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Synchronization of neuronal activity in the gamma frequency range as possible solution to the binding problem: An EEG biofeedback study

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This work is dedicated to my grandmother, † 2001.

I would like to thank for all her support she gave in my life.

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Abstract

The binding problem deals with combination and integration of distributed network activities in our brain. Synchronization of neuronal activity in the gamma frequency range is the supposed underlying mechanism for this. The theory states the formation of assemblies through synchronous (in-cycle) firing of cortical neurons with a precision in the millisecond range. The present study examined if human subjects are able to gain control on synchronization in the gamma frequency range. To test this, an EEG biofeedback design was applied. EEG signals from the scalp were recorded from 20 healthy subjects. Between two electrodes, synchronization was calculated online and reported back to the clients in real-time. Synchronization was calculated with a simple correlation. Feedback was presented through a smiley on a screen and the participants were instructed to make the smiley as happy as possible. The obtained results clearly show that participants have not been able to gain control over synchronization. The correlations did not change during the experiment. None of the participants could report a successful strategy to manage this. On a critical view, the chosen design was very strenuous for the participants, suggesting some problems in motivation. Additionally, the training consisted of one session only but EEG biofeedback usually needs more to achieve success. Although this study could not provide support for the theory of gamma synchronization, the functional relevance of this phenomenon requires some further examination.

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1 Introduction

The aim of the present study is to examine if human subjects are able to gain control on synchronization in the gamma frequency range. Gamma synchrony is suggested as the most likely solution to the binding problem. The so-called binding problem involves scientists already since some decades. It is up to date one of the most interesting topics in neuroscience. Basically, it concerns the central question how our brain codes and combines its distributed network activities (Lee et al., 2003). Different solutions were presented during the last decades. Some of them propose the existence of highly selective single cells which code for specific features or feature combinations, respectively (e.g. Barlow, 1972; as cited in Engel et al., 1992). Others suggest neuronal assemblies as the most probable solution to this (Hebb, 1949). In that context, the Feature Integration Theory (Treisman, 1998) should be mentioned as an interesting theoretical model, too. Anyway, none of these approaches provided a satisfying solution at all. Thus, the discovery of neurons in the cortex which fire their action potentials in temporal synchrony with a precision in the millisecond range caused highest interest among different disciplines (e.g. Singer, 1993). It is suggested that our cortex uses this to tag responses as related and thereby solve the binding problem. Obviously an attractive solution and up to date a huge amount of empirical support exists in accordance with that. In the theoretical part of this work I will explain all this as detailed as possible. Anyway, some authors criticized this theory and do not believe in it. Indeed, so far no study is available which proves that our brain definitely uses this mechanism. Most of the empirical support is only correlative. We therefore decided to further examine this still controversially discussed theory. We were wondering if human subjects are able to gain control on synchrony in the gamma frequency range. To test this, an EEG biofeedback design will be applied. We record EEG signals from the scalp and measure between two chosen electrodes, namely F3 and P4, synchronization online. For the online calculation we will use the correlation. As feedback we choose a simple smiley and the participants are instructed to make them as happy as possible. Feedback is provided in real-time. Furthermore, different trials will be applied. After having a base-line, we will offer trials with training in which we give feedback to the participants. Other trials will not include them and therefore allow us to see if our participants are able to practice their experience without feedback, too. Anyway, if the proposed theory holds true, we expect that our participants are able to gain control over the smiley happiness and therefore over gamma synchronization between the two measured signals, too. The second part of this work will thus deal with our study in all details, ranging from the chosen design, hypotheses, and of course the outcome with the resulting implications.

2 The Binding Problem

The binding problem is one of the most intriguing topics in neuroscience. Essentially, it concerns the central question of how our brain codes and combines its distributed network activities. This, for example, includes perception, memory, and cognition (Lee et al., 2003). Our current knowledge about structural and functional qualities of single neurons and their connections is of high level. But there are still plenty of questions concerning integration of cortical activity which remain to be answered (Engel et al., 1992). At first time the binding problem was mentioned as a theoretical problem by von der Malsburg (1981; as cited in Roskies, 1999). Since that time, it has engaged awareness by different fields, including neuroscience, psychology, computer modeling, and even philosophy (Roskies, 1999).

2.1 Definition of the Binding Problem

The binding problem refers to our ability to select and integrate information in the distributed network activities of our brain (Treisman, 1999). In other words, one may say that binding is „combining stimulus features to form an object representation" (Scholz, 2001, p. 1). The basic question to be answered is our possibility to perceive a coherent world with integrated objects, instead of incorrect or by chance combined features (Treisman, 1998).

Binding can be temporal and spatial. It may need focused attention or just appear quick and without attention. Binding can demand cross modal integration or even take place within a single modality (Scholz, 2001).

A paradigmatic example of binding was already formulated by Rosenblatt (1961; as cited in Roskies, 1999). In this illustration, a visual feature had to be combined with another feature, so that finally a consistent representation was perceived. In addition, von der Malsburg and Schneider (1986) also identified the problems of binding and segmentation at an early time. They considered the so-called „cocktail-party effect", which simply means that we are able to follow one voice in a crowded place (for further information see also chapter 3.4.2).

For Treisman (1998) the binding problem isn´t an obvious problem nor how well our brains solve it. We even don´t realize that there is a problem which remains to be solved. But different disciplines (e.g. neuroscience, psychology, and computer modeling) all suggest that there is.

In the following I will exemplify the concept of temporal binding in detail. As one will see, the binding problem concerns almost all cognitive activities.

2.2 The concept of temporal binding

The organizational complexity of our cerebral cortex is amazing. In the past decades, a subdivision of cortical regions into always smaller areas took place. Each of these areas has typical response qualities and connections with other regions. Representative examples are the somatosensory, motor, and auditory cortex (Engel et al., 1997). It is suggested, therefore, that most cortical functions (e.g. sensory, cognitive, and motor processes) arise from parallel interactions from a large population of neurons, located at different regions in the brain (Engel et al., 1992; Scholz, 2001).

A typical example gives the vertebrate visual system which includes more than 30 different visual cortical areas. Neurons in each of these areas are selective for distinct object features. As example, some areas are responsible for the color of objects, while others code for the shape of objects, and other areas contain cells which respond to the motion of objects. This functional specialization results in the simultaneous activation of neurons in different cortical areas, for every object appearing in the visual field. And as mentioned before, these distributed neuronal responses require some binding, to receive coherent representations and store information about the external world (Engel et al., 1999). To imagine the importance of this point, consider the huge amount of possible objects that confront our visual system at any given time. Just a simple feature, such as a horizontally oriented line, can be combined with other line segments and thereby create an almost unlimited number of geometrical objects. And such objects can occur with a large amount of other possible objects in parallel. Singer and Gray (1995, p. 556) clearly mentioned: „The possible combinations that confront the visual system are virtually unlimited“.

Furthermore, response selection and binding are of high importance for perceptual grouping, too. After representation of the basic features of a visual scene, some grouping process is necessary.

Features belonging to a certain object must be separated from features belonging to another object or to the background (Singer & Gray, 1995). Otherwise, false conjunctions can appear (Fell et al., 2003). This is of special importance if more than one object is in the present visual field and if objects have exchangeable properties (Roskies, 1999; Treisman, 1998). To exemplify this, the feature motion and the feature color are active at a given time. In that case, we have to make a clear distinction which color belongs to the moving object and which color to the stationary object (Treisman, 1998). Erroneous combinations of features, otherwise known as illusory conjunctions, give a paradigmatic example that in some situations binding is in fact a problem for the brain (Roskies, 1999). Obviously, some binding process is of high importance.

In addition, our visual system is able to recognize novel objects, i.e. objects which have never seen before. To enable recognition, temporary representations must be formed to allow a comparison with stored representations. This makes perception of novel objects as well as perception of similar objects, i.e. objects which differ only in minor features to stored representations, possible (Treisman, 1996).

In summary, taking all this evidence and examples into consideration, one can see that our visual system has developed a highly flexible and effective mechanism for the integration of features (Singer & Gray, 1995).

Up to now, the discourse only concerned the visual system. But binding problems are not restricted to the visual system - similar problems arise in other systems, too. Visual feature integration is just an example and the problem of integration, therefore, a fundamental one. In any neuronal network which is based on distributed representations, similar problems occur. Thus, the motor system and other sensory modalities are concerned as well - just to have another few examples mentioned (Engel et al., 1997).

Moreover, language comprehension and thinking require binding of semantic and syntactic structures (Treisman, 1999). Binding processes must be stored in memory, too. This allows suitable responses to identified objects, once they disappear in the visual field (Treisman, 1998).

Of course, binding is of high importance to activate motor programs as well. We need to response in a useful way to any perceived object (Treisman, 1996). This requires a flexible and efficient coordination between sensory modalities and the motor system. Otherwise, no adaptive behavior is possible. This example already implies a major assumption. As one can see, binding processes have

to occur not only in different cortical systems, they have to take place between them as well (Engel et al., 1997).

These short illustrations offer a general idea about the importance of the binding process and its application in our brain, namely at almost all cognitive activities. Clearly, the binding problem is therefore one of the most interesting topics in neuroscience. In the following section I try to explain why binding is a problem, before I will move on with some fundamental examinations done by different authors.

2.3 Why is binding a problem?

In this short chapter I will list why binding is a problem, beside the illustrations I already have done above and which highlighted clearly that some binding process must exist. In general, there are two main points important to mention. First of all, our brain has troubles in binding. Paradigmatic examples are brain damages. They clearly show that binding is of high importance for regular cognitive operations. But sometimes normal brains have difficulties in binding, too. This can appear due to temporal or capacity limitations and results in errors such as illusory conjunctions (see Treisman, 1999). The second point is just a theoretical one. Normally, binding problems seldom appear. Our brain has developed a very efficient and flexible mechanism for the integration of its distributed representations. Anyway, we still have no definite answer how this works. Thus, binding is a problem and it needs a clarification (Roskies, 1999).

2.4 Division of the binding problem by Roskies (1999)

The American philosopher and neuroscientist Roskies (1999) has done fundamental work on the binding problem and yielded a basic examination. Roskies (1999) mentioned some hesitation with the singular term „problem“. Whereas this name implies a unitary problem, this author clearly emphasized a class of problems. And thus, in practice, some confusion in discussions could stem from

this false description. According to Roskies (1999, p. 7), binding is a process which takes place in different modalities.

First, there are perceptual binding problems, as they all include similar features of percepts:

- Visual Binding: This involves binding information across visual space, binding information across types of features, and binding neural signals across cortical space.

- Auditory Binding: Can be required to follow a single voice in a crowded place.

- Binding across time: Is necessary to explain object motion.

- Cross-modal binding: Is needed, for example, to relate an auditory stimulus to a visual perception. Finally, both are perceived as a single event (e.g. the sound of a motorcycle and the vision of it, and maybe the smell of its exhaust, too).

Furthermore, Roskies (1999, p. 7) lists cognitive binding problems which involve:

- Relating a concept to a percept: Such as connecting the visual representation of a special car to all the semantic knowledge stored about it (it is fast, how it sounds, the feeling to drive it first time, and so on).

- Cross-modal identification: Such as being able to recognize an object that has before only been known by how it sounds.

- Memory reconstruction: The connection of formerly encoded information to construct an organized and consistent representation.

- Sensory-motor binding: The relationship between the sensory representation of objects and the motor orders to act in relevance to those objects.

Of course, a division into perceptual and cognitive binding problems is to some extent hypothetical. But it clearly demonstrates that binding is involved in almost any brain process. All the different kinds of binding problems may have a common solution, although, on the other hand, Roskies (1999) don´t believe that something complex as binding can be solved by a single mechanism.

2.5 Division of the binding problem by Treisman (1996)

Another important work on the binding problem was provided by Treisman (1996). According to Treisman (1996, p. 171), at least seven different types of binding exist.

- Property binding: Different properties, such as color, shape, and motion, are bound to objects, which they characterize.

- Part binding: Different parts of an object are separated from the background and bound to an object.

- Range binding: Special values on a scale (e.g. square on the shape scale, orange on the color scale) are signaled by the relation of activity in a few specific populations of neurons (e.g. those sensitive to red and yellow to signal orange).

- Hierarchical binding: Features of shape-defining limits (e.g. closure, curvature, and orientation) are bound to the surface-defining properties which carry them (e.g. luminance, color, texture, motion, and stereoscopic depth).

- Conditional binding: The interpretation of one property (e.g. direction of motion) often depends on another (e.g. occlusion, transparency, or depth).

- Temporal binding: Consecutive conditions of an identical object are integrated across temporal intervals, in real and visible motion, and other transformations.

- Location binding: Objects are bound to their present location (often called as linking „what" to „where").

Furthermore, Treisman (1999, p. 105) divided any binding process into three distinct problems:

- Parsing: Concerns the question of selection and segregation of the relevant features of an object against features belonging to different objects, ideas, or events.

- Encoding: It deals with the way how binding is encoded. This is necessary to signal it to other brain systems which have to use this information.

- Structural description: This, finally, concerns the correct specification of relations between the bound features within a single object.

With the Feature Integration Theory (FIT) (Treisman, 1998) the author provided a possible solution to the binding problem. I will have a detailed look on this in chapter 3.3.

2.6 From perception to consciousness

In summary, the above given information clearly highlights that feature selection and integration is a highly important process in our brain. But with that, some more problems appear. Further questions arise with the interpretation and transformation of binding by other neurons so that finally perception and action become possible (Roskies, 1999). Moreover, of huge interest is the connection with binding in context of consciousness, feeling, and subjectivity (Singer, 2001). Of course, these are central questions which need to be considered in addition. However, in the following pages I will present at next the most important approaches to the binding problem.

3 Classical approaches to the Binding Problem

In the past decades, neuroscientists have developed two elementary but totally different theories about how the brain solves the binding problem. They are well known as „distributed coding“ and „grandmother cell“ theories (Lee et al., 2003). I will highlight both theories with their advantages and problems in the following.

3.1 Grandmother Cell Theory

An extreme solution of how the brain solves the binding problem is the grandmother cell theory, otherwise known as „gnostic“ or „cardinal“ cell hypothesis (Bauer & Dicke, 1997; Gross & Sergent, 1992; as cited in Lee et al., 2003), as well as „single neuron doctrine“ (Barlow, 1972; as cited in Engel et al., 1992). This theory proposes selective cells which code for highly specific feature constellations (Barlow, 1972; as cited in Engel et al., 1997), e.g. a man with a black suit who stands up with a glass of wine in his hands. If a particular cell fires, it causes a set of synapses which are relevant for a specific perception (Barlow, 1972; as cited in Lee et al., 2003). These cardinal cells are supposed to be located in higher integrative cortical areas. They should reach this high selectivity through convergence of the outputs of neurons located in lower (visual) areas (Engel et al., 1997).

Historically, the term grandmother cell arose in a story Jerry Lettvin (Barlow, 1995; as cited in Gross, 2002) told in 1969. Anyway, a similar concept was already developed through Jerzy Konorski (1967; as cited in Gross, 2002) who called such cells „gnostic units“. In origin the concept was multimodal, but at present the term is used mostly in relation with visual perception. The name grandmother cell arose because the first such neuron represented a grandmother. Finally, in the early 1970`s the concept came into neuroscience journals and serious discussions about pattern perception (Gross, 2002).

At first glance, this solution seems promising. Representing features in that way is fast, because it can be achieved through feed-forward processing. In addition, it`s reliable as the respond of a specific cell always includes the same content (labeled line coding) (Singer, 2003).

3.1.1 The Discovery of Face Selective Cells

Indeed, some early results with experiments on monkeys were seen as confirmation of the grandmother cell theory. Scientists showed highly complex stimuli such as faces and found cells which selectively enhanced their firing rate (Young & Yamane, 1992; as cited in Fell et al., 2003; Perret et al., 1987; as cited in Engel et al., 1992). However, the results were less successful with other specific neurons when showing some more visual objects which are common or important for monkeys (e.g. bananas, trees, and other items which do exist in their regular environment) (Gross, 2002). Furthermore, the discovered face-selective cells are not real cardinal cells. They did not code all different attributes and showed big invariance. As example, they were not affected by changes in the size of faces, which, of course, should have been the case (Fujita et al., 1992; as cited in Fell et al., 2003).

Besides that, there rests another big problem in relation with the grandmother cell theory. It is known as the combinatorial problem and I will outline this in the following.

3.1.2 The Combinatorial Problem

We live in a world full of objects. That means, if the grandmother cell theory holds true, every object and its possible constellations would have to be represented each by a specific cell. Definitely hard to imagine how this scheme could work. Just visualize the unbelievable high number of possible objects and their constellations that confront our visual system every day and in general, which exist in our world (Singer, 2003). In addition, as already mentioned above, the high selectivity of the feature specific cells should be reached through convergence of the outputs from cells located in lower (visual) areas (Engel et al., 1997). In practice, any neuron which is activated from a basic contour would have to send information to the next processing stage, if the receptive fields of the higher level neurons code for objects sharing this basic contour. This would lead to an unacceptable number of required connections, too (Scholz, 2001). These facts are well known and have been summarized under the term „the combinatorial problem" (Singer & Gray, 1995).

Of course, under consideration of these aspects, the grandmother cell theory has earned widespread criticism. It´s inefficient and inflexible and it´s not possible by the brain to solve the binding problem if this would be the single solution available (Jefferys et al., 1996).

3.1.3 Criticism of the Grandmother Cell Theory

It may be that some selective cells have specialized functions. But, in addition to the combinatorial problem and listed in the following, there are some more arguments which point against the grandmother cell theory as a perfect solution to the binding problem (Crick, 1984; Damasio, 1990; as cited in Engel et al., 1992).

- This model lacks directly experimental support (Engel et al., 1992).

- There are probably not enough cells in the brain if every object and its possible constellations would have to be represented each by a specialized cell (Singer, 1993).

- In addition, a huge number of connections are needed to represent the immense number of real objects and their possible constellations (Singer, 2003).

- Cells in higher integrative areas are often less selective for particular features than cells located in lower integrative regions of the processing hierarchy (Singer, 1993).

- This model has no explanation why objects, which have been seen for the first time, can be processed immediately by the brain (Fell et al., 2003).

- A high number of available cells are required for the representation of new objects (Engel et al., 1992).

- Beside some hand- and face-specific cells, no other object-specific cells have been identified so far (Baylis et al., 1985; Desimone et al., 1984; Gross et al., 1972; Perret et al., 1987; Rolls, 1991; as cited in Singer, 1993).

- Even if cells are added in small units to represent features in a more economical way, no such high integration area have been found so far which is able to hold so much required cells (Poggio, 1990; as cited in Singer, 1993).

- There rest some difficulties in representing modified patterns due to the inflexibility of the model (Singer & Gray, 1995).

- Another problem is the representation of relations between components of mixed objects such as visual scenes or sentences (Singer, 2003).

- Finally, the representation of particular feature constellations does not guarantee the possibility to represent alternating combinations of the same feature (Fodor & Pylyshyn, 1988; as cited in Engel et al., 1997).

Obviously, these arguments point clearly against a single solution for the binding problem named grandmother cell theory (Singer, 2003). One can see that this model „provide a rigid and hard-wired network in which the path of information flow and its destination is predetermined and unambiguously channeled“ (Lee et al., 2003, p. 59).

Without doubt, needed is another binding mechanism which avoids the immense number of required cells, and, of course, all the other mentioned problems belonging to the grandmother cell theory (Engel et al., 1997). Such a mechanism is assembly coding and I will move on with that.

3.2 Neuronal Assemblies

Assembly coding offers a more variable definition of relations and is therefore an attractive alternative to the cardinal cell model. This theory is based on the proposals made by Hebb (1949; as cited in Singer, 2003) and in meantime expanded by authors in great number.

3.2.1 Theory from Hebb (1949)

This theory explains feature perception through the activity of a population of distributed neurons, either within or across different cortical hierarchies. Instead of representing complex features by a few cells or even highly specific single cells in special cortical regions, this approach allows much more flexibility (Scholz, 2001). Any percept is therefore represented by a specific dynamic condition of a great number of cooperating but distributed neurons (Singer, 2001). The idea is that such

assemblies exist of neurons which encode elementary features. Thus, in turn, makes complex representations already at early stages in the processing hierarchy possible, which again contradicts with the cardinal cell model (Engel et al., 1997). The coupling of cells which code features of a particular object takes place through the common increase of their average firing rate (Engel et al., 1992).

3.2.2 Synaptic Plasticity

Synaptic plasticity simply means that a plastic change occurs in the synapse of neurons if they fire together (Hebb, 1949; as cited in Lee et al., 2003). In practice, the connections of neurons strengthen or weakens, dependent on the kind of neuronal activation. Long-term potentiation (LTP) relates to an increase in the synaptic connection of neurons. It is applied experimentally with short, high-frequency bursts. On the other hand, long-term depression (LTD) refers to a reduction in the synaptic efficacy and is experimentally produced with low-frequency stimulation. Synaptic plasticity is of high importance in context of the binding problem. More detailed information (e.g. in context of use-dependent plasticity with learning and memory) will be listed in chapter 4.7.2, here I will follow next with some general advantages of assembly coding (McEachern & Shaw, 1996; as cited in Lee et al., 2003).

3.2.3 Advantages with assembly coding

The most important advantage of assembly coding is, obviously, the practical use of required neurons. Any feature-selective cell can participate in any object representation which contains this feature. As example, cells which code for the color blue can participate in any object representation which contains this color, e.g. a blue car, a blue book, and so on. Thus, the combinatorial problem no longer exists. In addition, with such a scheme it´s easy to adjust new representations, i.e. objects which have not been experienced before. This model is more immune against the loss of cells, too. Furthermore, comparable objects (i.e. objects which differ only in few aspects) arouse representations which are similar rather than those which differ in more aspects. This is important because it allows generalization. Therefore, assembly coding looks like an efficient and flexible solution for the binding problem (Edelman, 1987; Gerstein et al., 1989; Palm, 1990; as cited in Engel et al., 1997).

3.2.4 The Superposition Problem

Although much more attractive than the cardinal cell model, assembly coding as well has a major drawback: It is the so-called superposition problem. The theory by Hebb (1949) implies only one active assembly in a certain region of the cortex at a given time. Other assemblies being suppressed (Palm, 1982; as cited in Engel et al., 1992). If we imagine our world full of objects that confront our visual system day by day, one can see that this won't hold true (although it could be the case at very high levels in the processing hierarchy). We have to process a huge crowd of objects at almost any visual scene and thus, many assemblies need to be active at the same time (Engel et al., 1992). But this leads to the so-called superposition catastrophe (von der Malsburg, 1981; as cited in Engel et al., 1997): Neurons, which respond to an object won't be distinguishable with neurons, which respond to another object (with the assumption, as mentioned before, that the coupling of cells takes place through the common increase of the average firing rate). Simply said, the information which feature belongs to which object is lost (Engel et al., 1997). This results in wrong connections of features and thus, object recognition won't be possible (von der Malsburg, 1986; von der Malsburg & Schneider, 1986; as cited in Engel et al., 1991a). Again, although attractive, this model is incomplete and not practicable. Clearly, needed is a mechanism which is able to make an explicit distinction between the different responses for different objects (Engel et al., 1997). Such a mechanism is distributed coding and builds up on the proposals made by Hebb (1949). Before I will dedicate to this model, I will give a short overview about the Feature Integration Theory, another interesting (theoretical) approach by Anne Treisman (1998) to solve the binding problem.

3.3 Feature Integration Theory (FIT)

The Feature Integration Theory (FIT) by Anne Treisman (1998) provides another possible solution to the binding problem. This theoretical model corresponds with the idea of distributed representations. The concept of the model, in brief, includes a so-called master map of locations. Through an adaptable window of attention, a serial scan of this map takes place. Additionally, there are some specialized feature maps and with the serial scan, currently active features are selected and, simultaneously, features in other locations suppressed. This avoids wrong binding. The selected features are combined and form a brief description of the object. The comparison with stored

representations finally makes object recognition possible. In this theory, as one can see, feature registration happens early, automatically and in parallel, whereas object identification takes place in a later step (Treisman & Gelade, 1980; Treisman, 1993; Treisman, 1988; as cited in Treisman, 1996).

Figure 3.1 illustrates this model. In the bottom the master map of locations is shown. The specialized feature maps are displayed above. They include two important informations: a banner (shown as a flag in the figure) which indicates if the feature is present anywhere in the field and information about the present spatial layout of the feature. The top of the figure (right side) shows the detailed information of the object, currently available in the attention window. And, in addition, that green and vertical are present elsewhere. Perhaps there are also representations from former attended objects, although, some evidence showed that bindings are lost as soon as attention is removed (Wolfe, 1998; as cited in Treisman, 1998). Finally, illustrated on the top of the figure on the left side, comparison with stored objects takes place and allows for object identification (Treisman, 1998).

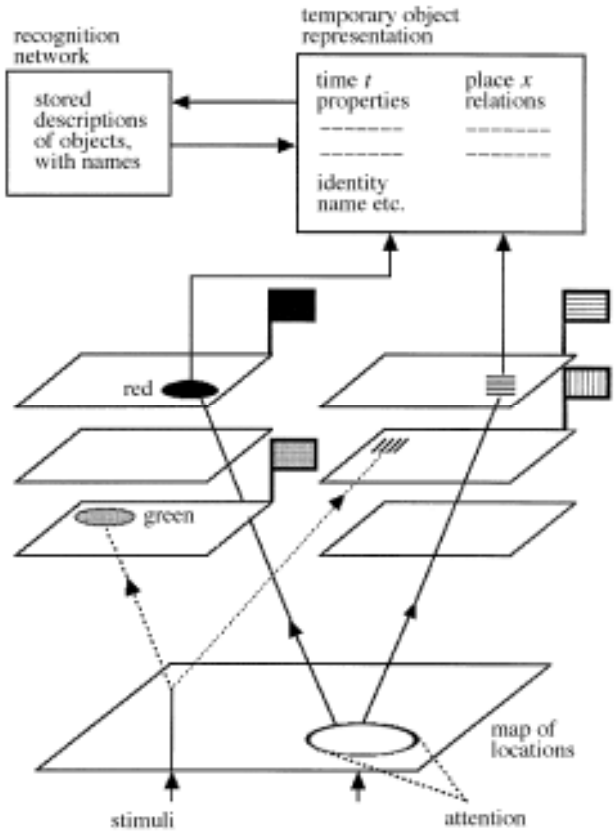

Figure 3.1: Model suggesting the relation between feature coding, spatial attention, and binding in object perception (Treisman, 1998, page 1296)

3.3.1 Evidence obtained for FIT

A huge amount of visual experiments have been examined in accordance with FIT. Most of them are in good agreement with the concept of this theory. In one example, people were instructed to find a red X in a large quantity of red O´s and blue X`s as quick as possible. As this approach contains the features color and shape, it requires binding. In this case, binding is needed to specify if the color red goes with the X shape, otherwise, the target can´t be found. Tasks like that require more time than tasks which include a feature that is totally different to others. In the latter case, the task is possibly solved by a feature map alone, i.e. without adding attention to it. The theory implies that attention checks any location in the feature map as long as all the features are bound and, thus, the target is found. This, of course, requires more time, as the binding step only takes place at one location at a given time. Anyway, the results of such visual search experiments are exactly in agreement with that. Further and more detailed evidence obtained for FIT (e.g. from parietal lesions and illusory conjunctions) is listed elsewhere (Treisman, 1996; Treisman, 1998; Treisman, 1999). But there is some criticism about this theory, too. I will outline this in the following (Holcombe, 2009).

3.3.2 Criticism of FIT

With the FIT a clear explanation of visual search results is possible. Anyway, other existing models provide proper descriptions for visual search performance as well, but without the need of attention in binding (Rolls & Deco, 2002; as cited in Holcombe, 2009). It´s most unlikely that the binding process is set on visual search results alone. Visual search results are influenced by different components and thus, complicated to separate the binding process (Holcombe, 2009). Another problem is the assumption of the attention window, which is necessary to place around the interesting object. This might cause troubles if the brief description of the object is inconsistent or if other different objects are close by. Further restrictions result through the limitation of the attention window to a single percept at a given time. This causes quite problems, especially if an object is partly covered with other objects. In that case, the adjacent parts of the object must be integrated to a coherent perception. Another drawback is the representation of relations. In case of having more than one object in the window of attention, segmentation of an image into an inherent object and its background is actually a requirement for the placement of the attention focus. Therefore, the binding problem has to be solved by another mechanism. This mechanism must take place before attention arises. The attention-driven mechanism may only contribute to stabilize representations, as soon as perceptual grouping and scene segmentation have appeared (Engel et al., 1997).

3.4 Distributed Coding

After the short discourse on the Feature Integration Theory, I want to move on with the mechanism of distributed coding in more detail. The Hebb model already was a quite attractive approach, but the superposition problem has to be solved. Therefore, another solution is needed which is based on the assumptions of Hebb, but with an additional possibility to mark which feature belongs to which object (Singer, 2001).

3.4.1 Temporal binding

Such a possible solution was suggested by von der Malsburg (1981; 1995), Abeles (1982a), and, in an early form, as well by Milner (1974) (as cited in Engel et al., 1997).

Instead of the average increase of the firing rates, these authors proposed the formation of assemblies through synchronous (in-cycle) firing of cortical neurons (Engel et al., 1992). In detail, those neurons coding for one object, fire their action potentials in temporal synchrony. This happens with a precision in the millisecond range (see figure 3.2). On the other hand, no temporal synchrony takes place between neurons coding for different objects (Engel et al., 1999). Therefore, this coding mechanism is time-based (Fell et al., 2003). The same neurons can code for different objects and combinations of objects, as long as those objects and combinations are represented by them. Of course, this strategy of distributed synchronized networks makes great flexibility possible (Lee et al., 2003).

Obviously, this temporal mechanism of selection and integration could be a convenient approach to solve the binding problem. Synchrony labels those neurons which fire for the same object, whereas responses from neurons activated by different objects will be separated (Engel et al., 1999). In that way, the advantages of a distributed coding scheme could be used and the superposition problem no longer exists (Engel et al., 1997).

The lady and the cat in figure 3.2 give an illustration of this scheme. Both are represented by an own assembly which is signed each in the figure by white or black circles. The neurons which are part of an assembly code for features of sensory objects (e.g. the orientation of contour segments, as

illustrated), appearing in their receptive fields (see figure 3.2, at the left bottom). Through temporal correlation among these neurons, object perception takes place (see figure 3.2, at the right bottom). Neurons belonging to one assembly fire their action potentials in synchrony. According to the theory, no temporal correlation occurs between cells which code features for other objects (Engel et al., 1999).

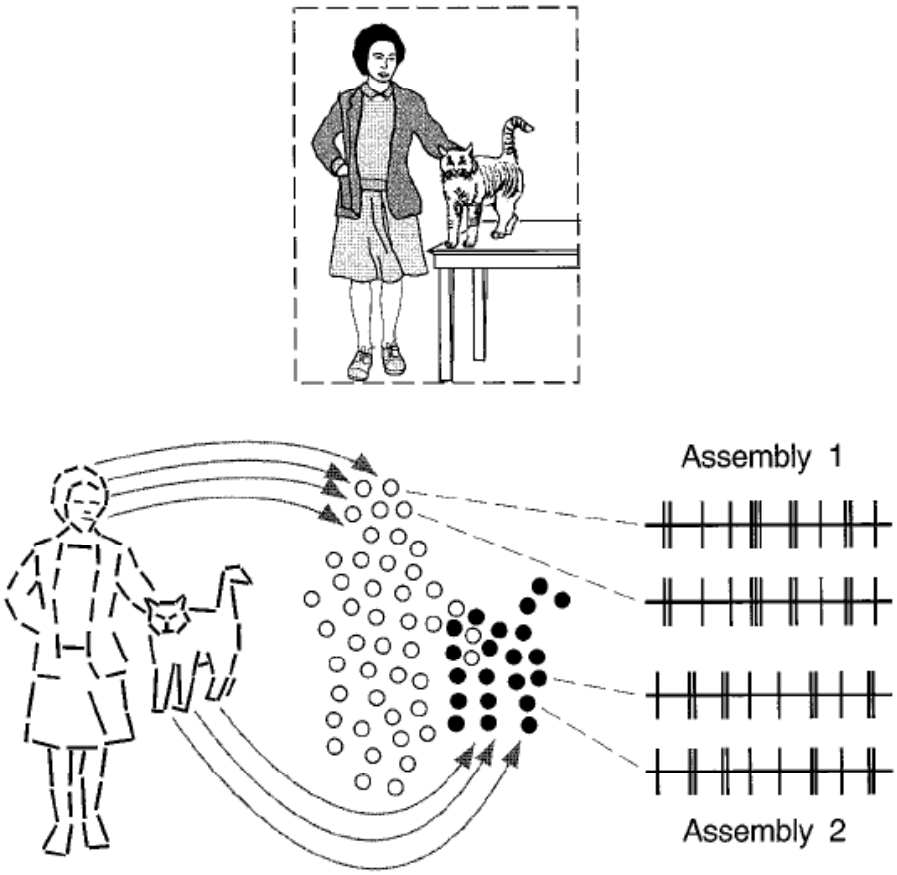

Figure 3.2: Feature binding by synchronization (Engel et al., 1997, page 572)

3.4.2 The model from von der Malsburg and Schneider (1986)

Von der Malsburg and Schneider (1986) have done fundamental work in context of temporal binding. Thus, I would like to offer a more detailed look on their basic ideas. In their model, perception is separated into three processes, each of them depending on the others. These processes are segmentation, pattern recognition, and integration of patterns into a scene.

Through segmentation, the sensory information is divided into segments which create patterns. Von der Malsburg and Schneider (1986) mention two references for segmentation, namely peripheral and central. The peripheral reference depends on similarity within a pattern, whereas the central reference depends on knowledge about patterns, i.e. about stored information of past experiences.

I already have mentioned the so-called „cocktail-party effect" (Cherry, 1953; Cherry & Taylor, 1954; as cited in von der Malsburg & Schneider, 1986) before. Remember, it deals with the way how it´s possible to follow one voice in a crowded place, for example, as in a cocktail party. According to the model from von der Malsburg and Schneider (1986), the phonetic information is encoded in spectral components. Through segmentation, the spectral components are rebound. In that case, the authors called this a „cocktail-party processor". And with peripheral reference, the spectral components differ from other sound events by being similar (McAdams, 1982; as cited in von der Malsburg & Schneider, 1986). Thus, their model provides a suitable explanation for the cocktail-party effect.

As illustrated in figure 3.3, the model includes some excitatory cells („E-cells") and one inhibitory cell („H-cell"). Every component is typified by an E-cell. In addition, every E-cell is linked with any other E-cells with an excitatory synaptic link. The inhibitory cell is linked with all E-cells, too. It sends inhibitory connections and receives excitatory connections (von der Malsburg & Schneider, 1986).

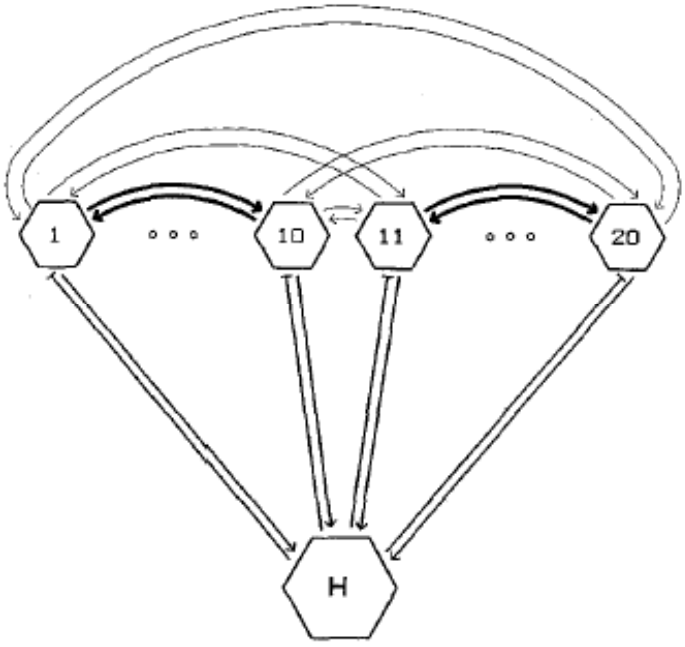

Figure 3.3: The Model (von der Malsburg & Schneider, 1986, page 31)

Every E-cell receives input from the periphery. In case of more inputs from different events, those inputs belonging to the same event change their values simultaneously and correlate, respectively. No correlation takes place between inputs belonging to different events. In practice, all cells which are activated at the same time synchronize their activity with each other, while desynchronizing with cells belonging to different events. Thus, those cells which fire in synchrony form an assembly (von der Malsburg & Schneider, 1986).

Through synchrony, the synaptic strength in the E-cells will increase. On the other hand, asynchronous activity leads to a decrease in the synaptic strength between the cells. These processes occur within a millisecond range. When the synchronous activity ends between cells, a reduction of the synaptic strength to a resting state takes place (von der Malsburg & Schneider, 1986).

3.4.3 Synchrony as a code for the definition of relations

Wolf Singer is one of the most important promoters for the theory that binding is achieved through synchronous rhythmic firing of neurons (von der Malsburg, 1981; Gray et al., 1989; as cited in Holcombe, 2009). In addition, he was the first who reported empirical support. Among others, Wolf Singer extended the basic concept from von der Malsburg and Schneider (1986) and provided up to date a huge amount of experiments. Of course, I will have the most important collected in chapter 5. Anyway, it´s a matter of fact that synchronization between groups of neurons in most parts of the brain frequently appears (Fries et al., 2001b; Thiele & Stoner, 2003; Dong et al., 2008; as cited in Holcombe, 2009). In the next chapter I will list some advantages with temporal binding.

3.4.4 Advantages of Temporal Binding

If the binding problem is solved through the common activity of neuronal assemblies, firing their action potentials in temporal synchrony, various advantages arise (Hebb, 1949; Braitenberg, 1978; Ballard et al., 1983; Singer, 1985; Singer, 1990; von der Malsburg, 1985; Edelmann, 1987; Gerstein et al., 1989; Grossberg, 1980; Palm, 1990; Abeles, 1991; as cited in Singer & Gray, 1995).

- Each cell codes, at different times, for different representations. This makes an economical use of required cells possible (Singer & Gray, 1995).

- This binding scheme is most flexible in adjusting new representations, i.e. objects which haven´t been experienced before (Singer & Gray, 1995).

- Such a strategy is very robust against the loss of individual cells (Engel et al., 1992).

- This binding process is immune to amplitude fluctuations (Engel et al., 1992).

- The grouping process is extremely dynamical. Individual cells can change very quickly to different assemblies by simply adjusting their firing pattern (Engel et al., 1992).

- Many assemblies can coexist, even in the same region of the brain, because cells belonging to different assemblies are labeled through synchrony (Engel et al., 1992).

- Binding takes place already with the first spikes of a response. Therefore, the processing speed is increased (Singer et al., 1997; Fries et al., 1997; as cited in Engel et al., 1999).

- The individual cells contain information about object features, although they do not code for the entire object. This is usually termed as „richness" of representations (Engel et al., 1999).

- The superposition problem no longer exists. Synchronization of neuronal responses acts as an additional binding code and labels all participating cells (Engel et al., 1999).

- This strategy allows binding even over large distances in the brain. Most likely, it´s advantageous for neural transmission and learning, too (Treisman, 1996).

- Finally, further processing of assemblies is enhanced (Singer & Gray, 1995; Singer et al., 1997; as cited in Engel et al., 1999). The detection of very precise synchronized spikes is relieved in other brain regions (Abeles, 1982b; König et al., 1996; as cited in Engel et al., 1999)

Considering all these numerous advantages, binding cells into assemblies by synchronization of their firing rate could be a highly interesting solution (Engel et al., 1992).

In the following pages I will consider any assumptions and their resulting consequences in context of this model in more detail, before I will move on with the up to date most important experiments and empirical support, respectively.

4 Gamma Synchrony and the Binding Problem

4.1 Introduction

The discovery of neurons in the cortex which fire their action potentials in temporal synchrony caused high interest among different disciplines. The idea, as already mentioned in the chapter of distributed coding, is a very simple one. It is suggested that our cerebral cortex uses synchronization to tag responses as related and thereby solve the binding problem (Singer, 2003).

Wolf Singer and colleagues (Gray et al., 1989; Gray & Singer, 1989) were first to obtain empirical support for this theory. In their experiment in the visual cortex of cats, synchronous gamma activity was closely related on features of visual stimulation, e.g. movement. Synchronization of responses took place in the millisecond range, even between neurons located in different columns or hemispheres, respectively (Engel et al., 1997; Singer & Gray, 1995; Lee et al., 2003).

The following sections of this chapter will deal with this model as detailed as possible.

4.2 Gamma frequency, oscillations, and synchrony

In the study from Singer and colleagues (Gray et al., 1989; Gray & Singer, 1989), as mentioned above, synchronization occurred in the gamma frequency range. Thus, I would like to start with a short explanation about this frequency band, followed by a very important distinction of gamma activity, gamma oscillations, and gamma synchrony.

Adrian (1950; as cited in Jefferys et al., 1996) first of all reported about fast gamma rhythms in the olfactory bulb. Since that time, they are a well-known phenomenon in higher cognitive function. Beside the olfactory bulb, fast gamma rhythms have been identified in the auditory cortex, motor cortex, visual cortex, and somatosensory cortex. They are as well known as „40-Hz" rhythms,

although they vary from 30 to 100 Hz and possibly differ in frequency during a response. The occurrence in humans and other mammals often follows sensory stimulation and fast gamma rhythms frequently appear in brief runs (Jefferys et al., 1996).

Most importantly, there is a major difference between gamma activity, gamma oscillations, and gamma synchrony. With gamma activity and gamma oscillations, the appearance of signals in the gamma frequency range is described. No relationship to each other is necessary.

Gammy synchrony, on the other hand, means the simultaneous (in-cycle) firing of two or more neurons (Singer, 2003). In other words, the rhythms of two or more signals coincide. Thus, synchrony measures the relation of signals, without regard of signal amplitude (Varela et al., 2001).

4.3 Why should synchrony occur in the gamma frequency range?

The segmentation of perceptual scenes happens very quickly, in general within 100 to 200 milliseconds. The theory states that various assemblies, active at the same time, should be separated. In that short time frame the first successive synchronous bursts already have to be evaluated, otherwise no such quick separation is possible. Consequently, synchrony in the alpha and beta frequency range is therefore excluded. These frequency bands are simply too slow. On the other hand, too high frequencies won't be possible, too. The conduction times in the synapses would not permit synchronization. The gamma frequency band is therefore a suitable solution which makes long range synchronization very quickly and with high temporal resolution possible (Singer, 1993). In practice, the discharges of synchronous activity can change with every cycle. Thus, if synchrony appears in the 40 Hz range, 40 different assemblies are possible within a second (Singer et al., 1997).

However, a number of authors reported empirical support for an integrative role with other frequency bands and, moreover, cross-talk between a broad range of frequencies (e.g. Bressler et al., 1993). Thus, synchronous oscillations in different frequency bands than the gamma range may also be a factor for integration of distributed activity. Further investigations are necessary (Lee et al., 2003).

4.4 Different types of synchrony

In general, synchrony can be sub-classified into different types. Just for example, with regard to its origin (internally generated or externally imposed) or depending on the distance of neurons (local scale versus large scale). In the following sections I will list and explain the most important ones.

4.4.1 Stimulus-locked vs. non-stimulus-locked

Synchrony can be either externally forced (which means it is stimulus-locked) or internally caused (which means it is not stimulus-locked). Most of the experiments have concentrated on the latter type. It is suggested that internally generated synchronization is caused by lateral interactions in the particular structures (Engel et al., 1991a; Munk et al., 1995; as cited in Engel et al., 1999) while externally imposed synchrony is most likely established by feed-forward signal flow from perception (Engel et al., 1999).

4.4.2 Evoked response vs. induced gamma activity

Another common used differentiation is between evoked responses versus induced gamma activity. These different activity types most likely have separated functions in information processing. The evoked response appears up to 150 ms past presentation of stimuli. This type serves for integration of sensory information, is modulated by attention, and exactly time locked with the stimulus. The induced gamma activity follows the evoked response, often observed up to 400 ms past stimulus presentation. The induced activity is not time locked to the stimulus and is suggested to underlie a more global integration function. Thus, most empirical support for the synchronization of activity is related to the latter type (Lee et al., 2003; Fell et al., 2003).

4.4.3 Four types of gamma activity by Galambos (1992)

According to Galambos (1992, p. 201-216), four different types of gamma activity can be distinguished:

- Spontaneous activity which is not related to external stimuli.
- Evoked activity, which is time-locked to a stimulus.
- Emitted gamma-band oscillations which are time-locked to a stimulus that has been omitted.
- Induced gamma band oscillations which are neither time-locked nor phase-locked to the stimulus.

4.4.4 Local and large scale integration

This type of differentiation refers to the distance between neurons which fire in synchrony.

Firstly, local integration takes place in a network with an area of approximately 1 cm. Synchronous activity is established through reciprocal connections in the particular areas of the network. The typical conduction delays are around 4-6 ms.

Large scale integration, on the other hand, relates to synchronous activity between distances more than 1 cm. It concerns, for example, assemblies across hemispheres. This type of synchrony is established through feedforward and feedback connections which link separated network levels in separated brain regions. The typical transmission delays are more than 8-10 ms.

Of course, the differentiation of local and large scale synchronization is somewhat artificial. There is no strictly index with local, regional, and long range synchrony and in practice neural synchrony often occurs on an intermediate spatial scale (Varela et al., 2001).

4.5 The substrate for response synchronization

In general, the organization of the brain is reciprocal. That means, as illustration, if an area A is linked to an area B, there are also links from area B to area A (van Essen et al., 1992; van Essen et al., 1994; as cited in Varela et al., 2001). In case of perception, the processing of information starts with periphery and leads from lower to higher levels in the brain. This type of information processing is known as feedforward or bottom-up activity. The processing of visual information is a typical illustration for this method and up to date the best elaborated one (Zeki 1993; as cited in Varela et al., 2001). Anyway, there is additional need of endogenous activity, responsible for emotion, anticipation, and preparation, for example. These activities provide another possible starting point for information processing with big distances to sensory inflow (e.g. limbic system). This type of information processing is called top-down or feedback activity and is involved already at very low levels of visual perception (Abeles, 1982a; von Stein et al., 2000; Steinmetz et al., 2000; Hupè et al., 1998; Roelfsema et al., 1998; as cited in Varela et al., 2001). In summary, both feedforward and feedback activity are responsible for the integration of sensory and endogenous information (Varela et al., 2001).

At first it was suggested that the synchronization of neuronal responses is achieved through oscillatory input from subcortical regions (Gerstein & Perkel, 1972; as cited in Singer, 1993). The finding of oscillatory activity in the gamma range in thalamic neurons was seen as confirmation of this hypothesis (Ghose & Freeman, 1990; Ghose & Freeman, 1992; Steriade et al., 1991; as cited in Singer, 1993). Anyway, this as single solution would not work at all. Synchronization solely by subcortical input would not be flexible enough nor allows for the required processing speed. It is necessary that binding of assemblies is additionally achieved by reciprocal links as described above. But this has been criticized. The establishment of synchrony with zero-time lag through reciprocal links is difficult, especially between neurons with large distance due to long connection delays. However, there is empirical support that synchronization in the millisecond range is possible through cortico-cortical connections, even over large distances and despite connection delays (e.g. König & Schillen, 1991; as cited in Singer, 1993). Oscillations do have an important role for this, especially for large scale integration. In the following chapter I will explain this in further detail (Singer, 1993).

4.6 Oscillations as a prerequisite for synchrony

Figure 4.1 illustrates an oscillatory response which was recorded from the visual cortex of an adult cat. An electrode was implanted to measure the activity of a small cluster of neurons (figure 4.1A). The raw electrode signal was filtered in different band passes. Figure 4.1B shows on the top the resulting local field potential and on the bottom multiunit spike activity. In this experiment, a light bar was moved over the receptive fields. One can see a plain oscillatory response in the local field potential which suggests that the recorded neurons fired their action potentials in a coherent and rhythmic manner (Engel et al., 1997).

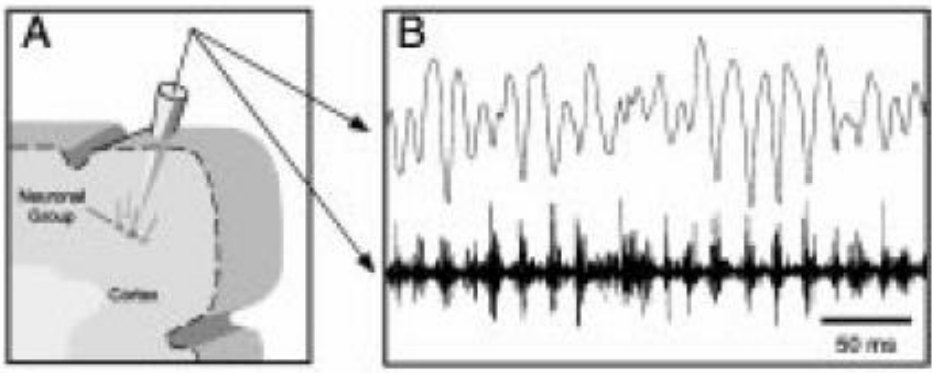

Figure 4.1: Example of an oscillatory response in cat primary visual cortex (Engel et al., 1997, page 576)

In fact, oscillatory activity is often related with synchrony. Apparently, a connection between oscillatory processes and synchronization is most likely and, of course, requires further information which I will provide in this chapter (Singer, 1993).

Indeed, this matter has been discussed contradictory. Some authors (e.g. Young et al., 1992; as cited in Engel et al., 1997) doubted the occurrence of stimulus-induced gamma oscillations at all. Other authors (e.g. Ghose & Freeman, 1992; Tovée & Rolls, 1992; as cited in Engel et al., 1997) accepted the phenomenon but questioned the functional relevance of it. These authors rated it as a result of cortical processing with no deeper meaning (Engel et al., 1997). But, on the other hand, some evidence obtained indicates that oscillatory activity is of functional relevance for the generation of internal synchronization (Singer et al., 1997).

In oscillatory responses, the appearance from burst to burst can be expected with some likelihood. Thus, some authors have reasoned that oscillatory responses are required to synchronize cell groups over large distances within the millisecond range (Engel et al., 1992; as cited in Singer, 1993). In such oscillatory networks, even if assemblies are not connected directly, could synchrony occur via intermediate oscillators (König & Schillen, 1991; as cited in Singer, 1993). This, for example, would be necessary to create relationships between neuronal groups distributed over different cortical regions, as is the case for processing of sensory features. In consequence, oscillations would not carry any important information from the stimulus, but have functional relevance for the synchronization of neuronal groups over large distances (Singer, 1993).

If these considerations are correct, cortical synchrony over large distances should be accompanied with oscillatory activity. Anyway, no such correlation is required for cell groups in proximity as there are strong relations without big connection delays. Indeed, König et al. (1995) obtained empirical evidence for this hypothesis. In their experiment, synchronization over large distances (e.g. between different areas or across the hemispheres) and oscillatory response patterns were strongly correlated. On the other hand, synchronization over short distances appeared either, with and without the modulation of oscillatory activity. Thus, the experiment confirmed the hypothesis that oscillatory patterns are necessary for the establishment of long-range synchronization (Engel et al., 1992; König et al., 1995).

Of course, the generation of assemblies through synchrony yields several predictions. In the following chapter I will list the most important ones.

4.7 Requirements for the generation of assembly codes

The following requirements have to be fulfilled if internally caused synchronization is responsible for the generation of assembly codes (Singer, 2003).

- Feature-selective neurons participate, at different times, in different assemblies (Singer et al., 1997).

- Grouping depends on usual Gestalt-criteria, i.e. it appears in a context-dependent way. Thus, each object always triggers the same assembly (Singer et al., 1997).

- In a visual scene with multiple objects, several different assemblies must exist. Synchrony takes place between neurons belonging to the same assembly, whereas no such synchronization should occur between neurons belonging to different assemblies (Singer & Gray, 1995).

- Synchronization must achieve very quick, i.e. in the millisecond range. Otherwise it can`t serve as the signature of relatedness, as processing speed is unbelievable fast (Rolls & Tovee, 1994; Thorpe et al., 1996; as cited in Singer, 1999).

- A strictly distinction of cells, belonging to one assembly against cells, belonging to different assemblies, must exist in following processing stages, too. If not, some confusion and consequently illusory conjunctions can appear (Singer, 2003).

- Synchronizing patterns should stay in connection with motor or perceptual processes. Thus, any changes of synchrony must consequently change motor or cognitive behavior, too (Singer, 2003).

- Synchrony and discharge rate should not depend on each other, i.e. they must be adjustable separately (Singer, 1999).

- The information of assemblies must be accessible at other processing stages. This allows most flexible information processing at higher cognitive levels (Singer, 2003).

- Synchronization must reflect some use-dependent modifications at the synapse. Thus, the synaptic connection from often together activated neurons should increase and consequently the probability of further synchronization, too. This is required for learning and memory (Singer, 1999).

- Synchronized activity, of course, should be more successful than non-synchronized activity (Singer, 2003).

In chapter 5 I have collected the most important evidence for synchrony up to date. But here I will follow first with more detailed information on two very important predictions, namely the feature dependence of response synchronization and temporal constraints of use-dependent modifications.

4.7.1 The feature dependence of response synchronization

The feature dependence of response synchronization is one of the most important predictions. Clearly, an invariable and stereotypical code would not be very helpful to obtain useful information in perception (Engel et al., 1992).

The so-called Gestalt criteria have already been described early last century (Koffka, 1935; as cited in Singer & Gray, 1995). These criteria include some general rules about feature grouping into objects. Thus, neurons which are part of an assembly should correspond to these criteria. The Gestalt criteria contain, among others, continuity, proximity, common fate, and similarity. These criteria indicate that objects usually include features which are in close distance, which have familiar qualities like color and form, which move in a common direction, and which are spatially contiguous (Singer & Gray, 1995).

Indeed, there is empirical support that all these criteria are fulfilled. That means, in practice, that universal qualities of visual stimuli affect the appearance of synchronization. Synchrony among corresponding cell groups is more likely between features which move in the same direction and thus appear as part of an object than oppositely moving features, just to mention an example. Therefore, the likelihood and extent of synchronization is also connected with the structure of the stimulus and not only dependent on the spatial distance of neurons or feature preferences (Singer & Gray, 1995).

In figure 4.2 one can see an illustration of this scheme. Figure 4.2A shows different aligned elements. According to feature dependent grouping, segments with corresponding orientation are grouped with higher probability than others. Thus, as illustrated in this example, synchrony should appear between neurons 1-2, 3-4, and 5-6. These elements form assemblies (at very low level of processing) which are shown in figure 4.2B. Finally, at higher levels of processing, a letter or a figure results, just to visualize a possible example. Moreover, if there are ambiguous perceptions, other grouping criteria can be added. This is shown in figure 4.2C, where motion is included as another grouping criterion. As illustrated in figure 4.2D, synchrony would occur in that case between neurons I, II, III,

and IV, while neurons V and VI would fire their action potentials in an uncorrelated manner. In combination of these grouping operations, at some higher level of processing, a perception of a clear stimulus or letter, for instance, becomes possible. The perception is illustrated finally in figure 4.2E, which shows in this example a resulting Z-letter (Singer et al., 1997).

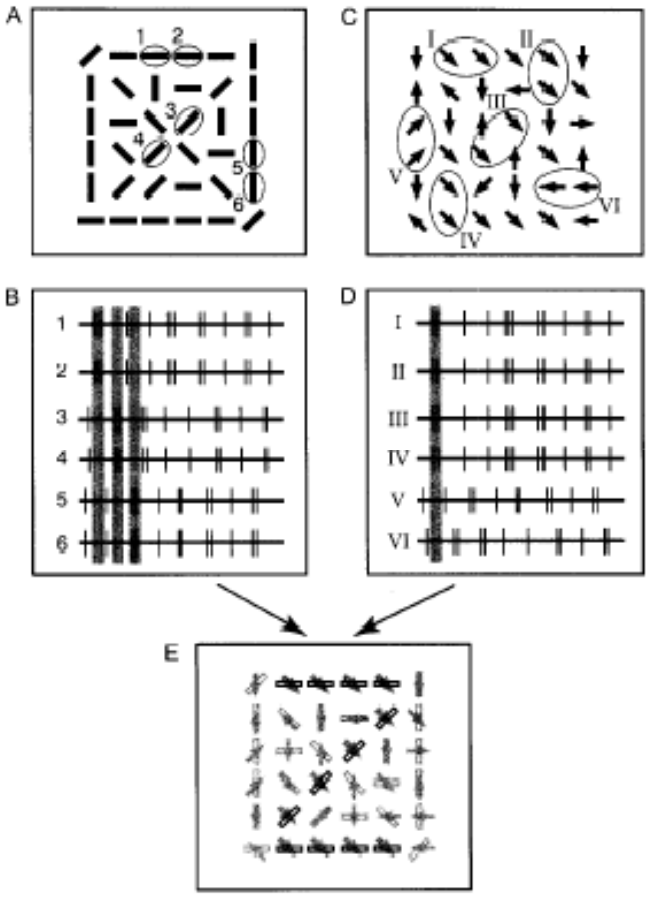

Figure 4.2: Context-dependent grouping of features by synchronization (Singer et al., 1997, page 256)

4.7.2 Temporal constraints of use-dependent plasticity

Another important prediction for the generation of assemblies through synchrony is use-dependent plasticity. This mechanism is highly important to add novel classification criteria through learning and to strengthen previously encountered assemblies. Use-dependent plasticity means that the probability of synchronization should be increased between neurons which already fired their action potentials in temporal synchrony. And the mechanism responsible for this use-dependent

modification has to occur within the same time range than the observed synchrony takes place (Singer, 1999).

Clearly, the generation of assemblies is connected with use-dependent modifications at the synapse. To make sure that certain features always activate the same assembly, often used connections between neurons should strengthen. As mentioned before, synchronization of responses is the suggested signature of neurons to group them into an assembly. Thus, at the same time, synchrony can be used in addition to differ between the connections which have to be strengthened or not (Singer, 1993).

Herculano et al. (1997; as cited in Singer, 1999) could obtain empirical support for these considerations. In their experiment, the probability of gamma synchrony was increased between groups of neurons which already fired their action potentials frequently in temporal synchrony. But if the same neurons fired their action potentials frequently in an uncorrelated manner, a reduction of the enhanced probability of synchronization took place. Herculano et al. (1997; as cited in Singer, 1999) could show that these changes of synaptic activity depended directly on synchronized oscillatory discharges (Singer, 1999).

4.8 Experience-dependent development of synchronizing connections

The generation of assemblies is suggested to arise through the connections between the participating neurons. Thus, the functional structure of the connections becomes an important criterion for the grouping of particular features. In detail, if this structure is genetically determined, perceptual grouping criteria would be fixed by a genetic code. But, on the other hand, if this structure is adjustable by experience and activity, perceptual grouping criteria could be obtained through learning. It is suggested, that typical concepts (e.g. laminar termination patterns, maximal spatial extent) are based on a genetic code. But also support for epigenetic adaptation is available. The development of cortico-cortical connections in mammals happens mainly postnatal (Callaway & Katz, 1991; Innocenti, 1981; Luhmann et al., 1986; 1990; Price & Blakemore, 1985; as cited in Singer, 1993). Thus, the resulting structure is based on a selection process by activity and experience (Singer, 1993).

4.9 Evidence for a functional role of precise timing

Up to date a huge amount of experimental support exists according to this theory. In this section I will just give a short overview about the occurrence of this phenomenon whereas in chapter 5 I will have more comprehensive information with the most important experiments in further detail.

The cat visual system is up to date the best elaborated one. Several studies could prove synchrony between spatially separated neurons located within visual areas (Toyama et al., 1981; Ts'o et al., 1986; Eckhorn et al., 1988; Gray et al., 1989; Engel et al., 1990; Schwarz & Bolz, 1991; Brosch et al., 1995; as cited in Engel et al., 1997). Further evidence is available that response synchronization is not restricted to a single visual area. It has been shown that even neurons located at different hemispheres synchronized their discharges with almost zero phase lag (Engel et al., 1991a; Nowak et al., 1995; as cited in Engel et al., 1997).

Beside the visual system, stimulus-dependent phase synchronization was proved within the olfactory (Bressler, 1987; Freeman, 1978; as cited in Fell et al., 2003), the auditory (Brosch et al., 2002; as cited in Fell et al., 2003), and the somatosensory (Desmedt & Tomberg, 1994; Lebedev & Nelson, 1995; as cited in Fell et al., 2003) system. Additional evidence for an involvement of gamma synchronization is available in visual working memory (Pesaran et al., 2002; as cited in Fell et al., 2003), in learning visuotactile associations (Miltner et al., 1999; as cited in Fell et al., 2003), and in the linking of hippocampus and rhinal cortex during formation of memory (Fell et al., 2001; as cited in Fell et al., 2003). Furthermore, gamma synchronization was also proved in the motor system of monkeys (Murthy & Fetz, 1996; Sanes & Donoghue, 1993; as cited in Singer, 2001) and cats (Steriade et al., 1996a; as cited in Singer, 2001). Moreover, direct evidence for an integrative function of synchrony was obtained in an experiment on insects. Odor discrimination worsened, as soon as synchronization was pharmacologically blocked in neurons in the olfactory system (Stopfer et al., 1997; as cited in Fell et al., 2003). In general, phase desynchronization is suggested to terminate the connection between neuronal assemblies and thus prevent perceptual and cognitive operations (Fell et al., 2001; Rodriguez et al., 1999; as cited in Fell et al., 2003).

Additional evidence suggests another important role of synchronization in the coupling between cortical assemblies and subcortical structures. Temporal synchronization was found between neurons in the visual cortex and the superior colliculus (Brecht et al., 1998; as cited in Singer, 2001).

Most importantly, gamma synchronization was proved as well in human EEG. Several studies yielded evidence for a functional activity in human visual cortex, suggesting an integrative role in perception (Tallon-Baudry et al., 1996; 1997; 1998; Rodriguez et al., 1999; Miltner et al., 1999; as cited in Singer, 2001).

Essentially, synchronization of responses took place with zero phase lag, even between neurons which are located in larger distances (Gray et al., 1989; Engel et al., 1990; as cited in Engel et al., 1992).

In summary, then, empirical support obtained suggests an integrative function of the synchronization phenomenon in a millisecond time range. With such a temporal code, the problem of the distributed activity of the brain could be solved without the assumption of cardinal cells or single integrating cortical areas, respectively (Engel et al., 1992).

4.10 Conclusion

In conclusion, then, it seems that phase synchronization in the gamma range serves as the underlying mechanism which enables the grouping of cortical assemblies (Engel & Singer, 2001; Varela et al., 2001; as cited in Fell et al., 2003). This is neither restricted to perception nor to a given distance of cortical areas. Thus, gamma synchrony most likely has a fundamental function in processing of cortical information (Fell et al., 2003).

In summary, it is suggested that the brain uses two elementary but totally different coding strategies. On the one hand the representation of explicit features through specific cells or populations of such cells, respectively. This strategy is reserved for restricted features and therefore applied only for objects which are repeatedly used or for objects which are of high importance. On the other hand the representation of connected features through the grouping of transient assemblies. This strategy is used for all other representations for which no specialized neurons exist, e.g. for the coding of new objects, or for the representation of objects which seldom occur (Singer, 2003).

In the following chapter 5 I have collected the most important experiments. One can see that up to date a huge amount of empirical support exists.

5 Empirical support for the significance of gamma synchrony

5.1 Introduction

The measurement of phase synchrony requires the recording from participating neurons at the same time. The position of electrodes as well as the experimental design are therefore of high importance in any attempt to measure synchrony. In that context, Singer et al. (1997) mentioned that some discrimination tasks, particularly those that have been repeated often, do not require the formation of assemblies. Such tasks are probably represented by individual cells or population of specialized cells.

The transient state of assemblies is a further problem in the measurement of synchrony. The duration of individual assemblies is often very short, in particular if the tasks are overtrained, demand no studying, do not contain obscurity, and require not much time to solve. But even such assemblies of short duration are in many cases of high importance for the brain and probably include a huge amount of neurons. Thus, the risk to miss phases of synchrony has to be considered. For Singer et al. (1997) it is therefore important to interpret negative results with some care.

Singer et al. (1997, p. 259) mentioned some strategies to encourage the discovery of assemblies:

- The design of the task should require dynamic binding. Tasks which do not involve the formation of assemblies, because the representation is possible through individual cells or population of specialized cells, should be avoided.

- The recording should be done in a compact constellation of cells. Although the response of neurons alone does not mean the formation of an assembly, the selection of a tight constellation of cells is a successful strategy. Such responses often indicate that a cell is part of an assembly of longer duration or that a cell participates in a series of different assemblies.

- Tasks are needed which enhance the duration of individual assemblies. This is possible through the establishment of ambiguous conditions, for example. Another possibility is to increase the difficulty of a task, e.g. create tasks which require learning of conjunctions or tasks where content must be hold in memory.

- The recording should involve as many cells as possible. This strategy increases the probability to detect neurons which actually fire in synchrony.

5.2 Visual Binding

One of the first experiments was carried out by Eckhorn et al. (1988). They recorded from various locations in area 17 and area 18 in the visual cortex of cats. These authors discovered stimulus-evoked (SE)-resonances in a frequency of 35-85 Hz when the receptive fields were activated with the preferred stimulus. The measured signals were single and multiple spikes and local field potentials.

Figure 5.1 illustrates the difference in amplitude between binocular and monocular stimulation. In this example, binocular stimulation was almost three times higher than monocular stimulation, as was the usual case in most of the samples.

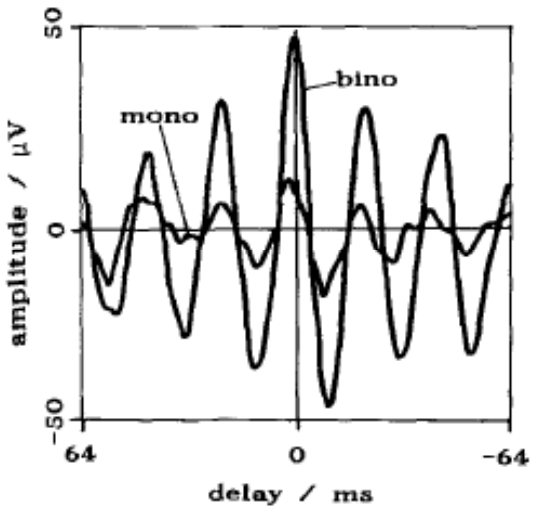

Figure 5.1: Enhanced oscillation amplitudes with binocular compared to monocular stimulation (Eckhorn et al., 1988, page 125)

Coherent responses appeared within a column, between neighboring columns, and even between different areas in the cortex with almost zero phase-lag. The phases of the oscillations were not locked to the stimulus and therefore determined through the neuronal network. This showed stimulus-locked averaging of the resonances of the local field potentials which had no oscillating components.

Figure 5.2 illustrates the time schedule of oscillations of LFPs from two correlated locations in area 17 and area 18. Binocular stimulation elicited oscillations around 45 Hz, as shown in figure 5.2A. As soon as the movement of the stimulus stopped, broad-band activity appeared, being more stochastic (see figure 5.2B and 5.2C). The measured correlation during the full stimulus interval was quite high, ranging from 0.4 for the time of stationary presentation up to 0.6 in stimulus movement. In figure 5.2D one can see the cross-correlograms. They clearly show dependence on stimulus configuration (moving versus stationary).

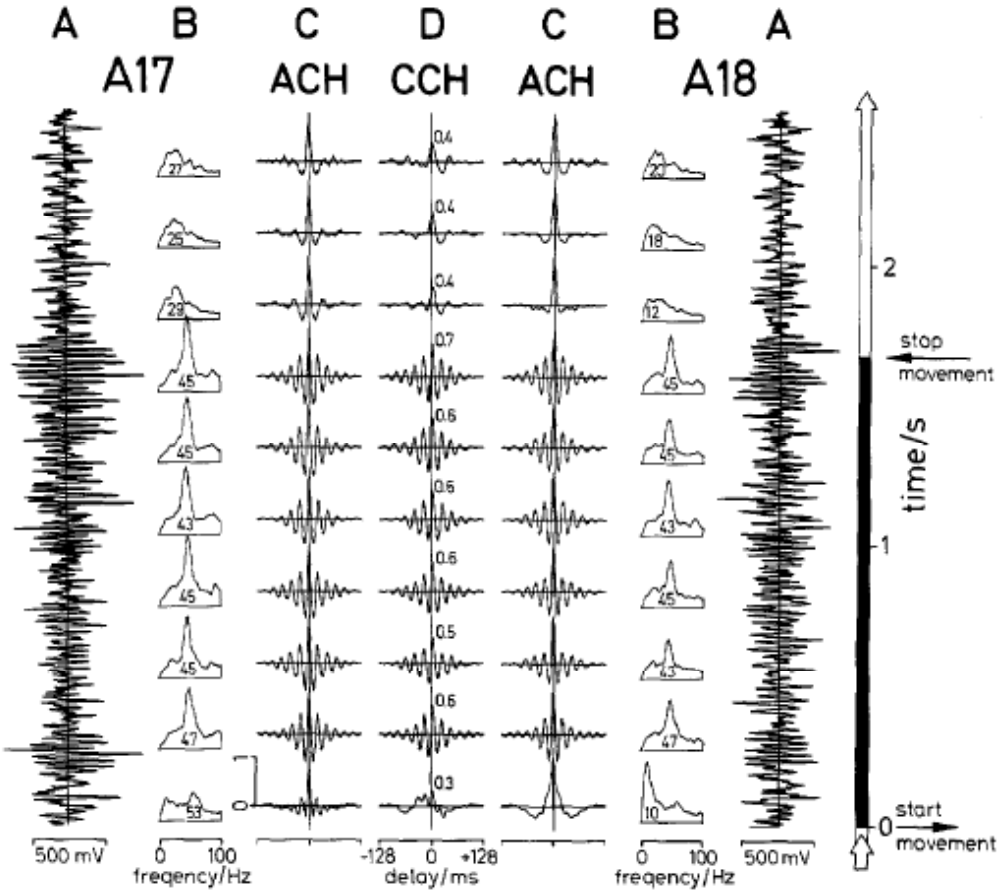

Figure 5.2: Time course of coherent oscillations at corresponding positions in two different visual cortical areas (Eckhorn et al., 1988, page 127)

Eckhorn et al. (1988) concluded that reciprocal connections are responsible for the coherent SE-resonances. Phase-locking between assemblies is established to join features of a visual scene. Thus, the transient association is signalized through a temporal code.

Another experiment in the visual cortex of cats was done by Gray and Singer (1989). They used different conditions of anesthesia to reduce a possible effect of that. Gray and Singer (1989) presented optimally adapted light stimuli and measured synchronous activity in areas 17 and 18. The stimulus-specific oscillations had a frequency around 40 Hz. On the other hand, thalamic input to visual cortex showed no such oscillations. Thus, reciprocal cortical connections are the suggested mechanism. Gray and Singer (1989) follow that synchronization of activity is used as neuronal code.

Figure 5.3A presents a typical response from area 17. On the top, multiunit activity (MUA) and LFP are shown when an optimally aligned light bar was passed through the receptive fields. The recorded neurons showed rhythmic firing patterns which were associated with gamma oscillations in the LFP. In the bottom of figure 5.3A the activity is displayed in an expanded time scale. Figure 5.3B illustrates a poststimulus time histogram which was measured over ten trials. One can see a clear directional preference. The power spectrum of the LFPs is shown in figure 5.3C. The oscillatory responses were stimulus-dependent. The presentation of the stimulus led to a broad spectrum increase in the amplitude, whereas in the absence of the stimulus large amplitude fluctuations in a frequency range of 1-10 Hz appeared.

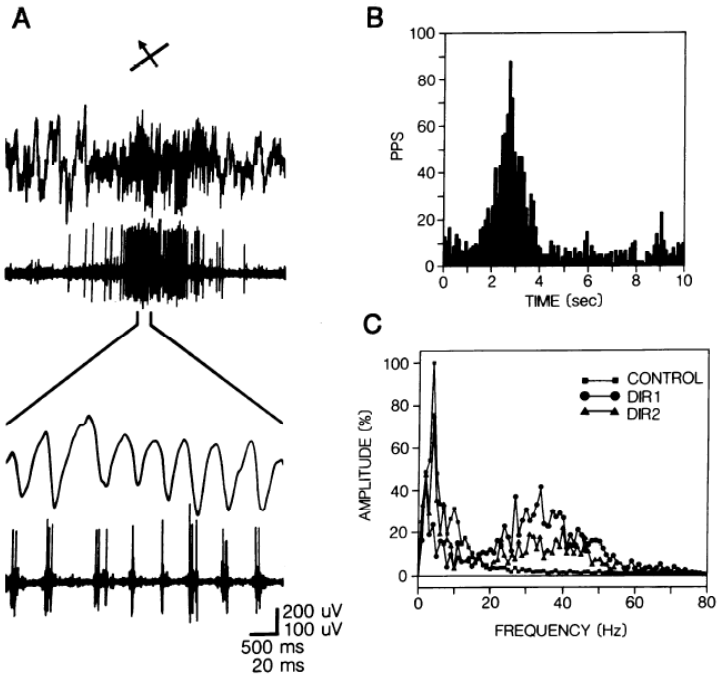

Figure 5.3: MUA and LFP responses recorded from area 17 in an adult cat
(Gray & Singer, 1989, page 1699)

Further support gives an experiment from Gray et al. (1989). Again, cats have been examined, in particular area 17 of the visual cortex. These authors recorded multi-unit responses at the same time from 5 to 7 spatially separated positions in different columns. Gray et al. (1989) presented optimally adapted moving light bars. Neurons synchronized their oscillatory responses in a frequency range of 40 to 60 Hz with no phase difference. The synchronization clearly was dependent on the orientation preference of the neurons, on the spatial location, and on global stimulus features.

Furthermore, Gray et al. (1989) measured in two cats larger separation, in particular at two positions separated through 7 mm. The receptive fields were non-overlapping, but with the same orientation preference and positioned co-linearly. Thus, activation of the two positions was possible at the same time, either with a long single light stimulus or with two separately moving stimuli, respectively (see figure 5.4). In both instances, oscillatory responses appeared at every site. Synchronized activity was observed when the single long light bar was moved over both receptive fields. No phase-locking occurred when the two separately moving stimuli were presented in different directions and only weak synchrony appeared when the two separately moving stimuli were presented in the same direction of the receptive fields. Thus, Gray et al. (1989) conclude that synchronization is influenced by global stimulus properties.

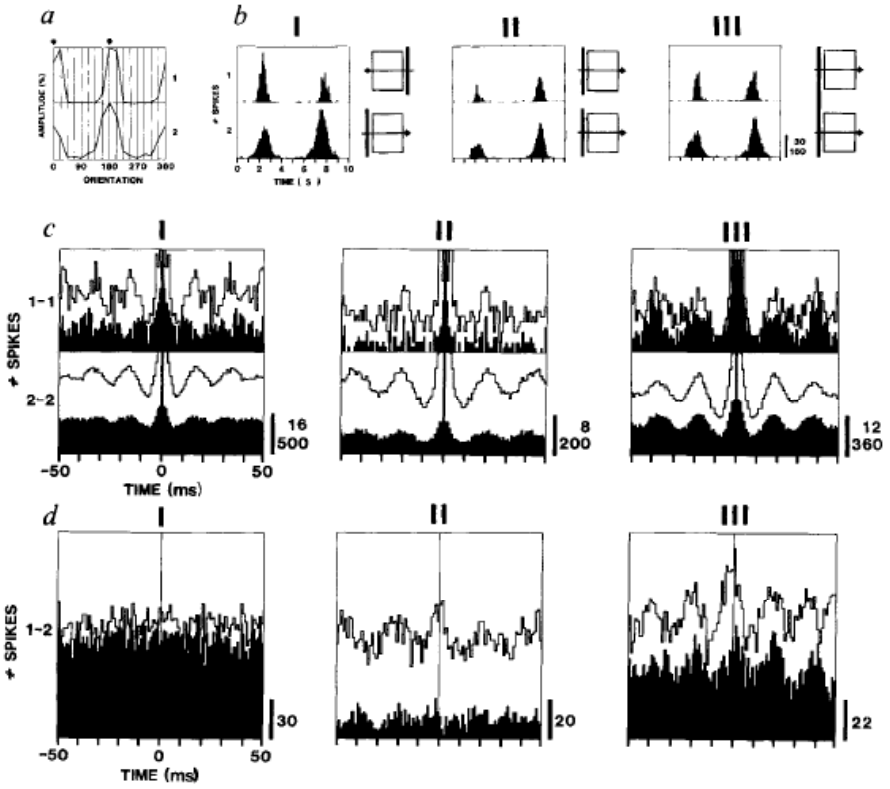

Figure 5.4: Long range oscillatory correlations reflect global stimulus properties
(Gray et al., 1989, page 336)

In figure 5.4A the orientation tuning curves are illustrated. Measured was with two electrodes (1, 2) which have been separated through 7 mm with vertical preferences (0 and 180°) at both sites. Beside the post-stimulus time histograms the three different stimulus sets are presented in figure 5.4B, too (illustrated on the right side of each histogram). Figure 5.4C presents the auto-correlation diagrams and in figure 5.4D one can see the cross-correlation diagrams between the two recording sites.

In this study, the appearance of synchrony was clearly influenced by the distance between electrode positions as well as by the angular difference of the favored stimulus orientations. No synchronization occurred between recording sites 7-12 mm apart. With a distance of 2-7 mm as well as 0.4-2.0 mm and non-overlapping receptive fields, synchrony was observed mostly between cell groups having corresponding orientation qualities. On average, synchronization occurred with zero time lag.

Gray et al. (1989) therefore indicate that the origin of phase locking between distant columns lies in the structure of intracortical connections or projections from other cortical areas, respectively. These authors excluded input from sub-cortical structures as the substrate for synchrony for different reasons.

In conclusion, then, it seems that phase locking of oscillatory activity in spatially apart regions of the cortex is responsible for the establishment of transient neuronal assemblies. Gray et al. (1989) could show that synchronization is dependent on global stimulus features and therefore most probably responsible for the selection and representation of features. Furthermore, Gray et al. (1989) suggest a more extensive function in cortical processing, as synchronization of oscillatory responses is a very powerful mechanism.

In chapter 4.6 I mentioned that oscillatory responses are required to synchronize cell groups over large distances. Empirical support for this hypothesis comes from König et al. (1995) who measured in cat visual cortex. They examined synchronization and oscillations in relation. Their results confirm above hypothesis. In their experiment, synchrony between neuronal groups with a distance of 2 mm and more as well as between the hemispheres occurred in general with oscillatory activity. This was not the case over short distances. Thus, the results obtained by König et al. (1995) indicate that oscillatory activity is of functional relevance for the establishment of synchrony over large distances in a network with reciprocal connections.

König et al. (1993; as cited in Engel et al., 1997) provided further support for neuronal synchronization in the visual domain in an experiment on cats with divergent squint. The characteristic feature of divergent strabismus is a changing fixation between the two eyes. Subjects who suffer on this are unable to integrate visual information if presented simultaneously at both eyes. On the other hand, monocular vision works in order. König et al. (1993; as cited in Engel et al., 1997) could not find synchronization in concerned animals between cells which represent both eyes. This is another indication for the importance of synchronization in common visual perception.

Another interesting correlation study was done by Roelfsema et al. (1994; as cited in Engel et al., 1997). These authors examined cats with convergent squint. In contrast to divergent strabismus, subjects with convergent squint normally fixate with one eye only. On the eye which is not used for fixation some deficits in perception emerge, well known as strabismic amblyopia. Typical symptoms are a decrease in visual acuity in the non-fixating eye, spatial misrepresentations of visual objects, temporal instability, and problems in the distinction of details. Obviously, some of these symptoms suggest a disturbance in visual integration and feature binding. The outcome of the experiment by Roelfsema et al. (1994; as cited in Engel et al., 1997) suggests an impairment of intracortical interactions as cause of the mentioned perceptual deficits.

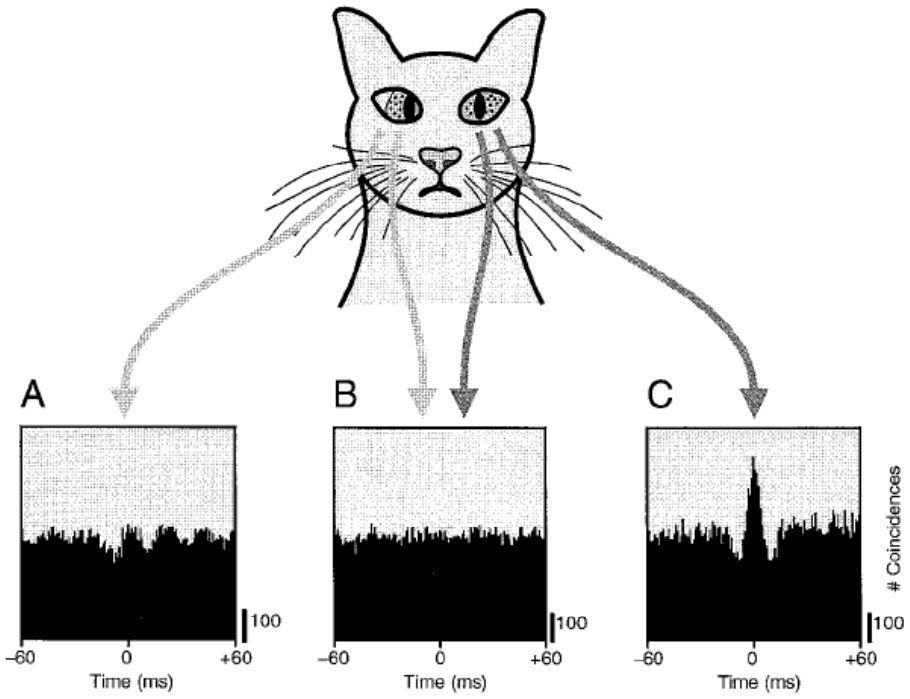

Figure 5.5: Neuronal synchronization in the primary visual cortex of cats with strabismic amblyopia (Roelfsema et al., 1994; as cited in Engel et al., 1997, page 574)

Figure 5.5 illustrates the difference in synchronization of neurons between the normal and the amblyopic eye. Synchronization was much stronger from neurons activated by the normal eye (see figure 5.5C) as was the case from neurons activated by the amblyopic eye (see figure 5.5A). Furthermore, no synchronization appeared between cells activated by different eyes (see figure 5.5B). This is in harmony with the results in the above mentioned study by König et al. (1993; as cited in Engel et al., 1997) on cats with divergent strabismus. Moreover, no difference was found in average firing rate between the responses of cells activated through the amblyopic and normal eye, respectively. Roelfsema et al. (1994; as cited in Engel et al., 1997) suggest a disturbance of intracortical interactions which are responsible for synchronization as the main reason for the perceptual deficits. Thus, the correlation of reduced synchrony with deficits in perception is another support for the functional importance of synchrony for feature binding.

I would like to close the sample of experiments in the visual domain with an extensive one provided by Engel et al. (1990). These authors additionally investigated the stimulus conditions which result in intercolumnar synchronization. Engel et al. (1990) used various electrodes in distances ranging from 0.4 to 12 mm. They recorded local field potentials as well as multi-unit activity in area 17 of the cat visual cortex. The result of the cross-correlation analysis showed that in 90 from 200 instances a consistent phase-locking of the oscillatory responses occurred. This happened in most cases with zero time lag. In case of non-overlapping receptive fields, synchrony mostly appeared between neurons with corresponding orientation preferences. This was not the same in case of overlapping receptive fields. In this situation, synchrony occurred additionally between neurons with different orientation preferences. Monocular instead of binocular stimulation reduced oscillatory responses but had still a significant relationship in the cross-correlograms. A corresponding result showed the change from a moving to a stationary stimulus. Furthermore, synchronization of local field potentials occurred in 136 from 174 recording pairs. In this case, synchrony was clearly not affected by the orientation preferences of the neurons but depended on spatial distance. Synchronization was strongest between cells in proximity. Engel et al. (1990) could show that synchronization of local field potentials was not affected by volume conduction.

These results proved the occurrence of synchrony at different cortical sites. Synchronization of oscillatory responses was dependent on the orientation preferences of the neurons as well as on the spatial distance of the recorded sites. In case of cross-columnar activity, features of the stimulus additionally affected the synchronization. In conclusion, then, Engel et al. (1990) indicated that synchronization is responsible for the establishment of transient assemblies in the visual cortex.

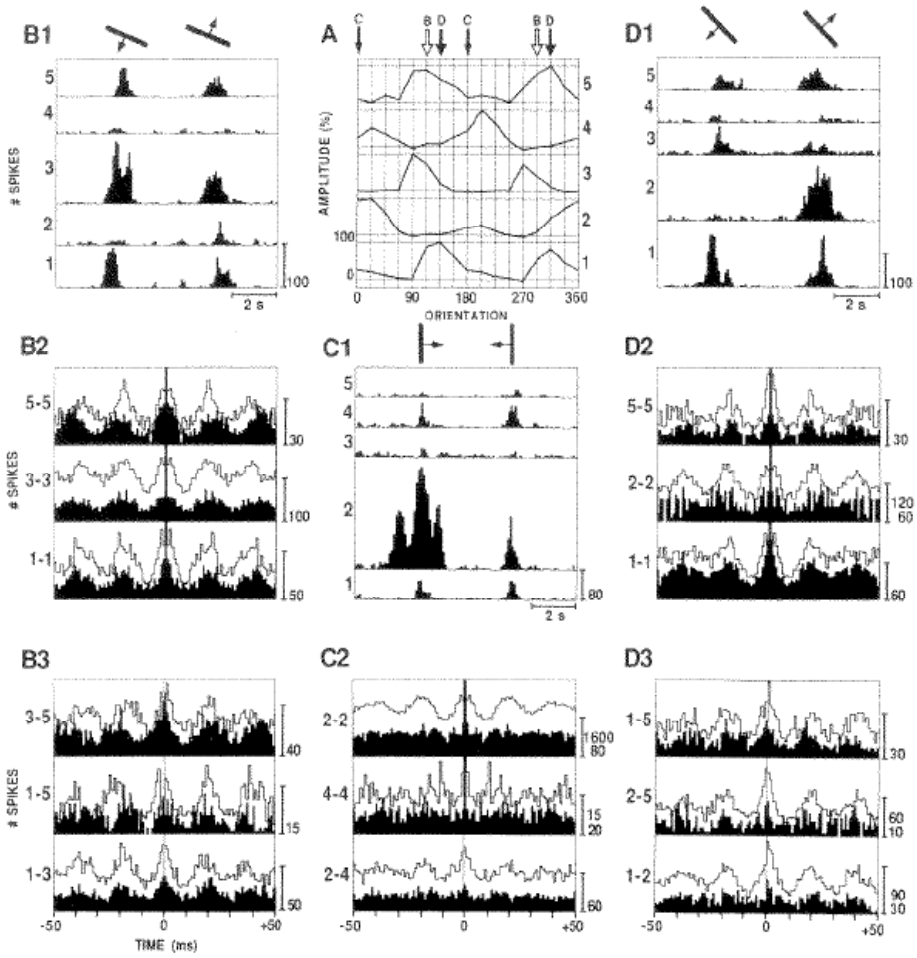

Figure 5.6: Synchronization of oscillatory MUA responses (Engel et al., 1990, page 593)

In figure 5.6 one can see synchronous responses recorded from five orientation columns having overlapping receptive fields but various orientation preferences. Figure 5.6A illustrates the normalized orientation tuning curves. The amplitude is shown on the ordinate and the stimulus orientation on the abscissa, separated for any recording site. The arrows on the top display the stimulus orientation used in B - D. Figure 5.6B1 shows the PSTHs in response to a light stimulus with 112° orientation and figure 5.6B2 illustrates the auto-correlations for responses at electrodes 1 (1-1), 3 (3-3), and 5 (5-5). The unfilled and filled representation displays the first and second direction of stimulus movement. The cross-correlation functions for the three possible combinations are shown in figure 5.6B3. Furthermore, in figure 5.6C1 strong responses at sites 2 and 4 are shown, obtained with a vertical (0°) light stimulus. The corresponding auto- and cross-correlation functions are illustrated in figure 5.6C2. Finally, figure 5.6D shows stimulation with a light stimulus of 135° orientation. Again, strong responses were obtained at sites 1, 2, and 5. Figure 5.6D2 illustrates the auto-correlograms whereas in figure 5.6D3 the cross-correlation function is shown. The number of spikes is displayed in the vertical scale bars.

5.3 LFPs in monkeys and surface recordings in humans

In the study of Bressler et al. (1993) three adult rhesus macaque monkeys had to carry out a visual discrimination task in which they had to separate between two visual figures and then act accordingly (GO and NO-GO paradigm). Local field potentials have been recorded from up to 15 sites which were all situated in the same hemisphere. In particular, posterior parietal, inferotemporal, superotemporal, striate, prestriate, somato-sensory, motor, and frontal cortices have been implicated. Bressler et al. (1993) observed various occurrences of coherence after stimulus presentation and successful discrimination of the visual task by the monkeys. The coherent periods lasted 50 to 200 ms and included various frequencies.

Figure 5.7A illustrates striate and motor sites during the response in the GO condition. One can see a big increase in broad-band coherence. Figure 5.7B illustrates the same striate site with a parietal site. Raised broad-band coherence occurred between 100 and 200 ms after stimulus onset.

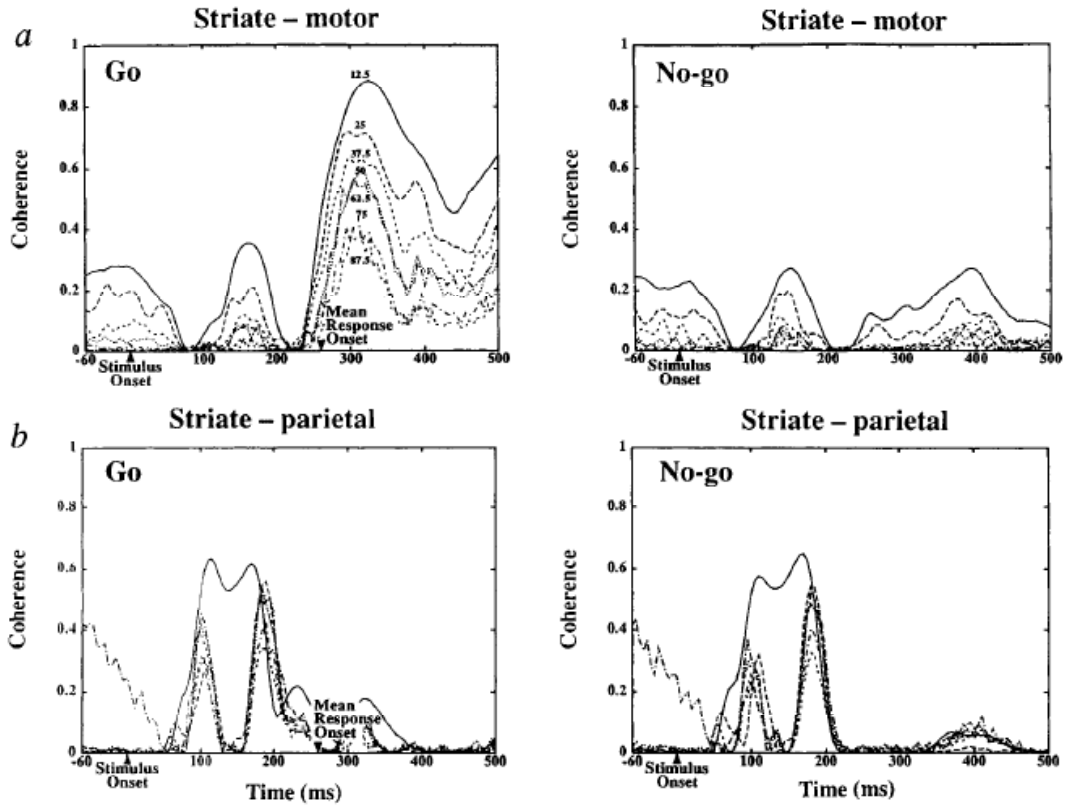

Figure 5.7: Coherence time-series for two different site pairs (Bressler et al., 1993, page 154)

The results obtained in the study by Bressler et al. (1993) confirm that perceptuomotor integration requires binding of various cortical areas. In addition, Bressler et al. (1993) conclude that synchronization of cortical activity can appear between various cortical regions and therefore serve as the underlying mechanism of binding.

Lutzenberger et al. (1995) measured with EEG on the scalp of 12 human subjects. They used 17 electrodes. The authors showed irregular changing visual patterns as well as coherently moving stimuli. Lutzenberger et al. (1995) measured increased 40 Hz activity over the occipital lobe in response to a regular pattern. This enhanced activity varied in dependence of the presentation in the visual field. Coherent stimulation in the upper visual field enhanced 40 Hz activity at lower occipital electrodes, while the opposite was observed in case of stimulation in the lower visual field. The results of Lutzenberger et al. (1995) proved that 40 Hz activity is closely linked with perception of regular moving stimuli in humans. In addition, these authors obtained evidence that gamma activity can be picked up with EEG even if measured at the scalp.

Anyway, a critical note has to be mentioned. Activity in higher visual areas could have contributed to the obtained variations in neural responses.

Another interesting study was carried out by Varela et al. (2001). These authors had possibility to examine subjects with implanted electrodes, which have been prepared for a surgery for epilepsy. While the subjects accomplished a visual discrimination task, reliable power emission occurred in the gamma frequency range. Furthermore, large-scale synchrony was observed between frontal and temporal lobes, but only while the subjects performed the discrimination task.

Another interesting study comes from Rodriguez et al. (1999). These authors presented to ten subjects so-called „Mooney" faces which are illustrated in figures 5.8A and 5.8B, respectively. Usually, these figures are simply recognized as faces in case of upright presentation, but considered as incoherent structures if shown upside-down. The subjects were instructed to inform as quick as possible if they recognize a face or not and act accordingly by pressing an appropriate button.

Rodriguez et al. (1999) found two induced gamma-activity peaks which are illustrated in figures 5.8C and 5.8D. The first induced peak ranged from 33 to 39 Hz for each condition and occurred around 230 ms past stimulus presentation. Gamma responses were significantly stronger in the perception condition. This induced activity most likely is in strong connection with the perception process itself. The second induced gamma response was obtained between 35 and 45 Hz and peaked around 800

ms. That induced gamma was larger in the no-perception condition, although not significant, and followed very close the reaction time of the subjects. A role in post-perceptual processes is suggested.

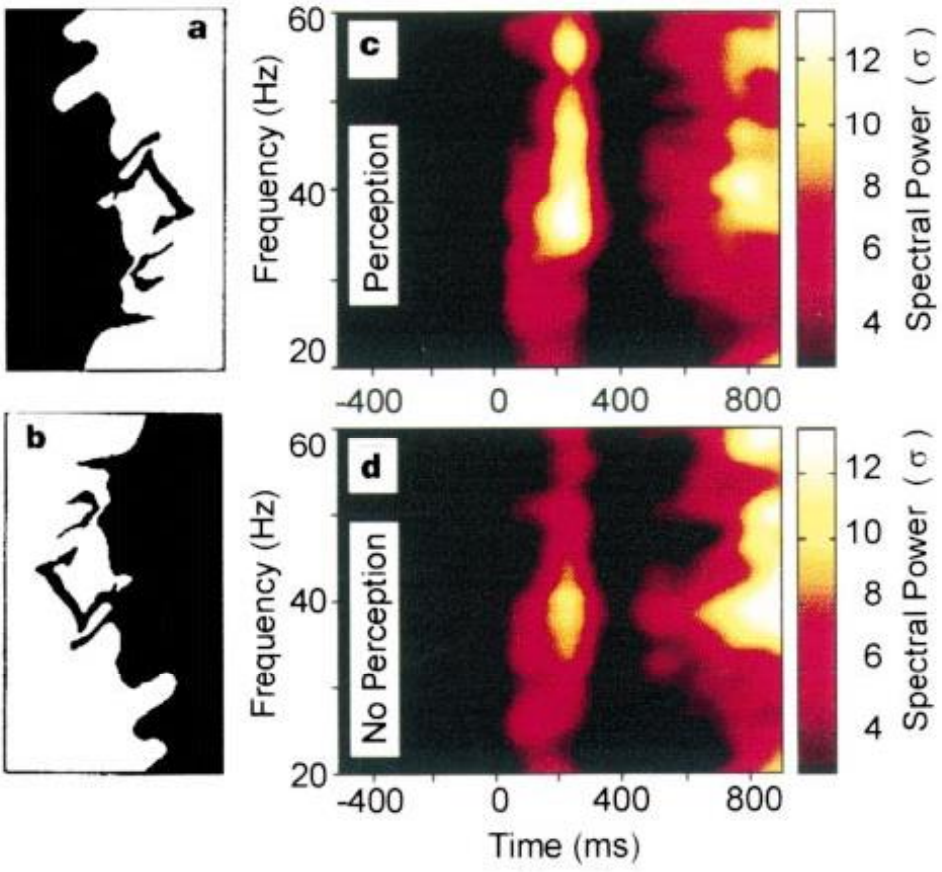

Figure 5.8: Stimuli and emission time-frequency charts (Rodriguez et al., 1999, page 431)

Moreover, Rodriguez et al. (1999) examined as well synchronization and found clear differences between the two conditions. Synchronization was prominent throughout the task only in the perception condition. A first significant extension occurred in the perception condition at around 200 to 260 ms past stimulus onset. This was followed by a pronounced reduction in synchrony, or de-synchronization, based around 500 ms. Another increase, for both the perception condition and the no-perception condition, appeared around the reaction time. In general, synchronization occurred with zero phase-lag.

In summary, gamma activity was quite similar in both conditions, except the difference in amplitude at around 230 ms, which contradicts with synchronization. The observed reduction in synchrony at around 500 ms is not equal with a simple return to a ground level. In contrast, Rodriguez et al. (1999) interpreted them as an active process of desynchronization. The current assembly (for face perception) was disintegrated to establish a new assembly (for motor response). Their results are thus another important support for the functional relevance of neural synchronization.

5.4 Evidence for large scale synchronization

Engel et al. (1991b) have done a study on three adult cats in which the occurrence of synchronization between the hemispheres was examined. Multiunit responses were recorded from cells of area 17 having the same orientation preferences. At 90 out of 109 recording sites the responses have been oscillatory. Furthermore, in 89 from 128 response pairs, which corresponds 70 %, synchronization occurred between the two hemispheres with zero time-lag. Inter-hemispheric synchrony appeared with similar strength as synchrony within one hemisphere.

Figure 5.9A illustrates the position of the electrodes in both hemispheres of area 17. Figure 5.9B shows that the recorded neurons had corresponding orientation preferences. Additionally, figure 5.9C presents the time histograms of responses, figure 5.9D the auto correlations, and figure 5.9E the cross correlations.

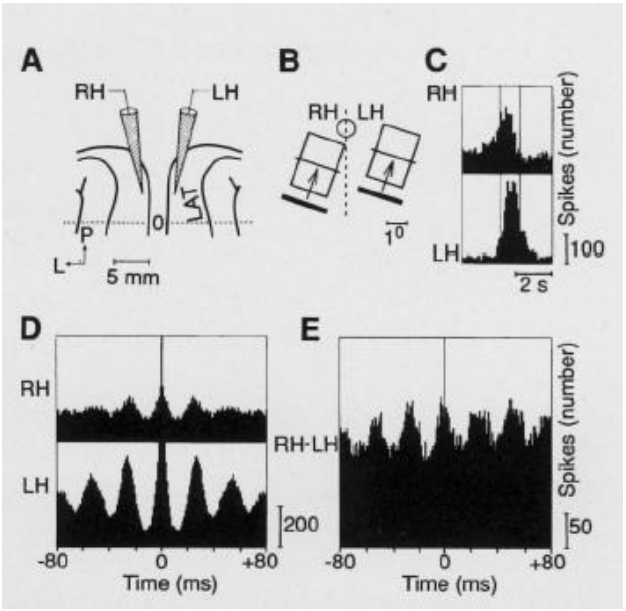

Figure 5.9: Interhemispheric synchronization of oscillatory responses
(Engel et. al, 1991b, page 1177)

Engel et al. (1991b) suggest the corpus callosum as the substrate for synchronization between the hemispheres. The authors tested this hypothesis and disconnected the corpus callosum in two further cats. The obtained results revealed again strong synchronization in each hemisphere. Anyway, no synchronization was evident between the hemispheres. Thus, synchronization between left and right hemisphere is most likely effected through the corpus callosum.

Figure 5.10 illustrates synchronization between the hemispheres in normal cats (left histogram) and cats with severed corpus callosum (right histogram) in comparison. Strong synchronization is shown with black histograms, weak synchronization with hatched histograms, and no synchronization with unfilled histograms, respectively.

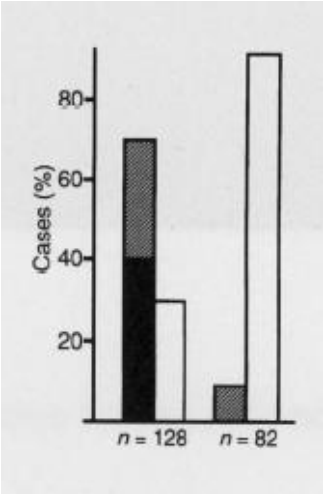

Figure 5.10: Comparison of interhemispheric synchronization (Engel et al., 1991b, page 1178)

5.5 Evidence for temporal binding

Engel et al. (1991a) obtained direct evidence for scene segmentation through synchronization of neuronal responses. The authors examined eight anesthetized and paralyzed cats and recorded from area 17 with overlapping receptive fields. The stimulation with a single light bar led to strong synchronized responses without regard to the orientation preferences of the cells. Anyway, the stimulation with two light bars with different orientations separated the same neurons into different assemblies. The responses in each of these assemblies again were synchronized but, importantly, no synchronization was evident between these assemblies. Engel et al. (1991a) could thus prove that scene segmentation is accomplished by a temporal code using synchronization of neuronal responses.

Figure 5.11 gives an example of the experiment by Engel et al. (1991a). The authors recorded from two to four sites. The thick line shown in figures 5.11A-D shows the orientation preferences of the cells. In particular, cells at sites 1 and 3 had orientation preferences close to vertical while cells at recording sites 2 and 4 preferred stimulus orientations close to horizontal. Figures 5.11A, 5.11B, and 5.11C illustrate synchronized responses between all recording sites during activation with a single light stimulus of 0°, 112°, and 135°, respectively. In case of simultaneous presentation of two superimposed stimuli having different orientations (e.g. 0° and 112°), synchronized responses were observed between sites 1 and 3 as well as between sites 2 and 4. Anyway, no significant synchronization was evident between these pairs. As example, figure 5.11D illustrates this at the bottom, showing not significant responses between sites 2 and 3.

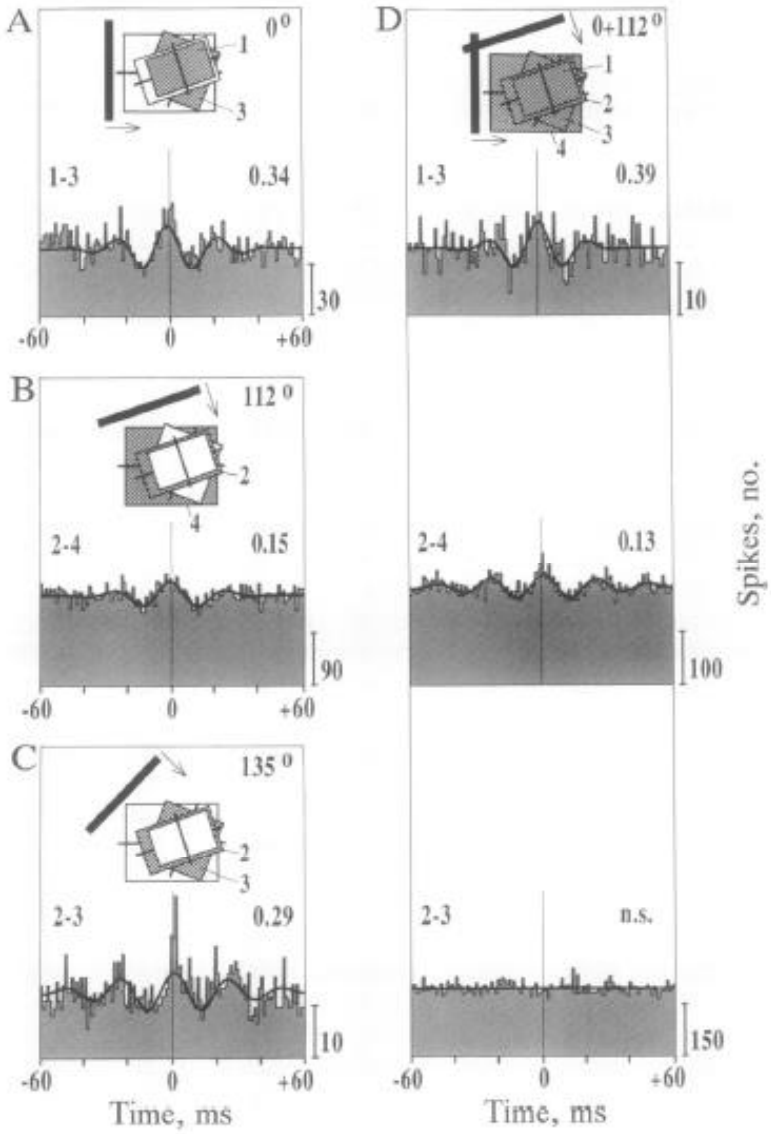

Figure 5.11: Conflicting stimuli alter the cross-columnar interaction
(Engel et al., 1991a, page 9138)

5.6 Visuo-Motor integration

Roelfsema et al. (1997) presented a study in which synchronization appeared between visual and parietal cortical sites, as well as between regions in parietal and motor cortex. The authors examined five cats which had to respond to a visual stimulus. Roelfsema et al. (1997) presented a grating with changing orientation and the cats had to react on this by either press or release a button with their forepaw. The cats received a reward on correct acting.

At time of the response by the cats, strong synchronization with zero time-lag occurred between the related cortical areas. On the other hand, this synchronization was replaced with activity having large and unsystematic time lags during reward period as well as during inter-trial phases.

Figure 5.12 shows correlations of field potentials obtained from visual, parietal, and motor cortical sites while the cat attended the grating. As illustrated, significant synchrony with zero time lag appeared between area 17 of the visual cortex and area 7 of the parietal cortex. On the other hand, area 7 showed significant synchronization with the lateral and medial subdivision of area 5 of the parietal cortex. Finally, further synchronization was evident between area 4 of the motor cortex and the lateral and medial subdivision of area 5 of the parietal cortex. Synchronization therefore was only existent between related areas.

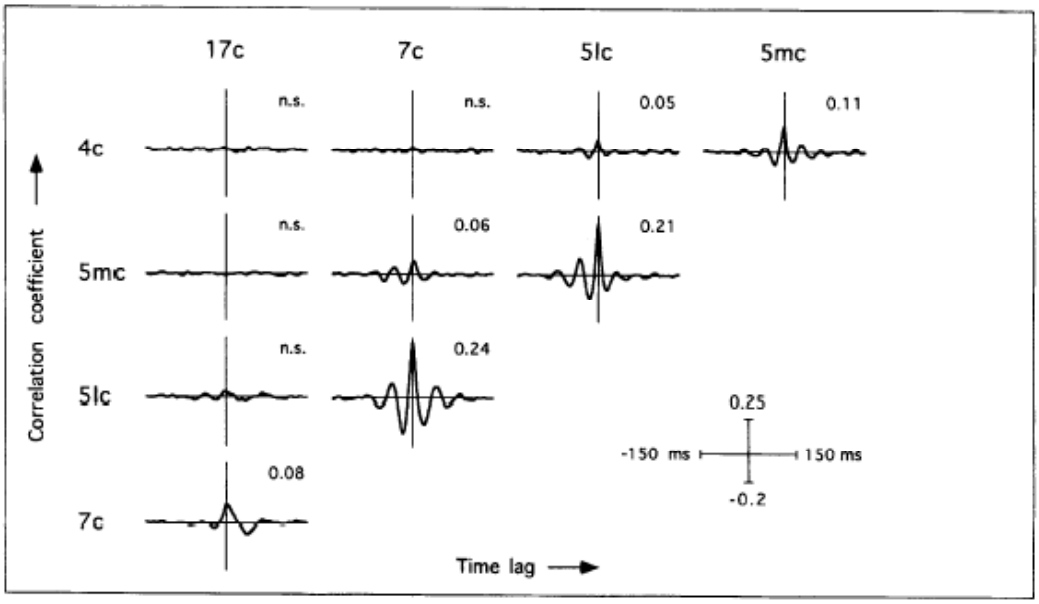

Figure 5.12: Pattern of interactions among areas of the visual, parietal, and motor cortex (Roelfsema et al., 1997, page 159)

Roelfsema et al. (1997) thus suggest that the obtained synchronization between parietal and motor sites is responsible for the integration of distributed neuronal activity which results in a compound movement.

Another confirmation for the integrative function in sensorimotor activity comes from Aoki et al. (1999) who recorded in 6 human subjects with intractable epilepsy electrocorticograms (ECoG) from 14 subdural sites. Each subject had to accomplish three different visuomotor tasks as squeezing some fingers serial on the thumb, just to mention one of them. During the control condition the subjects had just to relax and stretch out the wrist. Aoki et al. (1999) calculated the spectral power for five 10 Hz ranges from 10 to 60 Hz.

The results revealed a reduction of spectral power in the range from 11 to 20 Hz and, contrary, an increase of spectral power in the range from 31 to 60 Hz while the subjects accomplished the visuomotor tasks. The power changes were evident at forearm sites of sensorimotor cortex. During the control condition, almost no change in power occurred. Additionally, three subjects exhibited phases of clear gamma oscillations while performing the visuomotor tasks. Gamma-range power increased at different sites during various tasks, suggesting a particular function to the tasks. Furthermore, gamma activity was in phase between various sites during different tasks.

Thus, Aoki et al. (1999) conclude that synchronized gamma activity is of functional relevance for human sensorimotor integration.

5.7 Motor response

Similar evidence for a significant function of gamma synchronization is available for the motor system. In that context, Farmer (1998; as cited in Lee et al., 2003) presented some studies in which gamma activity was correlated with components of movement. To mention one example, Hamada et al. (1999; as cited in Lee et al., 2003) examined rats and found maximal gamma power at somatosensory cortex approximately 100 ms prior to exploratory whisking start. The authors suggest a connection with the motor order to prepare movement.

Additional support for the significance of gamma activity in motor systems comes from Jokeit and Makeig (1994; as cited in Lee et al., 2003). These authors reported stronger gamma activity in fast responders while slow responders had weaker gamma activity, measured close to reaction time. Further EEG and MEG studies obtained evidence for a temporary increase of gamma activity near to the movement of hands (e.g. Crone et al., 1998; Popivanov et al., 1999; as cited in Lee et al., 2003). Moreover, De Pascalis and Ray (1998; as cited in Lee et al., 2003) presented a study in which gamma activity showed a transient increase during movement (Go condition), while in the absence of movement (No-Go condition) this was not the case. Additionally, De Pascalis and Ray (1998; as cited in Lee et al., 2003) compared the pattern of gamma activity in connection with working memory load. Most interestingly, they found strong gamma activity during high memory load condition, in contrast to low memory load condition.

Further evidence is available showing synchronized gamma activity at time of muscle contraction. Baker et al. (2001; as cited in Lee et al., 2003) recorded from primary motor cortex. They examined monkeys which had to carry out a precision grip task. Gamma synchrony occurred and was strongest for the time of steady hold phases. These oscillations might have correlated activity with electromyographic (EMG) oscillations of muscle contractions. Brown et al. (1998; as cited in Lee et al., 2003) found a correlation between muscle activity in humans with MEG activity in motor cortex at approximately 40 Hz. Similar results obtained Mima and Hallett (1999; as cited in Lee et al., 2003), who indicate a functional role for gamma oscillations in driving muscle activity.

5.8 Learning

Gamma synchrony might have an important role in learning, too. Bauer and Jones (1976; as cited in Lee et al., 2003) could learn cats to raise gamma oscillations in visual cortex and hippocampus. They only needed 20 to 30 training lessons in which the cats were rewarded with milk when staring at a certain place. This behavior was associated with increased gamma activity. A similar experiment was presented by Amzica et al. (1997; as cited in Lee et al., 2003). These authors were able to condition cats to raise gamma oscillations in motor cortex with water reinforcement. Most interestingly, gamma power as well as gamma synchrony moved back to baseline level as soon as extinction took place. In addition, Amzica et al. (1997; as cited in Lee et al., 2003) reported different changes in motor and visual cortex and suggest that cats have been able to raise gamma oscillations in chosen cortical regions.

Another interesting study by Miltner et al. (1999) provides further support for the functional significance of gamma synchronization for associative learning which I will illustrate in more detail in the following.

Miltner et al. (1999) used a red or green light with 3 seconds duration as the conditioned stimulus (CS+) and induced an electric shock (UCS, unconditioned stimulus) at the end of this period. The electric shock was given either to the dominant (right hand) or non-dominant (left hand) finger. In summary, 60 trials with shock delivery and another 60 trials without shock delivery (CS-) and presentation of the alternate color have been applied in random order. Of course, at the end of the experiment another 80 trials were given to extinguish.

The occurrence of gamma activity was significantly greater for CS+ than for CS- during the first 2 seconds of the trial. In addition, 250 ms before and up to shock delivery, gamma coherence in the frequency range between 37 to 43 Hz was again significantly greater for CS+ than for CS-. Greater gamma coherence was also evident for CS+ than for CS- if the electric shock was applied to the non-dominant finger. Involved and measured areas were primary and association visual cortex as they receive visual input from CS+ and CS-. Input from the finger is presented at the contralateral (right) or midline pericentral cortex and concerned as well was the visual cortex with the contralateral posterior parietal somatosensory association area. If the electric shock was applied to the dominant (right) finger, the laterality of raised coherence altered.

Importantly, no increased coherence was evident for other frequency spectrums. Miltner et al. (1999) could not found differences between CS+ and CS- for delta, theta, or beta bands.

5.9 Language

Various experiments reported another involvement of gamma activity in language. Some authors compared words with pseudo-words and found increased gamma activity only for the word type. Evidence is available for either, visual and auditory domain. On the other hand, no difference was available in alpha activity (Krause et al., 1998; Pulvermuller et al., 1995; as cited in Lee et al., 2003). Further support comes from Pulvermuller et al. (1999; as cited in Lee et al., 2003) who recorded from the scalp. These authors showed a different topography of gamma oscillations. Nouns showed increased gamma activity at O1 and O2 whereas verbs revealed increased activity at C3 and C4. This provides further support for the importance of gamma activity in cortical processing.

5.10 Memory

The medial temporal lobe is responsible for conscious memory. In this region, neocortical inputs connect through the rhinal cortex with the hippocampus (Wagner, 2001).

A study by Fell et al. (2001; as cited in Wagner, 2001) examined patients with intractable epilepsy. The recording of field potentials took place from rhinal and hippocampal areas which have been seizure-free. The patients had to learn words and afterward recall them as good as possible. Fell et al. (2001; as cited in Wagner, 2001) found differences in the recorded regions in gamma synchronization between words that were later remembered or later forgotten. In particular, gamma synchronization was stronger for later remembered words in the time range 100 to 300 ms and 500 to 600 ms after word onset, suggesting a functional role in encoding. Furthermore, Fell et al. (2001; as cited in Wagner, 2001) observed a reduction in synchrony around 1,000 to 1,100 ms after the onset of later remembered words. Interestingly, the differences in synchronization were accompanied with temporary reductions in gamma power while patients encoded.

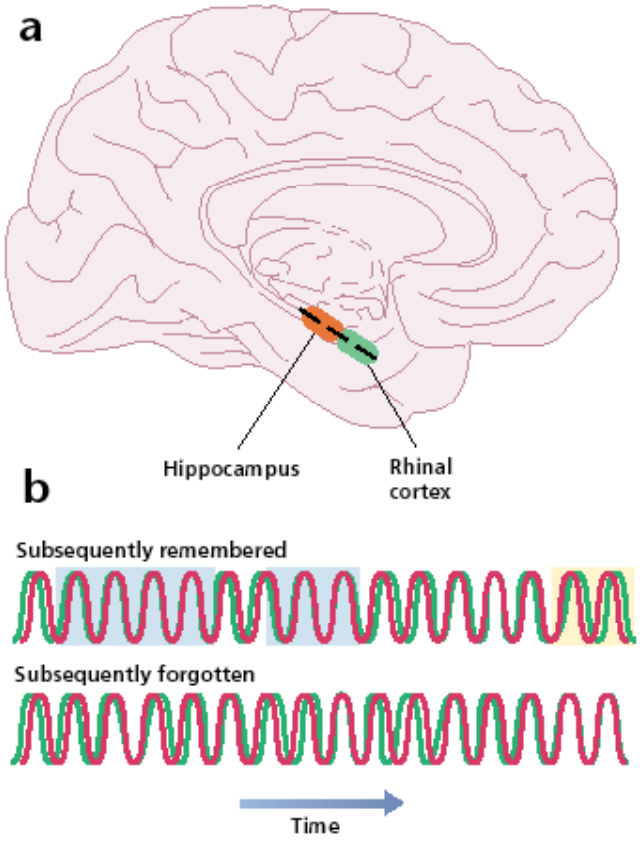

Figure 5.13: Gamma synchronization and desynchronization during the encoding of words later remembered compared to words later forgotten (Wagner, 2001, page 1160)

Figure 5.13A illustrates the recording from rhinal cortex and hippocampus. The black line shows the insertion of the electrodes. Figure 5.13B presents the differences in synchronization, between later remembered and later forgotten words. The phases of increased gamma synchronization during trials with words later remembered (in comparison to words later forgotten) are blue shaded whereas the decrease of synchronization is illustrated with yellow shading.

Importantly, the results are based on correlations and thus, lacking a causal explanation. Anyway, the obtained results suggest that a first synchronization, followed with desynchronization as well as a reduction in gamma power between rhinal and hippocampal neurons during encoding, facilitate the formation of declarative memory (Wagner, 2001).

5.11 Gamma synchronization in relation to Arousal and Attention

Studies are available showing a relation between neural synchronization and arousal and focused attention, too. For instance, synchronization in the gamma frequency range was increased during REM sleep as well as during waking in contrast to deep sleep. Such empirical support is evident for experiments in rats (Franken et al., 1994; as cited in Engel et al., 1999) and in cats (Steriade et al., 1996a; Steriade, 1997; as cited in Engel et al., 1999). Further support comes from Munk et al. (1996; as cited in Engel et al., 1999). These authors stimulated the midbrain reticular formation, which is responsible for the adaptation of vigilance. This resulted in a change from low to high frequency oscillations. In addition, Roelfsema et al. (1997; as cited in Engel et al., 1999) examined animals in an awake and behaving condition. They reported about increased gamma synchronization in the cortex throughout periods with focused attention.

Similar evidence is available with EEG and MEG experiments in human subjects. Schwender et al. (1994; as cited in Engel et al., 1999) could show that gamma synchronization disappeared with deep anesthesia. Desmedt and Tomberg (1994; as cited in Engel et al., 1999) demonstrated a clear correlation between increased gamma synchronization and arousal as well as focused attention. Additionally, Joliot et al. (1994; as cited in Engel et al., 1999) reported a connection with conscious auditory perception and Tallon-Baudry et al. (1997; as cited in Engel et al., 1999) with attentive visual search.

Another study in relation with attention comes from Fries et al. (2001a) who examined macaque monkeys and recorded from area V4 in the cortex. Fries et al. (2001a) found increased gamma synchronization in the range from 35 to 60 Hz while the monkeys were attending to behaviorally important stimuli whereas synchronization in the frequency range under 10 Hz was reduced. On the other hand, neurons activated by distracters did not yield differences in synchronization. Additionally, Fries et al. (2001a) could demonstrate that the firing rate did not increase at the same time, suggesting an independent function of gamma synchronization for selective attention. Fries et al. (2001a) concluded that gamma synchronization probably amplifies behaviorally important signals.

Further support demonstrated Gruber et al. (1999) who designed a visual attention task. The participants had to pay attention to colored squares which have been shown in alteration on the right or left side of the screen and additionally in rotation or motionless, respectively. Gruber et al. (1999) reported significantly increased gamma power in the range between 35 to 51 Hz while the participants paid attention to the stimulus (see figure 5.14). Moreover, gamma power was enhanced with the rotating stimulus in relation to the motionless stimulus, suggesting a connection with motion processing. In conclusion, Gruber et al. (1999) indicated that attention facilitate neuronal activity related to focused and selective cortical processing. And this enhancement most likely is based on synchronization in the gamma frequency range.

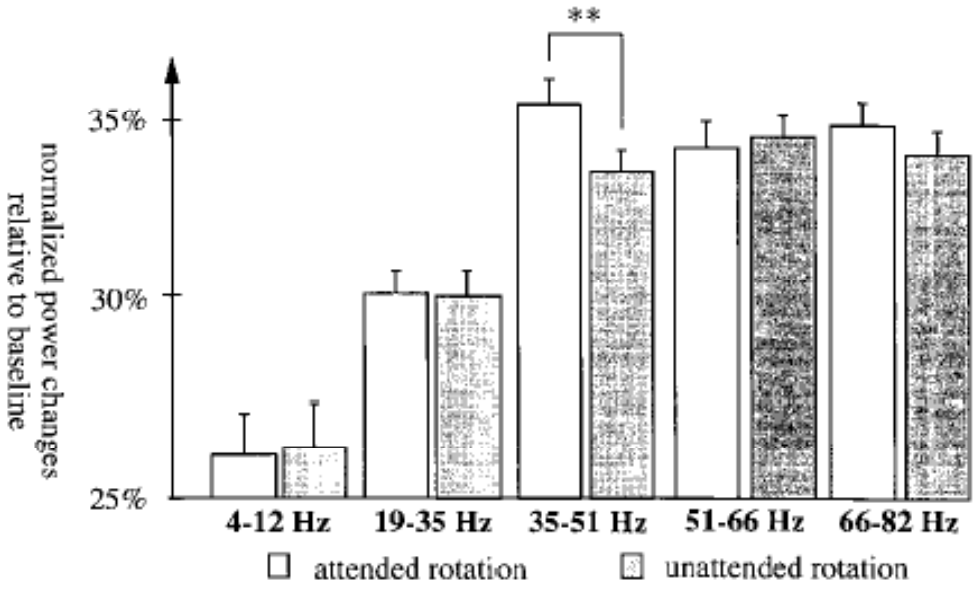

Figure 5.14: Normalized power changes across the left and right parieto-occipital regional means when subjects attended (white bars) or ignored (grey bars) the rotating screen (Gruber et al., 1999, page 2079)

Moreover, Tiitinen et al. (1993; as cited in Lee et al., 2003) used a dichotic listening task. They reported about increased Gamma activity recorded with EEG when the stimulus was displayed to the attentive ear in relation to the inattentive ear. Similar evidence is available in a study obtained by Sokolev et al. (1999; as cited in Lee et al., 2003). These authors presented increased MEG Gamma oscillations in a visual stimulus condition without distractor, compared to the same condition with an auditory distractor. Additionally, Shibata et al. (1999; as cited in Lee et al., 2003) designed a Go/No-Go task and demonstrated faster Gamma responses for the attended visual stimulus in relation to the unattended stimulus.

In summary, it seems that gamma phase synchronization is of functional relevance not only for information processing in the cortex, it is most likely implicated in arousal and attentional processes as well.

5.12 Other gamma synchronization in non-visual areas

Another interesting study comes from Haig et al. (2000) who examined 40 human subjects. They recorded from multiple sites and were interested in the time course of gamma activity. The participants had to react on two different tones which have been presented in random order. Two reaction-time buttons had to be pressed after presentation of the target-relevant tones which have been around 1,500 Hz, while the irrelevant tones ranging around 1,000 Hz should have been ignored.

In both conditions, gamma synchrony peaked in the latency window between -100 to 100 ms. Anyway, only the task-relevant condition revealed a late maximum between 250 to 450 ms after stimulus onset. Figure 5.15 shows both obtained results.

This late maximum possibly indicates features of post-discrimination activities and it is suggested to be in relation with N2 and P3 components and reaction time.

However, Haig et al. (2000) could obtain empirical support for the occurrence of synchronous gamma oscillations in connection with human cognition.

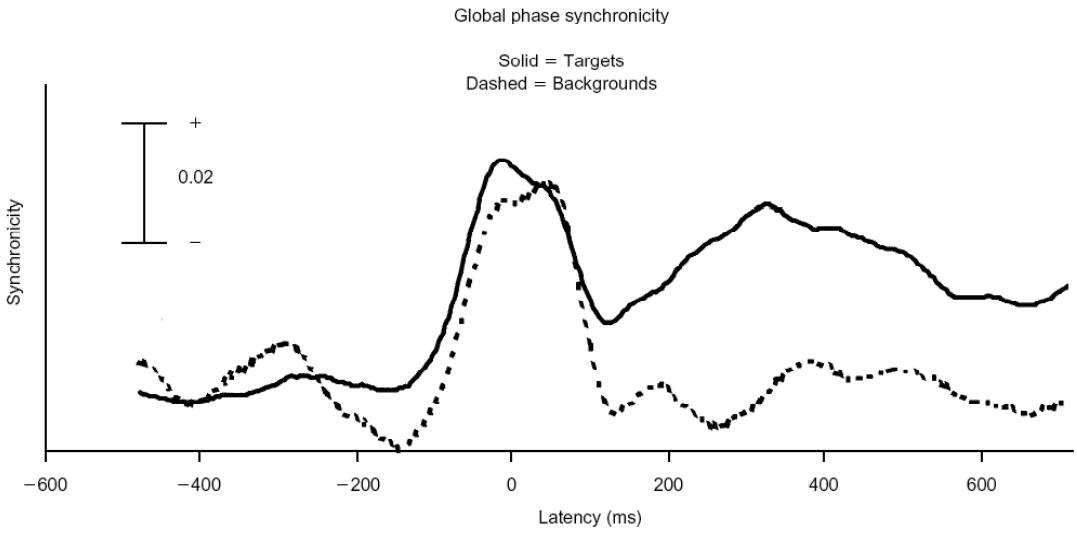

Figure 5.15: Grand average global gamma phase synchronicity waveforms in targets and backgrounds (Haig et al., 2000, page 672)

5.13 Gamma on the control of feature bindings and intelligence measures

So far, most of the experimental support for the functional significance of synchronization is correlative, which doesn`t allow causal conclusions. To test directly if gamma synchrony is related with binding, another experimental setting has to be applied. Thus, in a recent study, Keizer et al. (2010) varied synchronization and examined the effects on human performance.

The possible role of gamma synchronization for feature binding as well as for intelligence has already been discussed in more detail before. Keizer et al. (2010) tried to test this directly, using a neurofeedback paradigm with 8 sessions. In particular, the so-called Gamma-up group of participants was instructed to enhance gamma power while reducing beta activity. The second group, a classical control group, was trained to enhance beta activity at the expense of gamma power. Thus, Keizer et al. (2010) examined both frequency bands in competition and used one band as preference over the other one.

Feature integration was measured by a version of the task from Hommel (1998; as cited in Keizer et al., 2010) and for intelligence the authors used the Raven´s Standard Progressive Matrices (Raven, 1938; as cited in Keizer et al., 2010).

Gamma power was significant different between the two groups on session 8, while this difference was absent in the pretest. Another significant difference resulted in the 2 to 12 Hz activity in session 8, again without any differences in the pretest.

Keizer et al. (2010) additionally reported significant differences in visual binding costs in the posttest. In particular, the Gamma-up group showed a decrease on binding costs while the reverse was true for the control group. Anyway, it has to be noted that this effect was only significant in comparison of the first halves of pre- and posttest. The comparison of the second halves did not yield differences in binding costs.

Moreover, Keizer et al. (2010) reported a significant correlation in the Gamma-up group between the change in percent on the intelligence result, measured from pre- to posttest, and the change in percent on the gamma power. Keizer et al. (2010) found a peak already at 16 Hz, suggesting a functional role on intelligence for both, high-beta and gamma activity.

In summary, the study obtained by Keizer et al. (2010) shows that neurofeedback is an interesting method to investigate the functional importance of different frequency bands, measured with scalp EEG. The variation in gamma activity resulted in changes on intelligence score as well as in visual binding costs. Anyway, at this point it´s only possible to suggest a connection between gamma power with binding and intelligence. Further examination is required. However, the idea behind this experiment is similar with our own design and therefore this study a support for the experimental design which we have decided to apply.

5.14 Gamma synchronization and disorders

Beside the experimental support, also brain disorders indicate a functional relevance for neural synchronization (Mackey & Glass, 1977; Llinas et al., 1999; as cited in Varela et al., 2001). For instance, Tremor in Parkinson`s disease is suggested to arise due to irregular coupling patterns in

basal ganglia (Hurtado et al., 2000; as cited in Varela et al., 2001). Furthermore, the cognitive abnormalities in patients with schizophrenia are related with an interruption in synchrony (Hoffman & McGlashan, 1993; Tononi & Edelman, 2000; as cited in Varela et al., 2001). Moreover, intrinsic local frequencies change to slow and uniform oscillations with long duration in epileptic patients (Martinerie et al., 1998; Le Van Quyen et al., 2001; as cited in Varela et al., 2001). All these examples provide additional support for a functional significance of neural synchronization in our brain.

5.15 Conclusion

In summary, then, it seems that synchronization of neuronal activity is the most suitable solution to the binding problem. The above presented studies clearly show that synchrony is of functional relevance. This could be demonstrated with different recording methods, ranging from single cell studies up to EEG recordings in human subjects. So far, empirical support is available for almost any cognitive activities, from visual perception, over the motor system, up to arousal and attention. It seems that synchronization in the gamma frequency range is of general importance for integration and information processing. Additional support for this hypothesis comes from disorders, were disturbances in synchronization are often responsible for functional abnormalities (Lee et al., 2003).

Anyway, after all the experimental support, I will move on in chapter 6 with the possible measurement of gamma synchrony, followed by an illustration of its underlying mechanisms in chapter 7.

6 Measurement of gamma synchrony and gamma oscillations

6.1 Neural synchrony as a multi-scale phenomenon

According to Varela et al. (2001), neural synchrony can be measured at various scales. Of course, the most important option to measure integrated activity is the examination of the common response of a local group of neurons. The measurement of local field potentials (LFPs) is most suitable for that. LFPs emphasize the common response of a local neural group. For the calculation, a time frequency analysis is possible to measure the activity of neuronal populations. Synchrony can be calculated with a cross-correlation function whereas for oscillations an auto-correlation function is applied. Besides that, the recording of single-neuron activity is used to measure on the micro-scale level. On the macro-scale level, the application of surface electrodes is commonly used. EEG recordings represent the activity of multiple local clusters (Varela et al., 2001). Figure 6.1 illustrates neural synchrony as a multi-scale phenomenon.

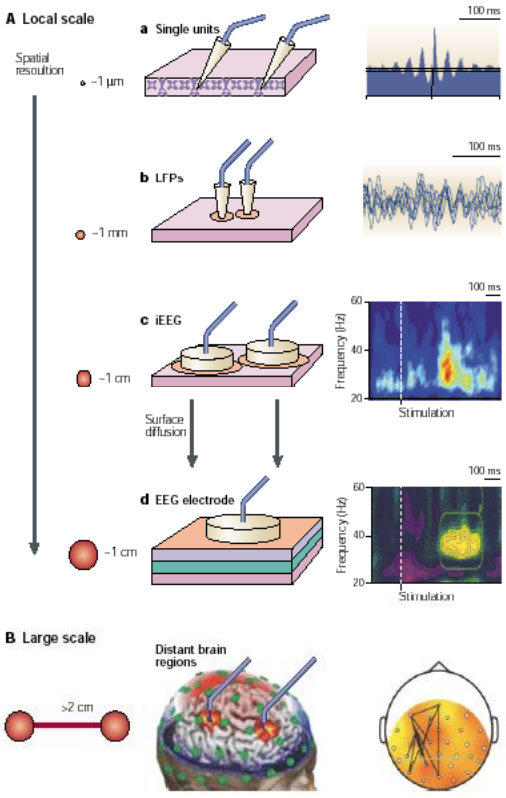

Figure 6.1: Neural synchrony as a multiscale phenomenon (Varela et al., 2001, page 232)

6.2 Methods for the study of phase synchrony

The study of synchrony is still a difficult intention. It requires the estimation of the present phase from every signal as well as the quantification of phase locking over a given period. For the latter one statistical criteria have aroused (see figure 6.2). In practical use, the cross-correlation function gives information about phase locking between single units. On the other hand, measuring on the meso- and macro scale is not that easy. Individual spikes are summed up and the measured signals contain various frequencies. Thus, new methods have been employed for the adequate measure of synchrony. These methods show suitable resolutions in frequency and time. Further developed models allow the estimation of synchrony online, having the advantage of calculation while the subject performs the task. The interested reader will find further information in more detail elsewhere (e.g. Lee et al., 2003; Varela et al., 2001).

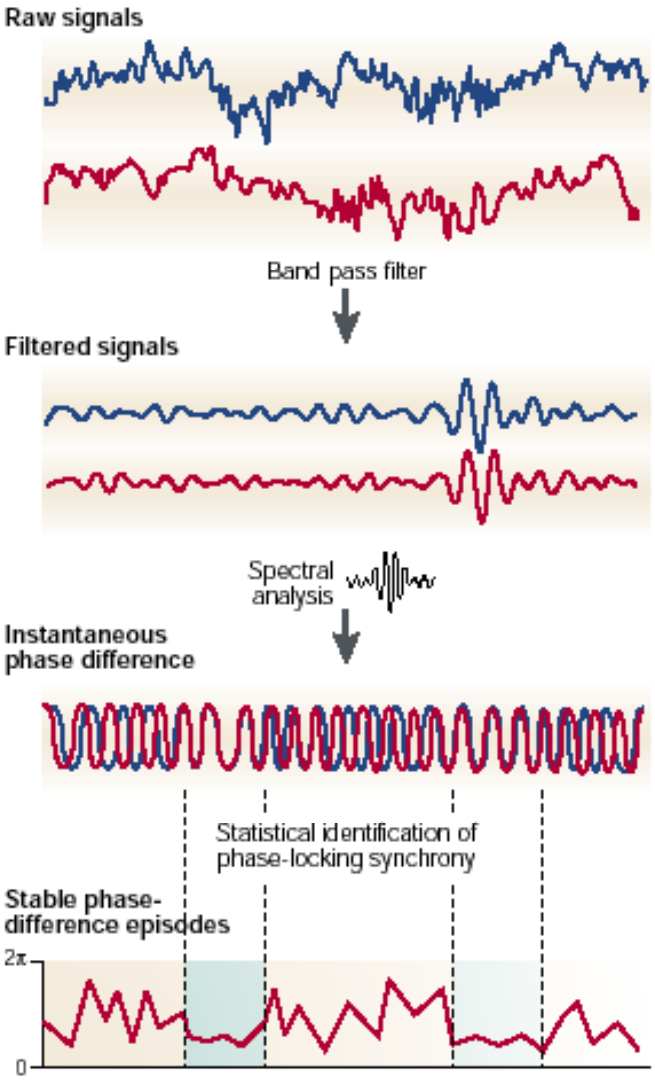

Figure 6.2: Methods for the study of phase synchrony (Varela et al., 2001, page 233)

On a critical view, regardless of the used method, problems rest with the background and intrinsic noise. In consequence, the measured phases vary between the recorded electrodes and the detection of synchrony therefore needs statistical assistance. Moreover, brain signals appear as broad band which makes it difficult to measure a present phase clearly. Most of the experimental support was therefore obtained with filtered signals, restricted to a small frequency range only. Further problems arise with the deficient spatial resolution of EEG and MEG studies, which are commonly used in healthy human subjects. This includes the risk that electrodes record from overlapping populations which may result in synchrony due to volume conduction. This problem as well requires the development of special techniques with better spatial resolutions. Although, in some cases it was possible to record directly with implanted electrodes - for instance on epileptic patients. Further detailed information on methodological issues and literature are listed, for instance, in Lee et al. (2003) and Varela et al. (2001). Here I will follow with another important distinction for the study of synchrony, namely the difference between coherence and correlation.

6.3 Coherence and Correlation

Historically, the use of the cross-correlation function to measure the relation between two signals recorded with EEG is familiar since the middle of last century (Brazier & Casby, 1951; 1952; as cited in Guevara & Corsi-Cabrera, 1996). The progress with fast computational algorithms resulted in a change to the alternative coherence spectrum. In general, the coherence provides comparable information, but additionally displays the covariation of two signals in a short time.

Although both, coherence and correlation, measure the relation of two signals, some important differences exist (Shaw, 1981; 1984; as cited in Guevara & Corsi-Cabrera, 1996). Coherence reflects both a variation in power as well as a variation in the phase relation. In consequence, the coherence value changes if either phase or power alternates. Furthermore, coherence gives information on stability between two signals over time. In particular, coherence does not reflect the true relation of two signals directly and its value for a given period is therefore always one, irrespective of alterations in power and phase relationships. Correlation, in contrast, reflects phase and polarity, regardless of amplitudes. The coherence is calculated by squaring the signal, resulting in values between 0 and 1 whereas the correlation values range from -1 to 1 and therefore consider polarity, too. The correlation is an easy method which does not require detailed mathematical knowledge while the coherence is not that simple and difficult to understand. Anyway, usually strong power asymmetries won't occur, resulting in comparable outcomes obtained with either, coherence or correlation, respectively (Guevara & Corsi-Cabrera, 1996).

Guevara and Corsi-Cabrera (1996) compared correlation and coherence in relation to phase and amplitude. Two signals of 2 Hz were used in different relationships. Figure 6.3 shows the values for correlation (r), coherence (Coh), and the average (r_m) for all together four periods of 1-s epochs. The coherence value, as expected, reflected the stability of the signals over the periods. In particular, the coherence was unaffected either by differences in phase (see figure 6.3B and 6.3C) or by differences in amplitude (see figure 6.3A and 6.3C), under consideration that the relationship between the signals did not change. Anyway, the coherence was sensitive to changes in phase or amplitude in a given channel and additionally in one of the periods, as this concerned the stability of the two signals (see figure 6.3E, 6.3F, 6.3G, and 6.3H). On the other hand, differences in amplitude did not change the correlation value (see figure 6.3A and 6.3D). But, in contrast, differences in phase (see figure 6.3B, 6.3C, 6.3E, and 6.3F) affected the correlation of the signals.

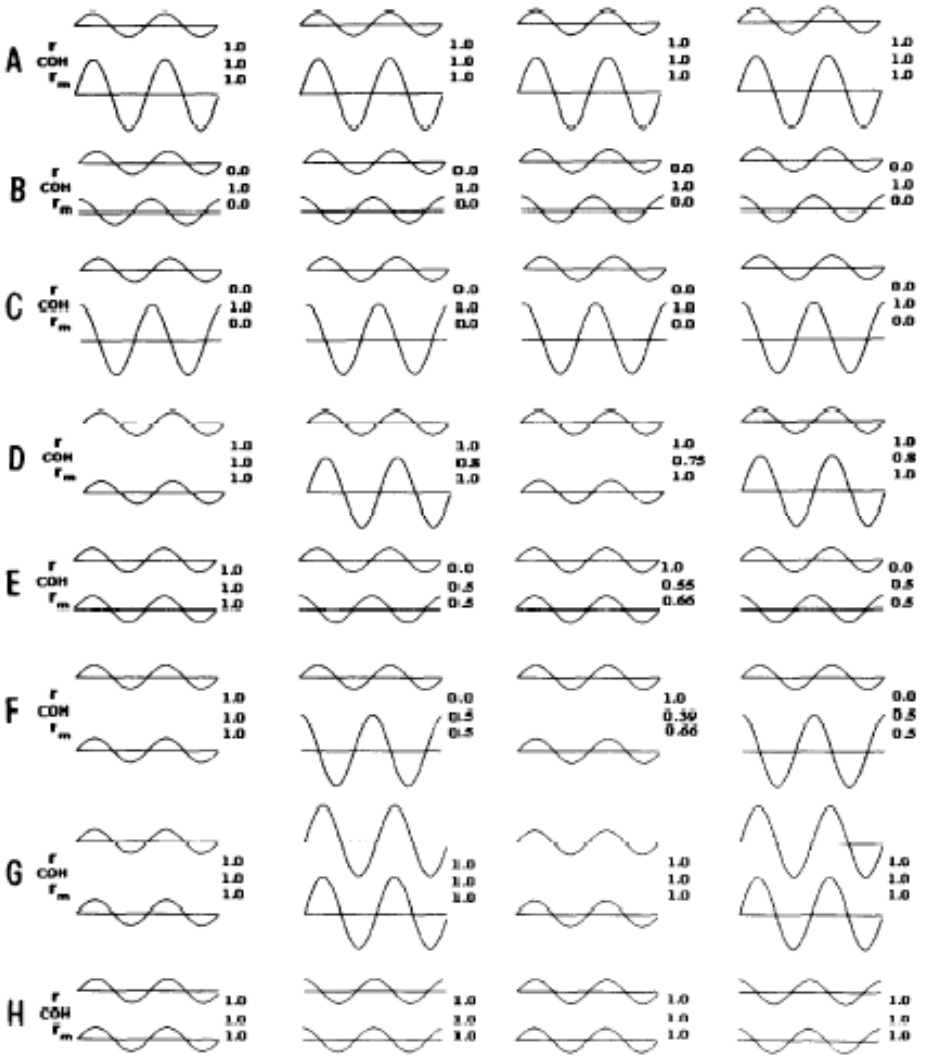

Figure 6.3: Differences and similarities between correlation and coherence
(Guevara & Corsi-Cabrera, 1996, page 147)

In summary, the results obtained by Guevara and Corsi-Cabrera (1996) clearly illustrate that correlation gives information about the phase of two signals, irrespective of the amplitudes. The coherence value, on the other hand, provides information about the stability of two signals and is thus sensitive to either a change in phase or amplitude. In conclusion, then, coherence is the better choice if the stability of two recording sites including differences in amplitude is of interest. Correlation is the better method if the interest is direct on phase relationship. We therefore have decided to use correlation for our study.

6.4 Gamma oscillation vs. Gamma synchrony

The important difference between gamma oscillation and gamma synchrony was already mentioned in chapter 4.2. Some studies exist which use the measure of gamma oscillations as an evidence for the occurrence of gamma synchrony. However, this is not correct. The appearance of gamma oscillations is not an indicator for the appearance of gamma synchrony, which reflects the relationship between two recorded signals, whereas gamma oscillations solely mean the occurrence of activity in the gamma frequency range, without regard to any phase relationship. As gamma synchrony is the suggested activity for an integrative function in cognition, only the direct measure of synchrony is of practical significance (Rodriguez et al., 1999).

6.5 Prominent alpha frequency

Activity in the alpha frequency range is the dominant one in adults, if measured with scalp EEG. Alpha regularly ranges between 7.5 to 12.5 Hz. The peak frequency means the largest amplitude within the mentioned frequency range (see figure 6.4).

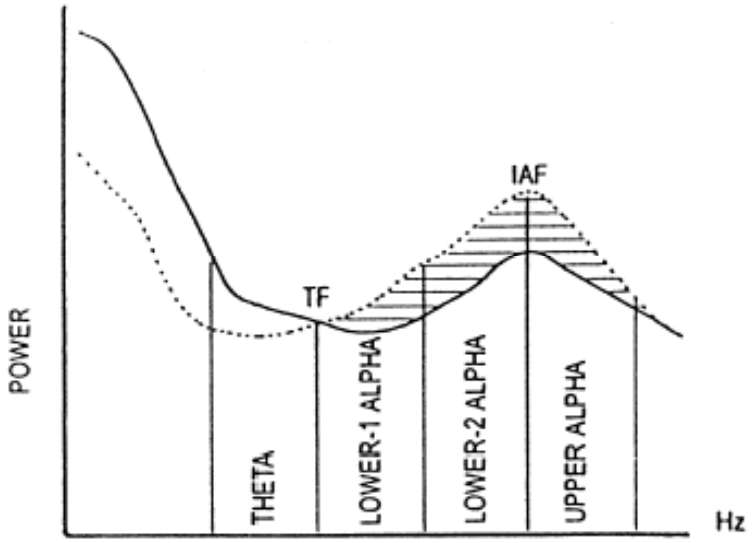

Figure 6.4: Individual alpha frequency (IAF) (Klimesch, 1999, page 171)

Most importantly, the individual alpha frequency (IAF) differs between subjects. The so-called transition frequency (TF) is the point where alpha and theta band cross. The individual adjustment of frequency bands for every participant is of high importance (Klimesch, 1999). This, of course, has been considered in the performance of the current study.

7 Underlying mechanisms of Gamma synchrony

So far, increasing evidence indicates a functional role of gamma synchrony in information processing. However, the accurate underlying mechanisms are still unknown. Lee et al. (2003, p. 65-67) provided a comprehensive overview of the most probable ones which I will summarize in this chapter.

7.1 GABA-ergic interneuron network model

Traub et al. (1999; as cited in Lee et al., 2003) provided fundamental work on the so-called network model which differs generally between two mechanisms responsible for gamma synchronization. Firstly, short-range synchrony, on a local scale of less than 2 mm, appears through the activation of GABA-ergic interneurons. This activation results in a continuous mutual inhibition of the postsynaptic potentials, occurring in synchrony with 40 cycles each second. Gamma synchronization is thus based on the repeated feedback loop of cortical interneurons (Whittington et al., 1995; as cited in Lee et al., 2003).

On the other hand, long-range synchrony, on a spatial scale of more than 2 mm, appears through the combined firing of interneuron networks with pyramidal cells (Traub et al., 1996; as cited in Lee et al., 2003). This synchronous rhythm of inhibition and excitation is the suggested mechanism for large scale gamma synchronization. Empirical evidence showed long-range gamma synchronization caused by repeated stimulation of the interneurons (Traub et al., 1996; as cited in Lee et al., 2003). Thus, it is suggested that gamma power in the interneuron network serves for the timing of pyramidal cells (Buzsaki & Chrobak, 1995; as cited in Lee et al., 2003). The first spike of the interneuron network could indicate the timing whereas the second spike of the interneuron network regulates the synchronization between interneuron networks and pyramidal cells (Jefferys et al., 1996; Traub et al., 1996; as cited in Lee et al., 2003).

So far, pharmacological studies support the model by Traub et al. (1999; as cited in Lee et al., 2003). As gamma synchronization is suggested to result from the activation of GABA-ergic interneurons, pharmacological instruments which disturb inhibitory postsynaptic potentials should thus inhibit gamma activity (Jefferys et al., 1996; as cited in Lee et al., 2003). Indeed, gamma activity in animals

was eliminated by bicuculline, which is a GABA A receptor antagonist (Boddeke et al., 1997; Colling et al., 1998; Taira et al., 1997; Whittington et al., 1995; 1996; as cited in Lee et al., 2003). Furthermore, Stopfer et al. (1997; as cited in Lee et al., 2003) used picrotoxin, a pharmacological agent which inhibits GABA-ergic activity, on honey bees and reported a disturbance in gamma synchrony, although the neurons fired still in order. Additionally, the honey bees lost their ability of odor discrimination, which is another important support for the functional role of gamma synchronization in perception.

7.2 Thalamo-cortical arousal model

This model, in short, proposes the resonance of thalamus and cortex as fundamental mechanism for gamma synchronization (Llinas et al., 1998; Steriade et al., 1996a; 1996b; as cited in Lee et al., 2003).

The thalamus is known as the core for processing and acts as relay for almost any sensory input. Although the exact synaptic mechanisms of the connecting neurons of thalamus and cortex are still unknown, probably some of them are responsible for the establishment of gamma oscillations. In fact, experimental evidence is available that various neurons exist which act as “intrinsic oscillators” and thereby generate repeated gamma oscillations. For instance, Gray and McCormick (1996; as cited in Lee et al., 2003) reported about pyramidal cells, located in the superficial layers of the visual cortex in cats, having repeated bursts within the gamma frequency range. These cells are known as pacemaker, as they have an impact on neighboring neurons.

Additional support for the thalamo-cortical model comes from Steriade et al. (1996a; 1996b; as cited in Lee et al., 2003) who reported synchronized gamma oscillations between thalamus and cortex. Furthermore, experiments showed an association between stimulation in the acoustic thalamus and gamma oscillations in auditory cortex, suggesting a more direct connection between thalamus and cortex (Barth & MacDonald, 1996; as cited in Lee et al., 2003). Consequently, a destruction of thalamus or cortex should affect gamma synchrony (Llinas et al., 1999; as cited in Lee et al., 2003). Indeed, it was shown that lesions in thalamus slowed gamma oscillations in response to 40 Hz tones (Spydell et al., 1985; as cited in Lee et al., 2003).

Another contribution to the thalamo-cortical model comes from Sheer (1984; as cited in Lee et al., 2003) who emphasized arousal in this context. In short, arousal should affect gamma synchronization through modulation of the ascending reticular activation system (ARAS) as well as through cholinergic activity on thalamo-cortical cells (Sheer, 1984; Steriade, 1997; as cited in Lee et al., 2003). Pharmacological studies proved this. Carbachol, a cholinergic agonist, increased gamma oscillations while atropine, a cholinergic antagonist, destroyed gamma oscillations (Buhl et al., 1998; Fisahn et al., 1998; as cited in Lee et al., 2003).

So far, the mechanisms responsible for gamma synchronization are yet not known in detail. Probably the network model and the thalamo-cortical model act in cooperation (Ritz & Sejnowski, 1997; as cited in Lee et al., 2003). If so, the thalamo-cortical mechanisms possibly work on multiple networks across the brain, whereas GABA-ergic interneuron mechanisms are responsible for the local networks. Anyway, another model is available which highlights inter-hemispheric gamma synchronization.

7.3 Corpus callosum model of inter-hemispheric Gamma activity

Some studies suggest the corpus callosum as functional important for gamma synchrony between the hemispheres. For instance, Engel et al. (1991b; as cited in Lee et al., 2003) examined cats and showed neural synchrony in response to a perceptual stimulus in both hemispheres. After separation of the corpus callosum, gamma synchrony still occurred within each hemisphere, but no longer between them. Similar evidence is available by Munk et al. (1995; as cited in Lee et al., 2003) who reported that neural synchronization between the hemispheres requires the corpus callosum. These authors again examined the visual cortex of the cat. Interestingly, gamma activity between the hemispheres is much more frequent as gamma activity within a hemisphere (Sil`kis & Bogdanova, 1998; as cited in Lee et al., 2003), suggesting a functional role in information processing which arise at both hemispheres in parallel (Sil`kis & Bogdanova, 1998; as cited in Lee et al., 2003).

8 Criticism of Gamma synchrony

So far, I have highlighted the binding problem and its possible solutions. The concept of temporal binding seemed very promising and up to date a huge amount of experimental support exists in accordance with this theory. Anyway, some studies showing different results and even studies where no gamma synchrony or gamma activity appeared are available. Thus, some authors criticized this theory and the functional relevance of gamma synchrony at all. In the following I will illustrate the most important studies and arguments which contradict with this theory.

Golledge et al. (1996) reported from various masking experiments and concluded an approximate time of only 20 to 30 ms for object recognition. Moreover, most of the neural information is accessible in less than 50 ms. This results in two spikes only, considering a neuron which fires at 40 Hz. Consequently, synchrony should appear as close as possible with stimulus onset. But this is not the case as synchrony starts some stage after stimulus onset and, additionally, is not phase-locked with the stimulus. Thus, Golledge et al. (1996) conclude that synchronization might not be that important as indicated for binding. Anyway, the authors suggested a functional role in learning which allows more time.

Furthermore, Golledge et al. (1996) reflected on the already present synchrony by chance, which is regularly excluded from the data. In particular, if two neurons discharge at approximately 40 Hz, the probability of correlated firing becomes 0.96 in less than 600 ms. Thus, Golledge et al. (1996) believe that this „background“ synchrony do not allow the signal of coherent features.

In conclusion, then, Golledge et al. (1996) doubted the functional importance of gamma synchrony. The authors argued that neural synchronization is certainly too slow in comparison with the known speed in object perception. Golledge et al. (1996) rated the appearance of synchrony simply as a side effect of common neuronal input with no specialized function at all.

Lamme and Spekreijse (1998) could not support the synchrony theory in their experiment. They examined the primary visual cortex of monkeys which were shown different textured scenes. The authors could not found a relationship between synchrony and the presented perceptual scenes. Thus, Lamme and Spekreijse (1998) concluded that neural synchrony might not be responsible for feature binding and texture segregation, at least not in monkey primary visual cortex.

Notably, Singer (1999) added a comment on this study. In dependence on the organization of the receptive fields, synchronization is different between pairs of neurons. Consequently, for the detection of synchrony, the selection of suitable cell pairs is of high importance, beside the processing stage of course. The use of averaged data over neurons with various receptive field organizations might hide dynamic variations in synchrony. Singer (1999) supposes such a problem in the study of Lamme and Spekreijse (1998).

Another negative result was reported by Young et al. (1992). These authors tried to replicate the huge amount of experiments in the visual cortex of cats as similar as possible on monkeys. Thus, Young et al. (1992) examined area V1, the middle-temporal area (MT), and the inferotemporal cortex (IT) of monkeys under anesthesia. They recorded multi-unit activity (MUA) and local field potentials (LFP). Additionally, further data were obtained from IT on behaving monkeys, performing a face discrimination task.

Their results were quite different to those reported in studies on the visual cortex of the cat. In the anesthetized condition, Young et al. (1992) reported broadband increases in area V1 and MT, ranging from 1 to 100 Hz, at time of visual stimulation. No power shift from low to middle frequencies appeared. In area V1 and MT, the auto-correlation functions displayed oscillations in the alpha range, but not as expected in the gamma frequency. In area IT, no oscillations appeared in multi-unit activity.

Furthermore, in the behaving monkey condition, only 2 from 50 recording sites showed oscillating responses in the frequency range of 44 and 48 Hz while only one of these responses was in relation with the stimulus.

In summary, only 2 of 424 recordings at all together 142 sites showed oscillatory responses in the gamma frequency range from 30 to 70 Hz. There was no dependence on stimulus configuration at all. Thus, Young et al. (1992) concluded that gamma oscillations might have no functional importance, at least not in the monkey visual cortex. The authors suggest a possible difference of neural activity in visual cortex between monkeys and cats.

Finally, Young et al. (1992) additionally noticed existing methodological differences between various authors. Thus, some authors could have over-estimated oscillatory activity or synchrony, respectively, resulting from the mis-consideration of the goodness-of-fit between the Gabor function and the auto-correlogram.

Freeman and van Dijk (1987) reported broad band power with various peaks at around 20 to 40 Hz, while they expected them in the gamma frequency range between 35 to 75 Hz. These authors examined an adult rhesus monkey, in particular the visual cortex. Freeman and van Dijk (1987) tried to replicate results obtained in the olfactory bulb, but could not confirm their intent.

Yuval-Greenberg et al. (2008; as cited in Keizer et al., 2010) also argue against the theory of neural synchrony. They suppose miniature saccades as cause for the gamma increase immediately after stimulus onset, and not increase of gamma synchrony.

Juergens et al. (1995; as cited in Aoki et al., 1999) criticized the poor spatial resolution, using EEG recorded on the scalp. Commonly, these signals are bandpass filtered afterward, which might include harmonics in lower frequency bands, too, and therefore involve another problem, in comparison to cortical recordings obtained in animals.

Juergens et al. (1999) collected various human EEG, MEG, and ECoG studies, examining activity in the gamma frequency range for the time of visual stimulation. They clearly demonstrated some inconsistent and contradicting results, some of them in comparison to animal studies. For instance, Lutzenberger et al. (1995; as cited in Juergens et al., 1999) reported increased activity in the gamma range between 35 to 45 Hz during presentation with a moving stimulus, whereas Vijn et al. (1991; as cited in Juergens et al., 1999) discovered a broad band reduction during presentation of a turning checkerboard. Juergens et al. (1999) mentioned another study by Müller et al. (1996), who reported a broad band power increase in the range between 40 to 96 Hz during stimulation with a single light bar, while no gamma modulation appeared during presentation of two incoherently light bars. Müller et al. (1997; as cited in Juergens et al., 1999) tried to replicate this experiment and found this time a reduction of gamma activity during the condition with incoherent moving light bars. Finally, to have another example mentioned, Menon et al. (1996; as cited in Juergens et al., 1999) as well as Juergens et al. (1995; as cited in Juergens et al., 1999) could not find gamma modulations in human ECoG and human EEG recordings, using a classic learning and retrieval task which included the presentation of visual items. On the other hand, Murthy and Fetz (1992; as cited in Juergens et al., 1999) as well as Sanes and Donoghue (1993; as cited in Juergens et al., 1999) demonstrated clear gamma modulations during somatosensory stimulation with intracortical recordings in monkeys.

Following the above mentioned inconsistent and contradicting results, Juergens et al. (1999) started an experiment which involved both, a man and a monkey. They recorded EEG on the scalp and additionally local field potentials in the monkey. The authors examined the visual cortex throughout

presentation of a visual stimulus, which has been identical for the man and the monkey, respectively. With that, Juergens et al. (1999) aimed to clarify existing different results and doubts, mostly available in relation with the functional significance of gamma synchrony in human EEG studies. The obtained results clearly showed an increase of gamma activity in relation to the visual stimulus in the local field potentials as well as on scalp EEG in the monkey. Gamma activity was phase-locked with the stimulus and peaked around 80 to 160 ms after onset. Anyway, no gamma modulation was evident on human EEG, which is in contradiction with different previous publications. Juergens et al. (1999) concluded that gamma modulations might not be accessible in human EEG, at least not that easy as for instance in monkeys.

Juergens et al. (1999) mentioned some possible reasons for their negative results on human EEG and listed explanations why other authors reported them.

One reason might be a reduction of the signals measured with scalp EEG. The typical radius of human EEG is around 20 to 30 mm, which possibly cause superposition of different signals. This, of course, will not appear with intracortical recordings, for instance in monkeys and cats. Thus, Juergens et al. (1999) believe that strong remote gamma activity degenerated the site they intended to record.

Furthermore, differences in cranial, cortical, and scalp anatomy have to be considered. Juergens et al. (1999) additionally mentioned different visual-field representations between humans and monkeys. Notably, area V1 in humans is located in the middle of the medial occipito-temporal gyrus, which might be difficult to measure. On the other hand, area V1 in monkeys is mainly located on the surface.

Moreover, Juergens et al. (1999) doubted at least some of the supportive publications of studies with human scalp EEG. Artifacts cause big problems in EEG recordings. Muscle activity, for instance, is difficult to discriminate from gamma-range activity. Low frequency harmonics can influence the gamma activity and lead often to misinterpretations. Ringing is an artifact coming from narrow-band filtered signals which frequently shows oscillatory time courses. Spurious significances often become another artifact which is difficult to control.

Finally, Juergens et al. (1999) wonder if positive results have a higher probability of publication than negative results. If so, some more negative results might be available, but became not published.

Kiper et al. (1996) have been interested in the underlying processes of perceptual grouping and visual segmentation. These authors criticized that, so far, no direct experimental support for the synchronization theory exists. Thus, Kiper et al. (1996) carried out two studies to test this directly. They used visual flickers as stimulus and expected an influence on visual tasks.

The first experiment was a texture segmentation task. The subjects had to separate between different adjusted line segments and the background. In every trial, the participants had to distinguish if the stimulus was vertically or horizontally orientated. The presentation flickered in a frequency from 15 to 60 Hz and should therefore cause different oscillatory responses. Kiper et al. (1996) modified the presentation in four conditions, namely in phase, out of phase, presentation with a constant value, or randomly out of phase, respectively.

The second experiment aimed to examine the functional significance of synchronized flicker on perceptual grouping. Kiper et al. (1996) presented various triangles showing all in the same direction. This image is not stable as the pointing direction changes spontaneously towards another one of three possible directions. The participants just had to indicate the suggested direction of the triangles. Kiper et al. (1996) flickered two sides of the triangles and thought that this should influence the subjects to prefer a certain direction.

In both experiments, Kiper et al. (1996) reported negative results. The authors did not find an effect of the flickered presentations on visual segmentation nor on perceptual grouping. The authors therefore concluded that temporal synchrony is not responsible for perceptual grouping or visual segmentation, respectively.

Criticism is summarized by Jefferys et al. (1996) who lack a definitive confirmation for the functional significance of gamma rhythms. Gamma synchrony therefore possibly serves as the neural code, has a central function for cognition, is important maybe for a different function, or solely a side effect with no special meaning (Jefferys et al., 1996).

Even Singer (1993, p. 360), up to date one of the most important supporter for this theory, considered the possibility „that synchrony and oscillations are epiphenomena of a system`s properties that have evolved for a completely different purpose“.

A similar careful skepticism can be found by Engel et al. (1997) who consider the temporal binding model as a very attractive solution, but also lack direct evidence about the functional relevance of this phenomenon.

Singer and Gray (1995) demanded experiments in which a direct test becomes possible. But exactly this, at given time, is not possible. It would require the recording from various sites on behaving animals at once as well as the analysis of synchronization with high resolution. With the currently given technical possibilities, this causes some problems. For instance, only a short occurrence of synchrony might be of high importance (Bressler et al., 1993; as cited in Singer & Gray, 1995). But scientists only have possibility to examine a few neurons, which increases the risk to miss such episodes. Consequently, new techniques are a much needed intention. Until the development of such devices, only conditions which require longer periods of synchronization allow a suitable detection. In practice, almost only difficult tasks which involve long periods of focused attention, meet this demand (Singer & Gray, 1995).

Finally, I would like to close this chapter with a cite from deCharms and Zador (2000, p. 627) who summarized their criticism as following: „However, there has been a failure thus far of the research community to come together as a whole in either accepting or rejecting this still-controversial view".

9 Outlook

Varela et al. (2001, p. 236-237) provided a collection of considerations. This list might be helpful for any future study in order to gain empirical support or rejection for this controversial theory. I will give a comprehensive overview in the following.

9.1 Direct evidence for the functional significance of synchrony

So far, almost any evidence for the functional significance of synchrony is just correlative. There is nearly no support in an experimental setting, i.e. experimental changes in synchrony cause changes in behavior, except one study by Stopfer et al. (1997; as cited in Varela et al., 2001). These authors examined insects, in particular the olfactory system. They interrupted synchrony in olfactory bulb neurons and reported degeneration of odor discrimination. More such studies in the vertebrate brain which provide direct evidence are of inevitable importance.

9.2 Large-scale synchrony across various frequencies

Some authors (e.g. Bressler et al., 1993; Fries et al., 2001a) reported the parallel synchrony among various frequency bands. In consequence of these observations, Varela et al. (2001) suggest that different frequency bands might be responsible for different features in brain integration. Interestingly, these frequency bands constantly occur among different participants at given behaviors. Further support for this view comes from Friston (1997; as cited in Varela et al., 2001) who reported correlated activity in the gamma frequency range in frontal cortex with beta activity in parietal cortex during hand movement. Similar evidence is available by von Stein et al. (2000; as cited in Varela et al., 2001) who found cross-talk between gamma oscillations in area 17 and beta oscillations in area 7 in cats. Thus, Varela et al. (2001) suggest further studies which examine synchrony in parallel over multiple frequencies.

9.3 Phase synchrony and phase scattering

Further evidence is available that also phase scattering is of functional importance (e.g. Rodriguez et al., 1999). Varela et al. (2001) rated this observation as an essential part of long range integration, which enables the reorganization of new assemblies. In practice, the whole process of brain integration might consist of a combination between phase synchrony and phase scattering among various frequency bands. Up to date, the responsible mechanisms for these inhibitory processes are still unknown in detail and therefore require further examination (Varela et al., 2001).

9.4 Cellular processes of phase synchrony

Recent studies analyzed the role of ion channels in connection with phase synchrony (e.g. Ermentrout & Kopell, 1998; Kopell et al., 2000; as cited in Varela et al., 2001). The results revealed that the beta frequency band most likely serves for the formation of long range synchrony while the gamma frequency band is possibly responsible for the buildup of more local synchronization (von Stein et al., 1999; as cited in Varela et al., 2001). In consequence, Varela et al. (2001) demand further studies examining the cellular mechanisms of phase synchrony in more detail.

9.5 Connection of fast and slow frequency bands

Varela et al. (2001) also see the alpha and theta frequencies as important for the formation of assemblies. The reciprocal connections between thalamus and cortex can influence various frequencies, responsible for excitatory postsynaptic potentials in pyramidal cells. The occurrence of theta band activity in limbic structures, responsible for memory integration, is well known. Varela et al. (2001) therefore request further research about the fast beta and gamma activities in the context of the slower theta and alpha frequencies.

10 Conclusion

In conclusion, then, the theoretical assumptions as well as the experimental support up to date are a good motivation for future studies to examine this still controversial hypothesis in more detail. Of course, some requirements, for instance those mentioned above, have to be considered and new methods need to be developed. So far, it`s most likely that synchronization of cortical activity is of functional significance for brain integration, although some authors reported negative results.

I would like to close the theoretical part of this work with a cite from Singer (1999, p. 65): „If it then turns out that the hypothesis falls short of the real complexity - which is bound to be the case - we will have learned something about the role of time in neuronal processing that we would not have learned otherwise. Based on current evidence, I consider it highly unlikely that self-paced temporal coordination of distributed activity will prove irrelevant for cortical processing; if it does, we nonetheless shall have made a great step forward, because it is the unexpected result that contains maximal information“.

II EXPERIMENTAL PART

11 Introduction

Synchronization of neuronal activity is the most likely solution to the binding problem. In short, the theory suggests the formation of transient cell assemblies which fire their action potentials in temporal synchrony in the gamma frequency range (Singer, 1993). This allows selection and integration of the distributed networks in our brain. Consequently, almost any cognitive act, as for instance perception, language, and memory, is concerned (Lee et al., 2003).

The general idea of the present study was to examine if human subjects are able to gain control on synchronization in the gamma frequency range. We recorded EEG signals from the scalp and measured synchrony between two selected electrodes. The success in controlling synchronization was reported back to the participants in real-time. Thus, a neurofeedback design was applied. We calculated synchronization with a simple correlation and presented feedback through a smiley on a screen. The participants were instructed to make the smiley as happy as possible and did not know the intention of the study.

So far, such an approach has not been done in the study of gamma synchronization. Most of the experimental support up to date is correlative and a more direct test of this still controversial theory therefore a much needed approach. Additionally, we explicitly concentrated on the occurrence of gamma phase synchronization, as this is the suggested phenomenon for the binding process. The sole appearance of gamma oscillations does not imply the existence of gamma synchronization. This was another important part in choosing our design, as most of the existing experimental support focused only on the occurrence of gamma oscillations.

We decided to examine long-range synchronization and thus have chosen two electrodes with long distance between them, namely one in the left hemisphere in the front of the head and one in the right hemisphere in the back of the head. This, of course, constitutes the most extreme case to establish synchronization, as the distance is long and the hemispheres have to be crossed additionally. On the other hand, there is almost no risk left that synchronization could be explained by volume conduction.

The participants had to complete 9 trials. The experiment with inserted breaks lasted around four hours. In addition with application and detachment of the electrodes, the subjects had to spend

around seven to eight hours. Obviously a strong burden for the participants. But it was important to give them enough time to train and thus a real chance to learn synchronization.

Gamma synchronization already has been referred to intelligence in the theory part of this work. If the participants are able to learn gamma synchronization in our experiment, we expect a possible effect on intelligence measure. Thus, similar as Keizer et al. (2010) have done in their study, we measured general intelligence before and after the training session, using Raven´s Matrices (1998).

It has to be mentioned that already one colleague at the Faculty of Psychology in the University of Vienna has done a quite similar study (Holzmayer, 2007). The results did not show that participants have been able to gain control over synchronization between the selected electrodes. Thus, we changed some settings (particularly more participants and a lower level of reinforcement) and start hereby with another attempt.

12 Methods

On short preview, this chapter of Methods will include detailed information about our experiment, including participants, materials, procedure, and evaluation of the data. The results are presented afterwards in chapter 13.

12.1 Participants

All together 20 healthy subjects (12 males and 8 females) in the age from 21 to 36 years (M = 27.30; SD = 3.59) voluntary attended in the present study. Written consent was obtained from all subjects who did not receive any compensation for their participation. Most of the subjects were students of psychology. No information about the aim of the experiment was given to them in advance. Furthermore, all subjects were proved on their handedness through a German version of the „Marian Annett Handedness Inventory" (Annett, 1970; 1985). The study was obtained in agreement with the ethical standards for participants of the 1964 Declaration of Helsinki.

12.2 Materials

In this chapter I will describe the materials we used in our experiment. These have been, in particular, EEG Biofeedback and Advanced Progressive Matrices (APM) by Raven (1998). Additionally, I will focus on the EEG application and measurement.

12.2.1 EEG application and measurement

The experiment took place at the Biological Psychology Department in the University of Vienna. The data have been collected during December 2004 and April 2005. Every participant was tested on a single day. The entire study was conducted in German language.

In preparation of the EEG measurement 40 Ag/AgCl scalp electrodes have been applied according to an expansion of the 10/20 system from Jasper (1958). Additionally, two reference electrodes were used as potentiometer. One electrode applied on the mastoid behind the left ear and another one on the mastoid behind the right ear. Another four electrodes were used for the electrooculogram (EOG), applied in a horizontal and vertical position of the eyes. Two of them approximately 1 cm above and below in the middle of the right eye, as well as two electrodes approximately 1 cm on the outer border of the left and right eye. These electrodes were used for the EOG calibration. Finally, another electrode was used for mass.

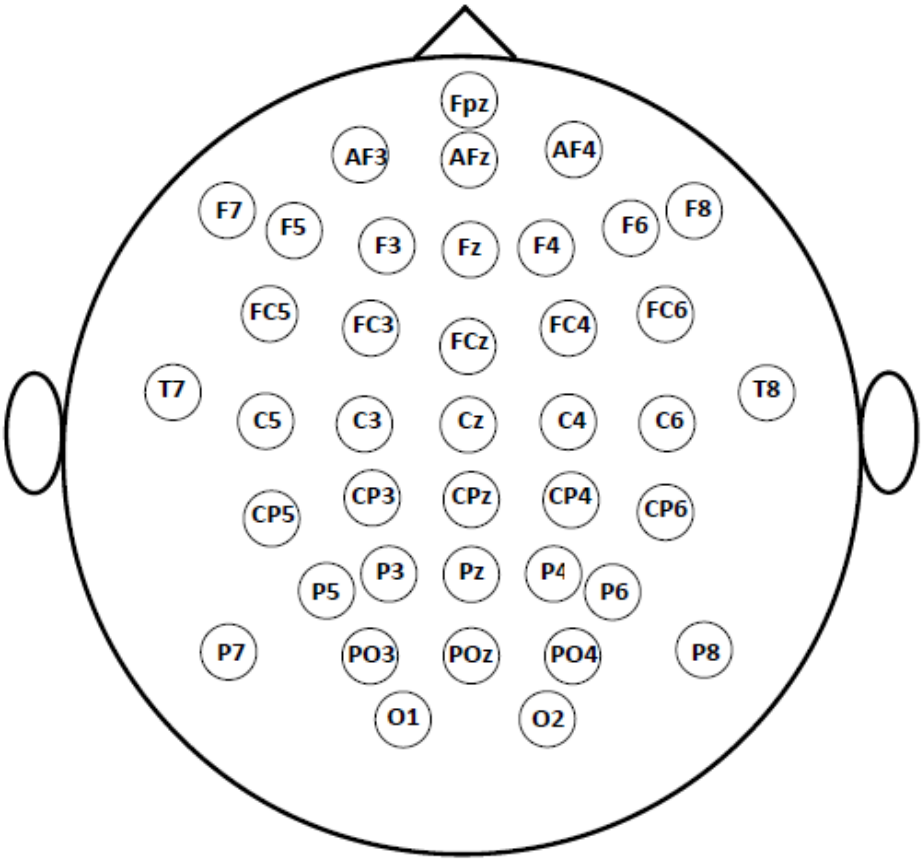

Figure 12.1: Electrode Positions

The electrode application started with the measurement of Nasion and Inion, as well as the distance between the pre-auricular points of the head. This position was signed for localization of the Cz electrode and all further electrodes have been applied equally spaced according to the mentioned expansion of the 10/20 system from Jasper (1958). This procedure ensures a similar position of the electrodes on different participants, independent of size and shape of the scalp.

In order to minimize skin resistance and to enhance the conduction between scalp and electrode, we used the following procedure. The hairs have been moved aside and the scalp was disinfected using 70 percent alcohol. Afterwards, the skin was scratched with a sterile needle and each electrode was filled with electro gel. The impedance was checked and these steps possibly repeated, until each electrode was below 2kΩ.

For the recording we used a 64 channel DC amplifier. The data were re-sampled to 250 Hz and to clean them from DC offsets and slow drifts, we used a highpass filter of < 1 Hz. The filter is calibrated to the gamma target frequency which we calculated before. Additionally, the channels were referenced to the average of the two mastoids and the cardiac activity and EOG signal calibrated.

The exact positions of the electrodes have been registered using a 3 Dimensional Photogrammetric Head Digitizer (3D-PHD) (Bauer et al., 2000). All together 12 cameras took pictures from different perspectives and angles, respectively.

Although we used only two electrodes to measure the correlation, we applied 40 electrodes to calculate a cortical source density (CSD) to smooth the measured signals. Artifacts possibly arise due to volume conduction in the brain, the scalp, and cerebral membrane. The CSD reduces the influence of distant sources which results in local and accurate signals. In comparison to average derivation, the CSD excludes sources in neighboring areas. The original potential pattern can be restored. It is a practical implementation of the Laplace operator which forms a star-like configuration around each electrode. This method tries to derive the source activity at the position of each individual electrode (Hjorth, 1975).

The application of the electrodes as well as the following pre-measurements lasted around three hours.

For the experiment we guided the participants into a sound-proof and semi-darkened room. All subjects were placed on a comfortable chair approximately 90 cm from the monitor. The feedback trials were presented on a 50 cm screen.

In order to minimize data artifacts, all participants were instructed to avoid movements and, so far it was possible, to sit still during the experiment. All subjects have been monitored by a camera and if necessary reminded on this. Additionally, we controlled the EEG signal during the experiment and had thus the possibility to change electrodes in case of problems. To make the experiment more comfortable, we inserted some breaks to refresh.

12.2.2 Biofeedback

12.2.2.1 Definition, purpose, and application

„Biofeedback is an operant conditioning technique in which participants (patients) learn to increase awareness and to gain voluntary control over physiological functions (e.g. muscle activity, respiration, heart rate, skin temperature, brainwaves) that usually are not consciously perceived or controlled" (Heinrich et al., 2007, p. 4). The participants receive continuing feedback about these functions through acoustic or visual stimuli in real time. Positive changes are immediately rewarded. With some training the desired changes can appear without the application of technical instruments and feedback. The general aim of biofeedback is to increase performance and health. Biofeedback is rated as a safe technique and no harmful spin-offs are known (Heinrich et al., 2007).

Biofeedback is applied for a very wide range of diseases and conditions, e.g. sleep disorders, depression, high blood pressure, stress, migraine headaches, traumatic brain injury, alcohol addiction, anxiety, epilepsy, chronic pain, urinary incontinence, respiratory problems, and attention deficit hyperactivity disorder (ADHD) (Heinrich et al., 2007).

12.2.2.2 Biofeedback with EEG (Neurofeedback)

Neurofeedback, also known as EEG biofeedback or EEG operant conditioning, is a subdivision of biofeedback. With neurofeedback participants (patients) learn to control electrophysiological processes in their brain. The EEG is used to show participants current patterns in their cortex. The general purpose is training of individual subjects to change abnormal patterns and to normalize or optimize brain functioning (Yucha & Montgomery, 2008).

In practice, total neurofeedback trainings consist of 25 to 50 sessions, each lasting around 45 to 60 minutes. Usually, transfer trials, i.e. trials which do not give feedback, are mixed with feedback trials. This ensures transfer into common situations. Additionally, participants are asked to train their skills at home and in real-life situations (Heinrich et al., 2007).

Research in the last decades concentrated also on healthy subjects. Results have been reported in which neurofeedback training was associated with enhanced attentional processing (Vernon et al., 2003). Nash (2000; as cited in Masterpasqua & Healey, 2003), for instance, collected various studies showing improvements after neurofeedback training, e.g. intelligence, academic skills, and continuous performance.

Thus, neurofeedback became a prominent technique used to adjust or stimulate brain activity. This, on the other hand, may affect cognitive processes (Vernon et al., 2003).

12.2.2.3 Biofeedback with EEG in the 40-Hz Domain

Bird et al. (1978) showed first that human subjects are able to gain control over high frequency components. All together 22 subjects participated in their EEG biofeedback study. The participants were separated into three different groups with different tasks. Group one had to increase 40 Hz EEG whereas group two had to suppress them. Group three was trained to increase 21 to 31 Hz EEG. Each subject had to participate on all together eight days. The biofeedback training included two sessions per day, each lasting around 15 minutes with a break of 2 minutes to relax. Bird et al. (1978) reported that eight participants were able to learn suppression and increases of their 40 Hz EEG. Additionally, these subjects successfully performed even without feedback after their biofeedback training. Interestingly, the participants could not report a common strategy how they managed to gain control over the target frequencies.

Keizer et al. (2010) examined gamma oscillations in connection with feature binding and intelligence. Using a neurofeedback design, these authors changed gamma power and analyzed the impact on feature binding and intelligence. All together 14 people participated in their experiment. The study consisted of 8 sessions on different days, each of them lasting 30 minutes. It took place within 10 to 11 days. Keizer et al. (2010) reported that participants were able to influence gamma power if trained with neurofeedback. Furthermore, the increase in gamma oscillations was connected with an increase of intelligence as well as a decrease of binding costs. Keizer et al. (2010) concluded that feature binding and intelligence use the same mechanism which most likely is gamma synchronization.

12.2.3 Advanced Progressive Matrices (APM)

Raven`s Advanced Progressive Matrices (1998) is a nonverbal intelligence test to measure cognitive abilities above average. The APM quantifies the intelligence factor „g" in Spearmans model (Spearman, 1938) and is therefore an indication of general intelligence. Originally it was developed in 1936 by John C. Raven. The current form contains 48 items in 2 sets with increasing difficulty. Set I consists of 12 items whereas set II consists of 36 items. In each of the items, subjects have to complete a missing element in a pattern from some given possible selections. The items are presented in black on a white background. Generally, three different versions of Raven`s matrices are available, namely Standard Progressive Matrices (SPM), Colored Progressive Matrices (CPM), and Advanced Progressive Matrices (APM). The latter one we used build up on the more general SPM version. Considering the subjects who participated in our study, we decided to use APM.

12.3 Experimental Procedure

In the following sections I will explain the experimental procedure as detailed as possible. In short preview, after application of the electrodes, we started to measure the individual alpha frequency and calculated the target frequency in the gamma range. This was followed by evaluation of the spontaneous synchronization between the selected electrodes. After these preliminary measures, the actual experiment started with the so-called „smiley" trial. During that, participants were trained to learn gamma synchronization and received feedback about their success. This trial was followed by a „transfer" trial. We still measured the correlation but did not provide any feedback. Smiley and transfer trial have been presented all together four times in alternated order. Additionally, we measured general intelligence using Raven´s Advanced Progressive Matrices (Raven, 1998). The participants had to solve the items with uneven numbers before the experiment and the ones with even numbers after the experiment. Finally, we interviewed all participants and noticed their experience with our attempt. The whole experiment for every subject took place on a single day. Figure 12.2 gives an overview about the course of the experiment. I will move on with more detailed information about the procedure in the following sections of this chapter.

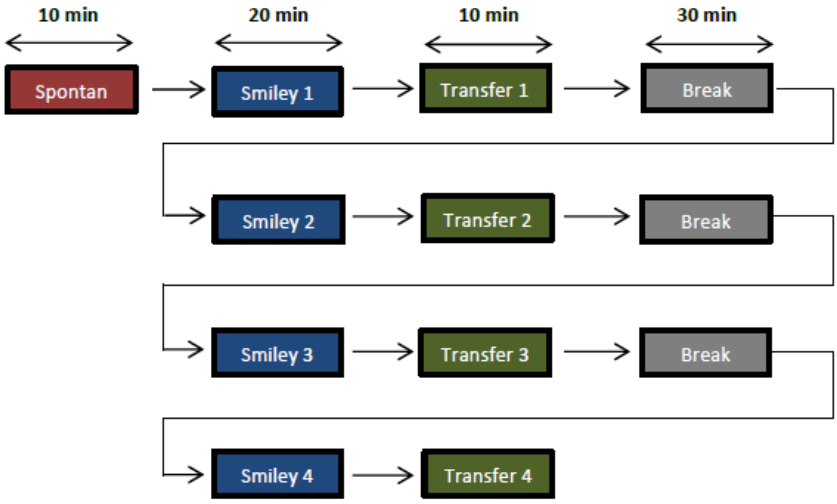

Figure 12.2: Graphical depiction of the experiment

12.3.1 Selection of the electrodes

Basically, we had to select the two electrodes between we measure and train the participants to learn synchronization. In general, we considered various different selections but did not follow any particular intention. One of the most important aspects was a long enough distance between them as we wanted to avoid two electrodes in proximity. We additionally thought to choose two electrodes in different hemispheres. Thus, our decision resulted in the choice of F3 and P4. This selection constitutes one of the most difficult cases to establish synchronization, but run away from synchrony due to volume conduction. Anyway, the participants did not know which electrodes were important nor the basic idea of the experiment in advance.

12.3.2 Feedback

Feedback was presented through a yellow shaped smiley on a computer screen. The smiley changed its appearance if the correlation between the measured electrodes was sufficiently high. All together 40 different gradations of the smiley have been available, starting from neutral looking to extremely happy. Figure 12.3A illustrates the feedback material with six different gradations of the smiley, just to give an impression of this. Feedback was provided directly after calculation, which is de facto in real-time.

During the transfer trials we did not provide feedback about the success in learning synchronization. Instead of the smileys we presented a white circle to signalize the beginning and end of an episode. Figure 12.3B illustrates this schematically.

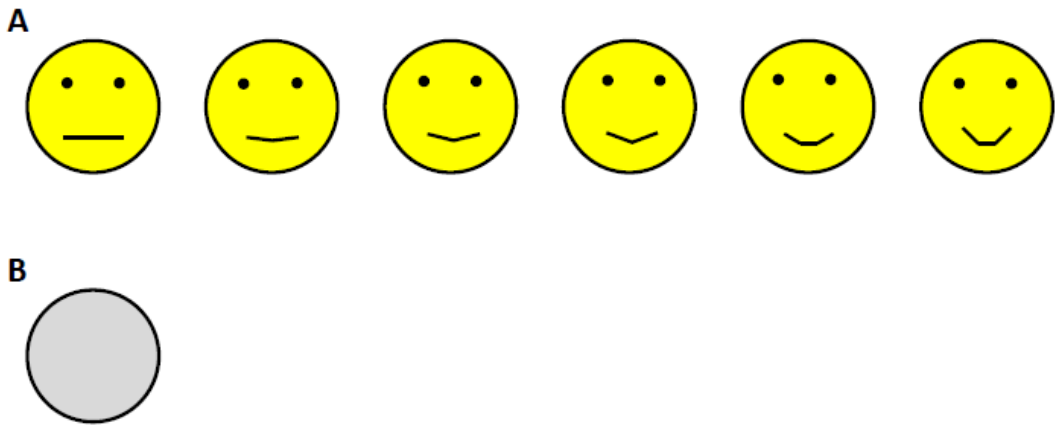

Figure 12.3: Example-Set of Smileys reduced to six
(Figure 12.3A in Feedback Trial and figure 12.3B in Transfer Trial)

12.3.3 Algorithm

I already illustrated the course of our experiment and I will move on with a detailed description of the trials in the next chapter. Here I would like to focus on the algorithm we used in our experiment.

Each of the nine trials we used consisted of 5 second episodes during which we measured synchronization. The spontaneous and transfer trials included 25 such episodes while the feedback (smiley) trials included 49 episodes. Each of the 5 second episodes was followed by a 10 second break to refresh.

We calculated 7-8 correlations every second, depending on the target gamma frequency (see figure 12.4). For any correlation, all together 7-8 data points were available between the two signals. Figure 12.5 illustrates one such period.

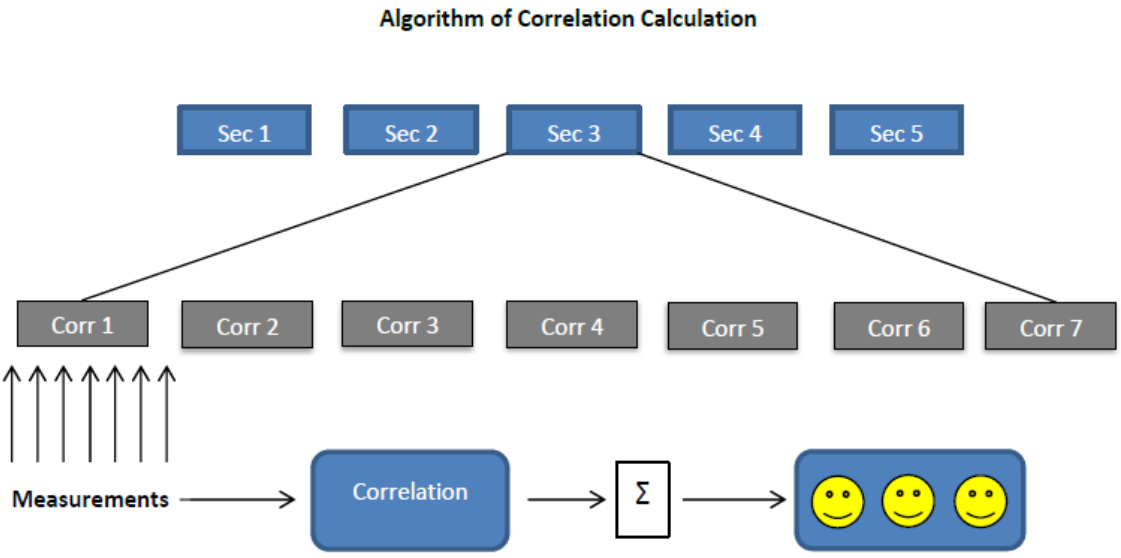

Figure 12.4: Five-Second Interval

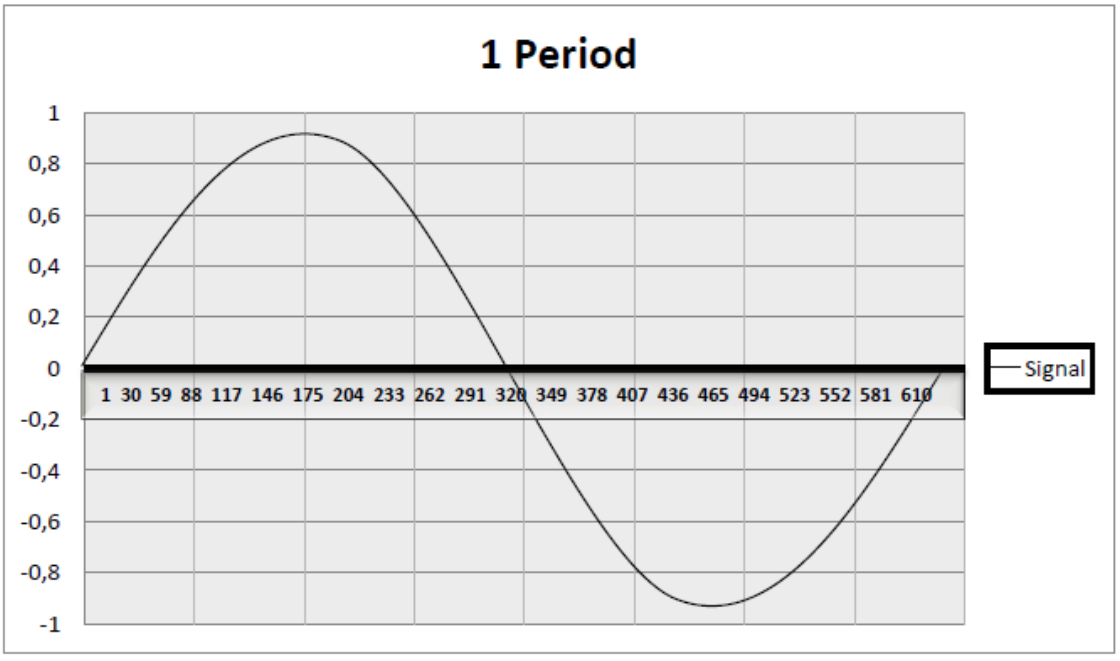

Figure 12.5: 1 Period

Feedback was presented through yellow shaped smileys. All together 40 different gradations of the smiley happiness were available, starting from neutral looking to extremely happy. In particular, any correlation above 0.90 created the next happier smiley stage on the computer screen. Correlations below 0.90 as well as negative correlations did not increase the smiley happiness. In other words, the smiley did not change. That means that the smiley happiness during every 5 second episode could not decrease. In summary, the smiley happiness could increase by eight gradations each second.

Additionally, we presented the current amount of smiley and their happiness at the end of each 5 second episode. For instance, if eight episodes are finished, then eight smileys with the achieved happiness are shown in the 10 second break on the screen. This gives the participants further feedback about their success as well as about the progress within each trial.

During the transfer trials we presented only white shaped circles to signalize the beginning and end of a 5 second episode. No feedback was provided. Anyway, the synchronization between the chosen electrodes was calculated with the same algorithm as explained above.

12.3.4 Description of the trials

Here I will follow with a detailed description of the trials we used in our experiment.

12.3.4.1 Evaluation of the dominant alpha frequency

The individual alpha frequency (IAF) differs between subjects and is the dominant one if measured with scalp EEG. It is of crucial importance to adjust this for every subject separately (Klimesch, 1999). Thus, our experiment started with the evaluation of this frequency. During calculation, which took around 2 minutes, the participants were asked to relax and to avoid movements.

12.3.4.2 Target gamma frequency

The gamma frequency is the suggested one responsible for brain integration and therefore our target frequency, too. Thus, we multiplied the calculated alpha by three, in order to receive a frequency in

the gamma range. We considered possible problems in the evaluation of the gamma frequency and decided in advance to use 33 Hz if any problems appear. Anyway, it did not become true.

12.3.4.3 Evaluation of the spontaneous synchronization

After these preliminary calculations, we started to measure the already existing synchronization. We suggested that the spontaneous synchronization will differ between participants. Thus, it was necessary to evaluate a basic value which additionally offers possibility to compare with the feedback trials after completion.

We presented a neutral looking smiley for a 5 second period followed by a break of 10 seconds. In summary this trial consisted of 25 such episodes and lasted therefore around 10 minutes. The smiley did not change its happiness nor was other feedback provided. The participants were instructed to look at the neutral smiley during the 5 second presentation and to avoid movements, as was the case during all feedback and transfer trials, too.

12.3.4.4 Feedback (smiley) trial

The actual training started with this trial. During that the participants could learn synchronization through the presented smiley feedback. Synchrony was calculated online and immediately fed back to the participants, which is in real-time. The subjects were instructed to make the smiley as happy as possible. They have been free in the choice of their way to manage this, except through movement. All participants were clearly instructed to avoid movements and have been monitored during the experiment. Furthermore, also the EEG signal was monitored during measurement. Anyway, the subjects did not know which electrodes were used to calculate synchronization, nor the aim of the experiment in advance. They simply had to make the smiley smile, for instance through ideas, thoughts, impressions, or images.

This trial consisted of 49 episodes. Each episode included a 5 second interval during the participants received smiley feedback and a 10 second break to recover afterwards. In summary, it took around 20 minutes. The feedback (smiley) trial was presented all together four times in alternated order with the transfer trial, which I will describe in the following.

12.3.4.5 Transfer trial

Every smiley trial was followed by a transfer trial. In general, we did the same as in the smiley trial, but without feedback provided. If the participants were able to learn synchronization in the smiley trials, they should be able to achieve the same synchrony score without feedback, if using the same strategy as before. The subjects were asked to do the same as in the previous smiley trials. In particular, use the same (successful) strategy as before.

We presented a white shaped circle during the 5 second periods to signalize the beginning and end of each interval. The 10 second break between these periods was identical. The transfer trial included only 25 episodes and lasted therefore approximately 10 minutes. The transfer trial, as mentioned already above, as well was presented four times in alternated order with the smiley trials. Immediately after each smiley and transfer period we inserted a 30 minutes break. This should give the participants enough time to recover and refresh.

12.3.5 Measurement of synchronization

Our chosen design requires the online calculation of synchrony. Two different measurements are currently available, namely correlation and coherence.

It was of crucial importance to calculate the synchronization directly during the experiment, to give the participants feedback in real-time. Additionally, we focused on gamma synchronization and not on the simply occurrence of gamma oscillations. Thus, differences in phase have to be considered and the measurement of stability alone is not enough. Clearly, we had to choose a calculation which does not require intensive computing.

Both, the coherence and correlation, measure the relation between two signals. Anyway, some differences exist. The coherence reflects variations in power as well as variations in phase. Thus, this value changes if either phase or power changes. Additionally, the coherence gives information of the stability between two signals over time. In contrast, the correlation reflects phase and polarity, regardless of the amplitude. In general, the correlation is an easy method and the online calculation does not require special technical knowledge (Guevara & Corsi-Cabrera, 1996).

Thus, we decided to use the correlation for the calculation of synchrony in our experiment.

12.3.6 Advanced Progressive Matrices

Gamma synchronization should also play a role in intelligence. Various authors could show a connection which I already reported in the theoretical part of this work. Thus, we thought to test this additionally. If the participants are able to learn synchronization in our biofeedback study, we expect an effect on intelligence measure. Thus, similar as Keizer et al. (2010) have done in their study, we measured general intelligence using Raven`s Matrices (1998). In contrast to these authors, we used the Advanced Progressive Matrices (APM). This version was constructed for people with an intelligence score above the average. As most of our participants have been students of psychology, we considered this as the more suitable version. All subjects had to solve the items with the uneven numbers before the experiment and the items with the even numbers after the experiment. Similar as Keizer et al. (2010) found in their study, we expect a better score after the experiment.

12.3.7 Feedback of the participants

Finally, after completion of the experiment, we interviewed all participants and asked for their strategies to gain control over the smiley happiness. We noticed for each person the subjective rating in order to control the smiley. This will allow a comparison of the results between subjects who rated their own control as high and subjects who rated themselves as unable to influence the smiley. Additionally, we invited the participants to report their general impression of the experiment, in particular their subjective experiences, ideas, feelings, and burden. Of course, immediately after completion, we informed all participants about the purpose of our study in all details.

12.4 Data evaluation and hypotheses

The analysis of the results will take place on different levels which I will describe in the following. Anyway, evaluation and calculation of the data will be done using IBM SPSS Statistics 20 and Microsoft Excel.

12.4.1 Analysis of the correlations

First of all, I will have a detailed look on the correlations. If the participants are able to gain control over the smiley happiness, the underlying correlations will increase. In more detail, the frequency of positive and high correlations will increase on the cost of negative and low correlations from trial to trial. During the spontaneous trial, the correlations will appear by chance whereas a trend toward higher correlations will appear with increasing duration of the experiment. These assumptions lead to the following hypotheses:

- H1: The correlations will increase from trial to trial.

- H2: The arithmetic mean of the correlations will differ between the trials.

To test H1 I will create histograms for each trial, including all correlations over all participants. I will divide them into 20 areas with same width. As the number of episodes differs between spontaneous trial, feedback (smiley) trial, and transfer trial, I will display the relative frequencies of the correlations instead of the absolute frequencies. I expect a clear trend toward higher correlations from trial to trial which should be visible in the histograms.

To test H2 I will first of all transform the correlations into Fishers z values. This transformation results in a Gaussian distribution of the data. Additionally, a metric scale can be supposed (Bortz, 1999). After calculation I will transfer the Fishers z values back to correlations (Silver & Dunlap, 1987; as cited in Bortz, 1999). A histogram showing the arithmetic mean between the trials should display a clear trend with increasing values. Furthermore, I will calculate an ANOVA for repeated measures with the 9 trials as within-subjects factors. This hypothesis will be tested one-tailored. Of course, I expect a significant difference between the trials.

12.4.2 Analysis of the achieved smiley stages

In a second step I will focus on the smiley stages achieved at the end of each 5 second episode. Remember, all together 40 different stages of the smiley happiness are available. Any correlation above 0.90 triggers the next higher smiley stage. The smileys are important as they have been the feedback for the clients about their success. And if the biofeedback design works, the smiley stages

should increase with duration of the experiment. In other words, the smiley stages should display a trend toward higher values from trial to trial. Similar as with the correlations, I expect a distribution by chance during the spontaneous trial. Most likely this distribution will differ from participant to participant and reflects the individual level of synchronization, i.e. some base-line. The feedback (smiley) trials will allow training of synchronization which gives the participants possibilities to gain control over the smiley happiness. If the participants reach the maximum level of smiley happiness, they are able to hold that stage. Furthermore, participants should be able to hold this level during transfer trials, where no feedback is available. I expect that most of the subjects have internalized their strategies to control the smiley and therefore are able to hold the level without feedback, too. Basically, the evaluation of the smiley stages should include the same information and results as the evaluation of the correlations will do, because the smiley stages will result from the correlation values. In summary, these considerations will lead to the following hypotheses:

- H3: The smiley stages will increase from trial to trial.

- H4: The arithmetic mean of the smiley stages will differ between the trials.

- H5: The smiley stages will display a temporal trend over the experiment.

To test H3 I will create histograms showing the relative frequencies of all 40 smiley stages over all participants. I will display each trial in an own histogram and expect a trend toward higher values from trial to trial which should be visible in them. Again I have to display the relative frequencies instead of the absolute frequencies because the number of episodes varies between the different trials.

Another histogram will include the arithmetic means over all participants between the nine trials. This will help to test H4. Additionally, I will calculate one-way ANOVA for repeated measures and expect a significant difference between the trials.

Finally, a histogram showing the temporal trend of the smiley stages over all person and trials should help to test H5. This histogram should display a clear trend with increasing values.

12.4.3 Analysis of the APM scores

Of further interests are the APM scores, too. The successful influence of smiley happiness corresponds with a successful influence of gamma synchronization between the chosen electrodes. And synchronization in the gamma frequency range is associated with intelligence. Thus, if this comes true, I expect higher scores in the APM task after than before the experiment. Therefore another hypothesis will be:

- H6: The APM scores increase in the second measurement after the experiment.

I will test this hypothesis with one-way paired t-test between the two measurements and expect a significant difference.

12.4.4 Analysis of the verbal feedback of the participants

Finally, I will analyze the verbal feedback given from the participants after the experiment. At the start the subjects have to figure out a method or strategy which works to gain control over the smiley happiness. With some time they should find a solution to manage this. Clearly, this can vary between the participants. Thus, the last hypothesis will be:

- H7: After the experiment the participants are able to verbalize a successful strategy to influence or control the smiley happiness.

To evaluate this hypothesis, I will interview all participants carefully after the experiment. I will ask them in detail about their impressions of the experiment and of course about any method or strategy they worked out. Of additional interest will be the way they have gone to find their own successful tactic. Moreover, I will notice the personal rating of success to have a comparison with the achieved success in the experiment. Of course, I expect a clear verbalized tactic of influence or control, respectively, which finally was successful, too.

13 Results

This chapter includes all the detailed results. Before presentation I focus on some missing values which appeared due to various reasons.

13.1 Missing values

During EEG recording some technical problems appeared and a few participants had to break earlier due to time limits. Thus, some data are missing. In particular, participants 1, 2, 7, and 19 asked to break the experiment after transfer trial three which we, of course, did immediately. Thus, for these people we miss the data for the trials smiley 4 and transfer 4. Additionally, technical problems appeared during EEG recording at participants 12, 14, 15, 16, and 17. We therefore miss further data for the last trials from these participants. Table 13.1 gives an overview about the mean correlations over all person and trials, including the missing values. Of course, for any further calculation I have considered this, e.g. calculating relative frequencies instead of absolute frequencies.

Participant	SP	SM1	TR1	SM2	TR2	SM3	TR3	SM4	TR4
P 01	0.10	0.10	0.08	0.09	0.13	0.03	0.01	m.v.	m.v.
P 02	-0.11	-0.03	0.12	0.01	-0.10	-0.03	0.08	m.v.	m.v.
P 03	0.09	0.02	0.01	-0.07	0.04	-0.03	0.00	0.03	0.01
P 04	0.07	0.03	-0.10	0.11	0.04	0.02	0.22	0.36	0.25
P 05	0.18	0.42	0.38	0.42	0.35	0.38	0.31	0.31	0.23
P 06	-0.04	-0.01	-0.11	-0.01	-0.09	-0.02	-0.16	-0.02	-0.07
P 07	0.24	0.40	0.08	0.49	0.55	0.49	0.29	m.v.	m.v.
P 08	0.01	0.09	0.07	0.17	0.12	0.05	0.05	0.20	0.02
P 09	0.16	0.27	0.10	0.19	0.14	0.23	0.24	0.18	0.28
P 10	0.37	0.43	0.44	0.32	0.27	0.28	0.25	0.24	0.39

P=Participant, SP=Spontaneous trial, SM=Smiley trials, TR=Transfer trials, m.v.=missing values.

Participant	SP	SM1	TR1	SM2	TR2	SM3	TR3	SM4	TR4
P 11	0.64	0.68	0.51	0.26	0.12	0.33	0.11	0.10	-0.03
P 12	0.30	0.28	0.23	0.14	0.18	m.v.	m.v.	m.v.	m.v.
P 13	0.24	0.34	0.26	0.24	0.17	0.18	0.23	0.21	0.02
P 14	-0.06	-0.11	-0.10	0.03	0.01	m.v.	m.v.	m.v.	m.v.
P 15	0.90	0.92	0.91	0.90	0.89	0.90	m.v.	m.v.	m.v.
P 16	0.03	0.05	0.21	0.02	m.v.	m.v.	m.v.	m.v.	m.v.
P 17	0.12	0.12	0.30	0.10	m.v.	m.v.	m.v.	m.v.	m.v.
P 18	-0.02	-0.06	0.00	0.05	0.03	-0.08	0.28	0.01	0.16
P 19	0.17	0.18	0.07	0.20	0.12	0.16	0.22	m.v.	m.v.
P 20	-0.03	0.13	0.10	0.05	0.06	0.22	0.06	0.11	0.00

P=Participant, SP=Spontaneous trial, SM=Smiley trials, TR=Transfer trials, m.v.=missing values.

Table 13.1: Mean correlations for all person and trials including missing values

13.2 Result of the correlations

The visual inspection of the 9 histograms does not show any trend toward higher correlations. Generally, the distribution is what I expected with more correlations in the positive range close to 1. But this does not change from trial to trial. All histograms contain basically the same distribution as the spontaneous trial does which means that participants have not been able to influence the smiley happiness. Contrary, starting with trial transfer 3 a slightly decrease of the higher correlations is visible. Thus, hypothesis 1 is not supported by these data and has to be rejected.

Figures 13.1 to 13.9 show the histograms in detail. The correlations are divided into 20 areas with same width. In particular, these areas are -1 to -0.9, -0.9 to -0.8, -0.8 to -0.7, which follows up to 0.8 to 0.9 and 0.9 to 1.

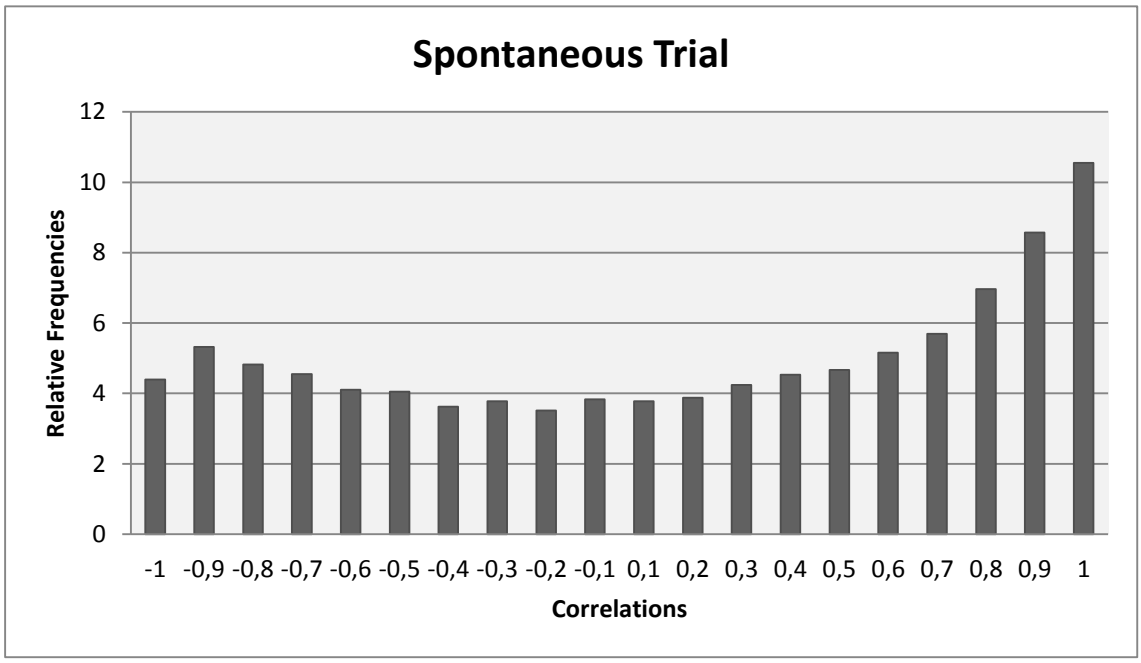

Figure 13.1: Spontaneous Trial: Correlations over all participants

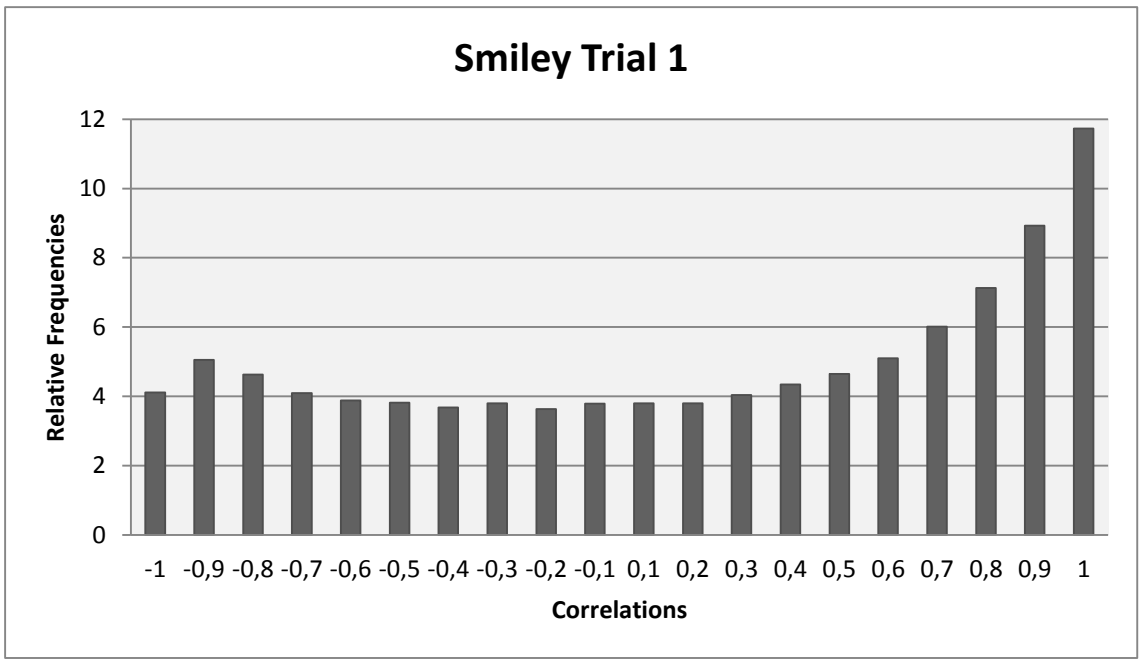

Figure 13.2: Smiley Trial 1: Correlations over all participants

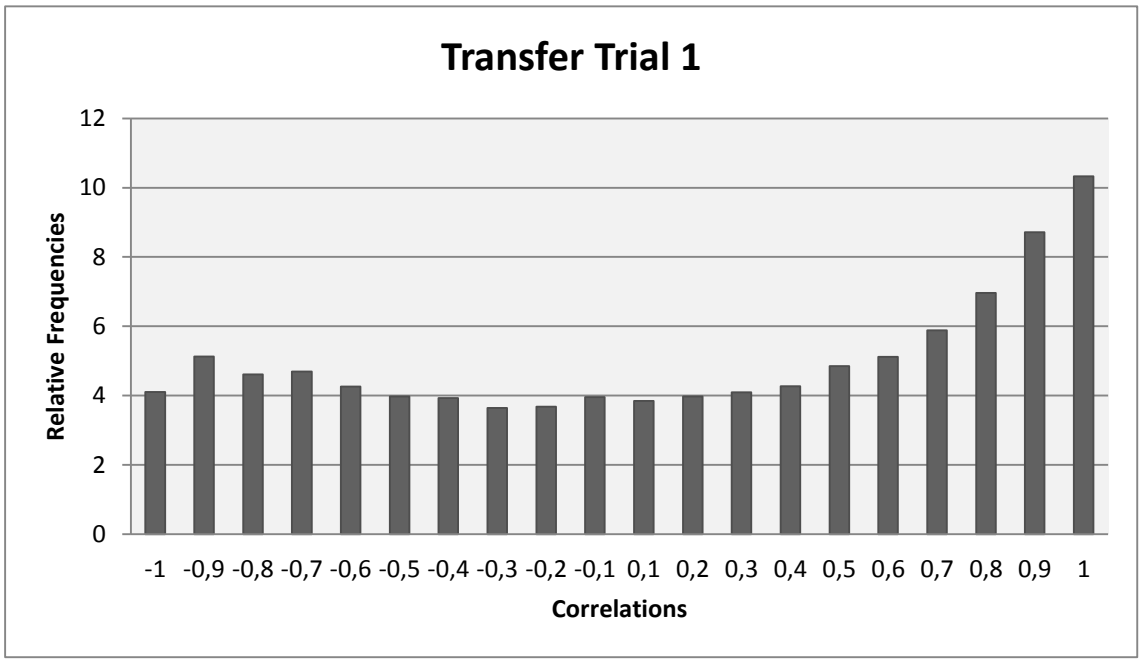

Figure 13.3: Transfer Trial 1: Correlations over all participants

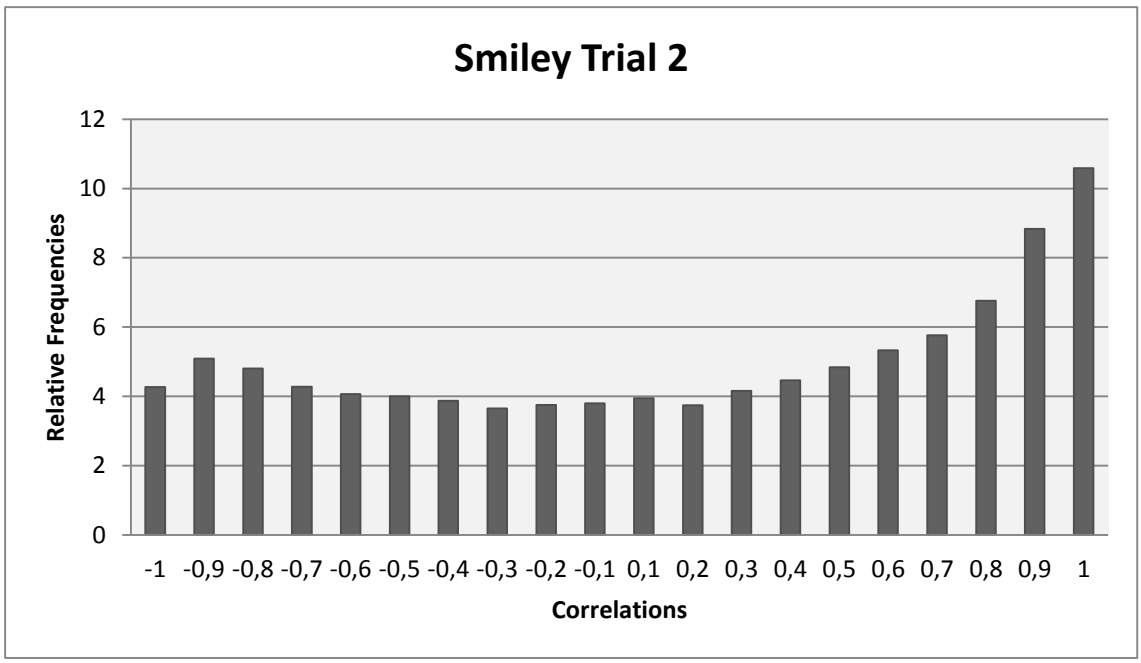

Figure 13.4: Smiley Trial 2: Correlations over all participants

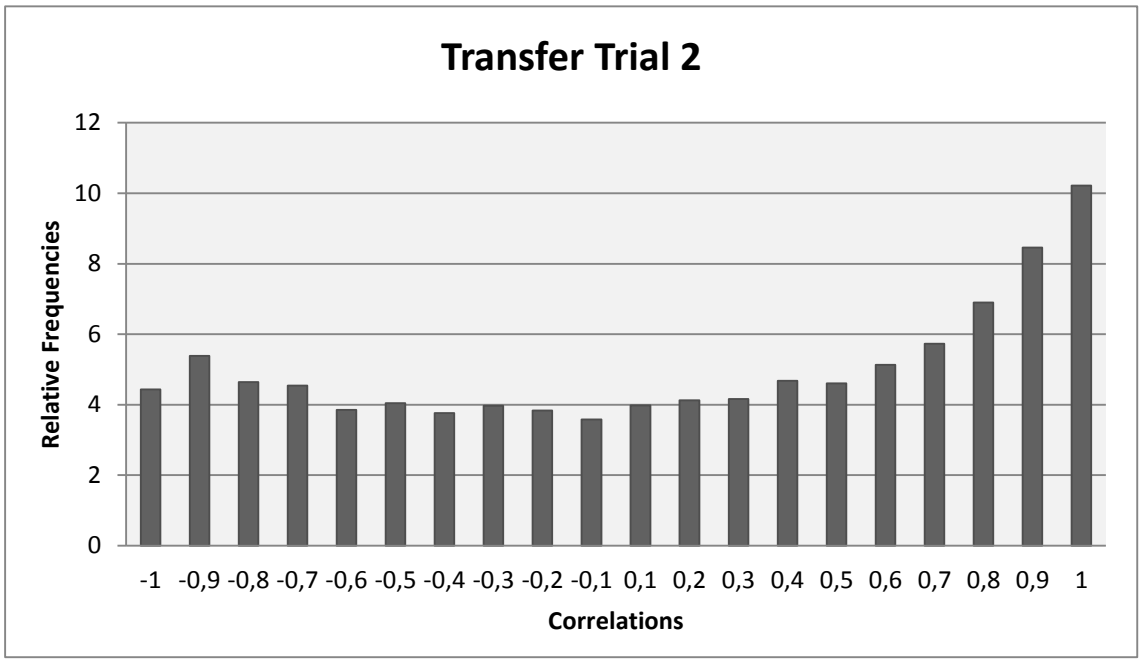

Figure 13.5: Transfer Trial 2: Correlations over all participants

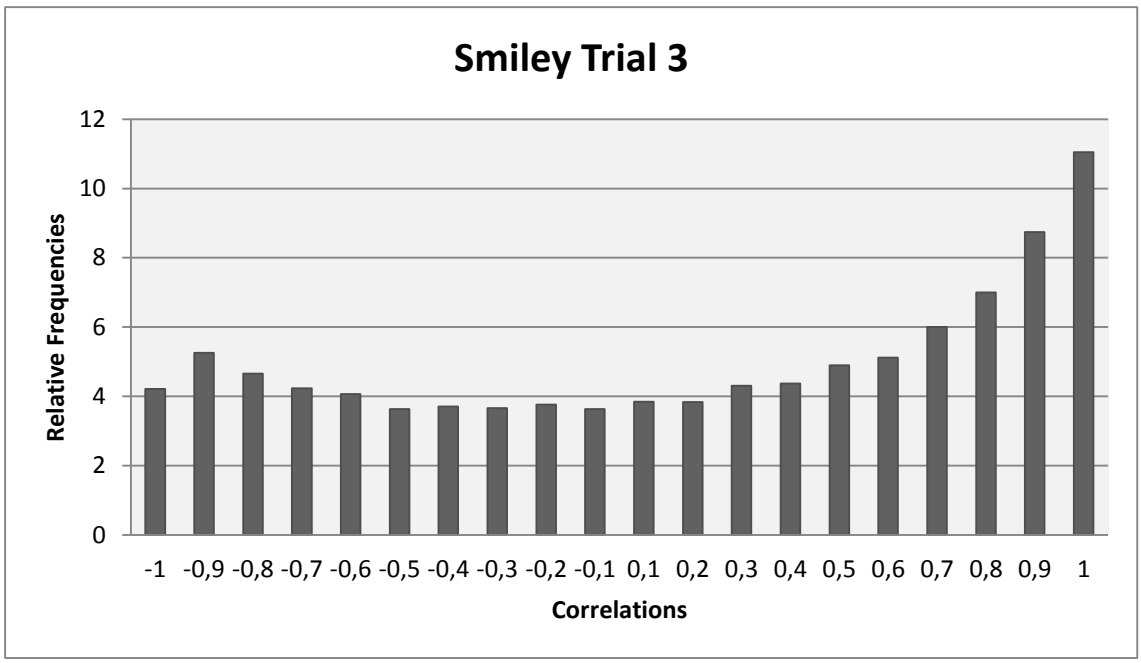

Figure 13.6: Smiley Trial 3: Correlations over all participants

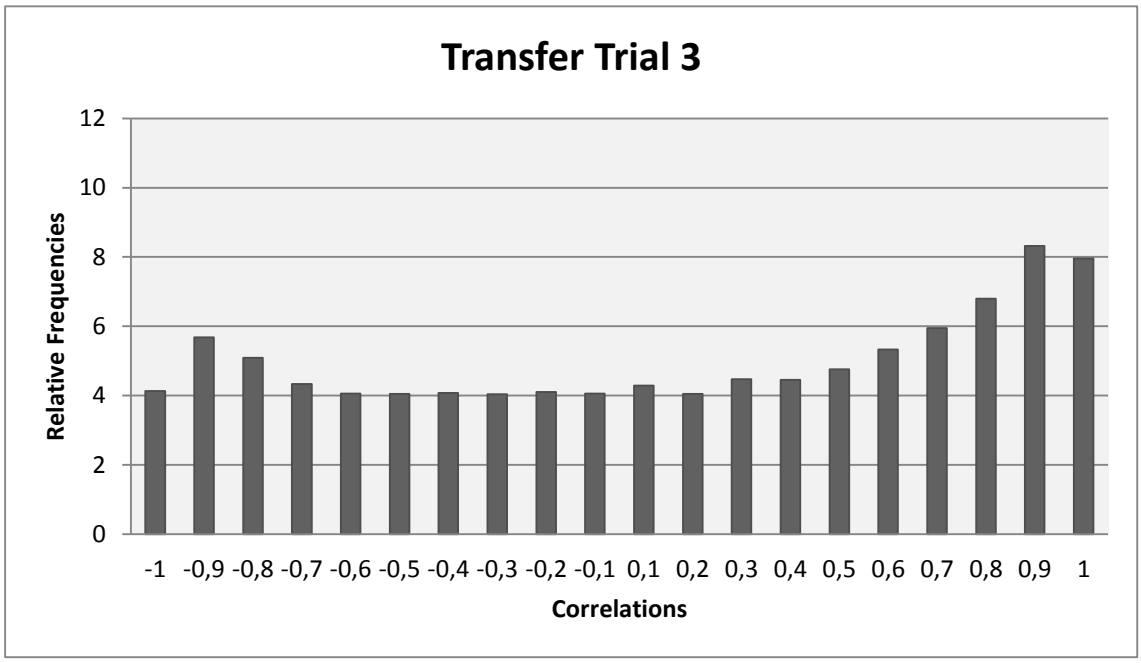

Figure 13.7: Transfer Trial 3: Correlations over all participants

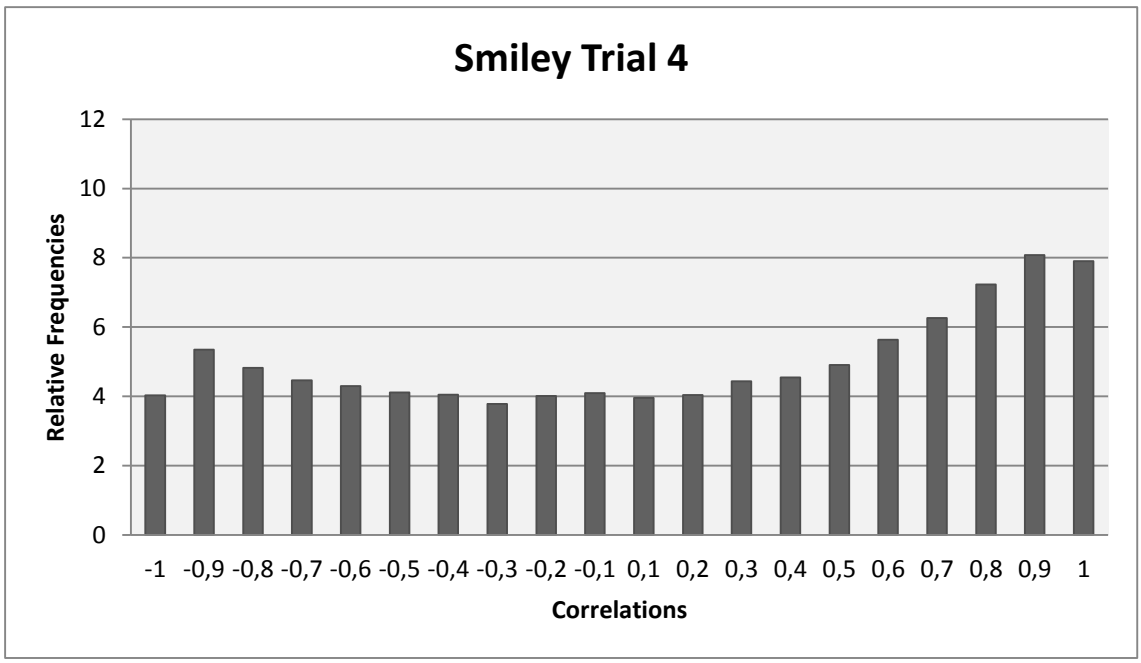

Figure 13.8: Smiley Trial 4: Correlations over all participants

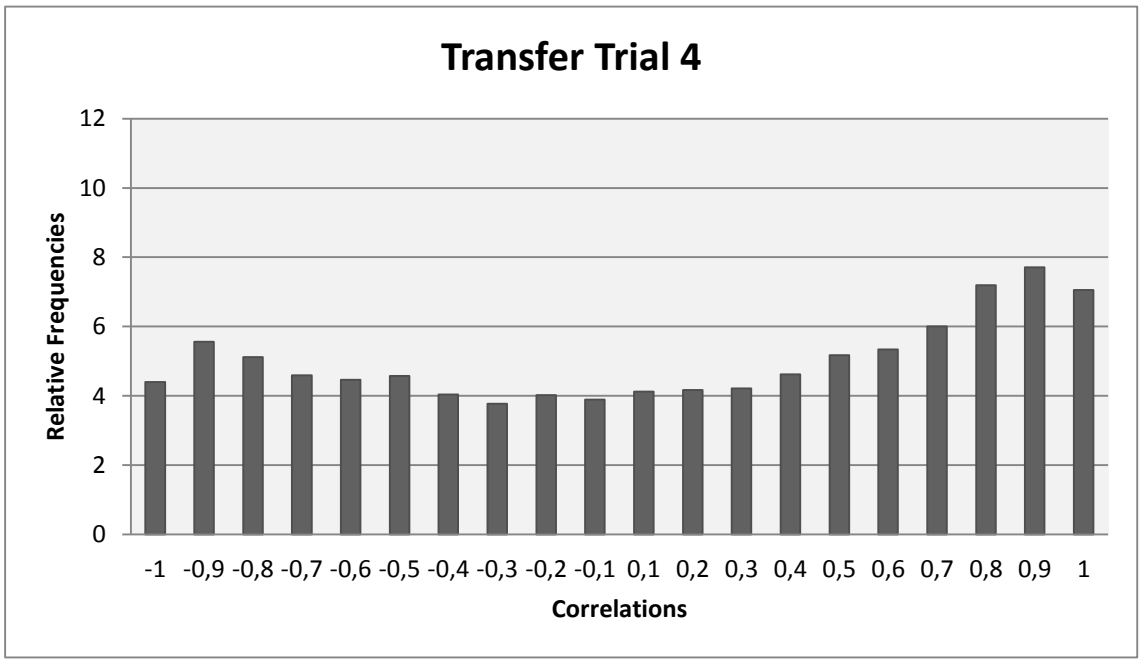

Figure 13.9: Transfer Trial 4: Correlations over all participants

Furthermore, the result of the repeated measure ANOVA showed no differences between the 9 trials, $F = 0.815$, $df = 1,908$, $p < 0.452$. Mauchly`s test of sphericity was significant ($p = 0.001$) and therefore the equality of variances of the differences between the trials not given. Thus, the Greenhouse-Geisser correction was used.

Table 13.2 includes the mean correlations over all participants and trials whereas figure 13.10 shows them in a histogram. As one can see, no trend toward higher correlations is visible. Contrary, the values at the last trials fall down which most likely shows that the participants became tired. Anyway, the results are far from expectation and hypothesis 2 has to be rejected as well.

Trials	Correlations
Spontan	0.20232
Smiley 1	0.25367
Smiley 2	0.21578
Smiley 3	0.23127
Smiley 4	0.16038
Transfer 1	0.21225
Transfer 2	0.20094
Transfer 3	0.14796
Transfer 4	0.11847

Table 13.2: Mean correlations over all participants and trials

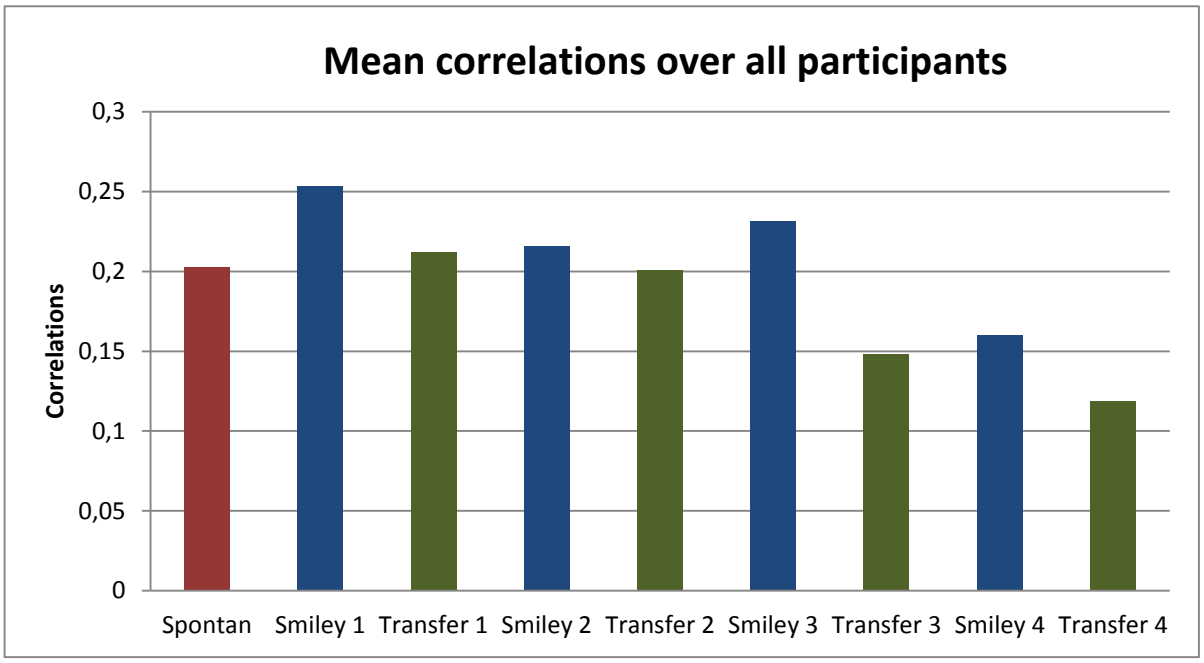

Figure 13.10: Mean correlations over all participants and trials

Generally, the distribution of the mean correlations does not support any trend. It looks as a distribution received by chance. There is only one increase between the spontaneous trial and smiley trial 1 which follows basically my expectation. Although the difference is not significant in a statistical sense, I was wondering if an increase in the 49 episodes of smiley trial 1 is responsible for that difference. Thus, I created another histogram showing the temporal trend of the 49 episodes of this trial which is shown in figure 13.11.

However, if there is a trend at all it would be rather toward lower values than to the expected higher values. This again clearly demonstrates that no learning took place, i.e. participants have not been able to gain control over synchronization in the gamma frequency range between the measured signals. The underlying correlations vary more or less by chance.

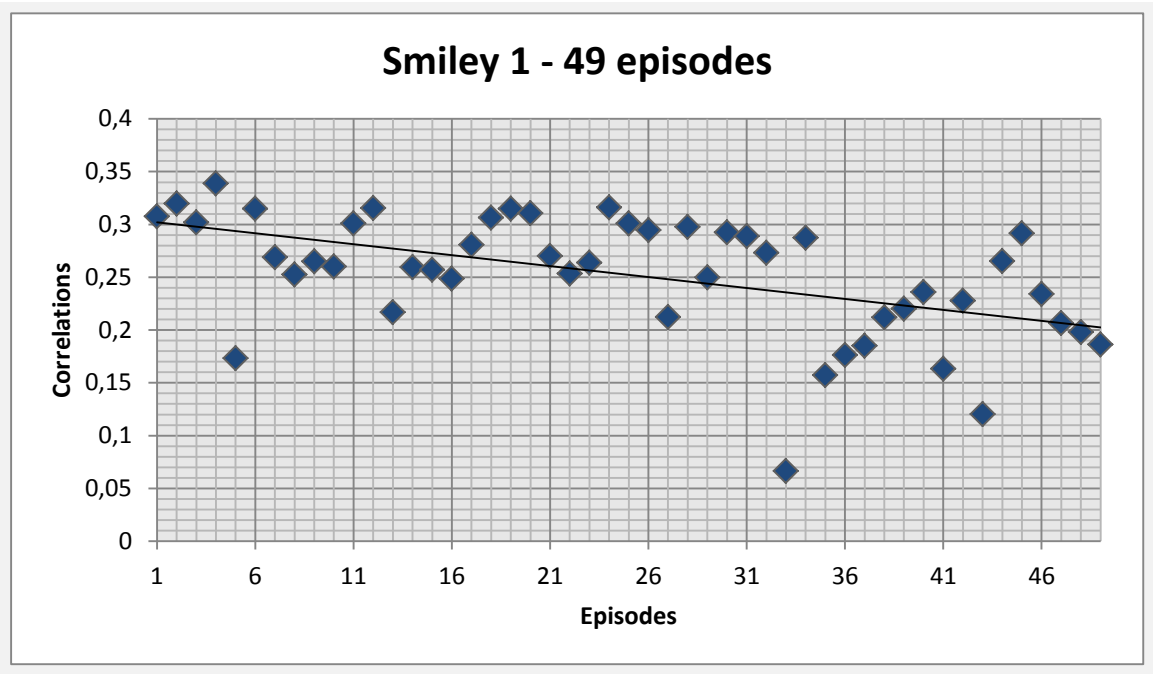

Figure 13.11: Temporal trend of the 49 episodes in smiley trial 1 over all participants

In summary, then, the result of the correlations does not correspond with the expectations and both hypotheses had to be rejected. Next I will have a detailed look on the results of the achieved smiley stages.

13.3 Result of the achieved smiley stages

Generally, the analysis of the achieved smiley stages should not reveal a different result than the result of the correlations did. Both are related to the underlying synchronization and should therefore display the same result. Figures 13.12 to 13.20 present the results of the achieved smiley stages over all participants, each trial in an own histogram. Following the histograms of the correlations, no trend toward higher smiley stages is visible. They look rather similar and do not support hypothesis 3 which has to be rejected.

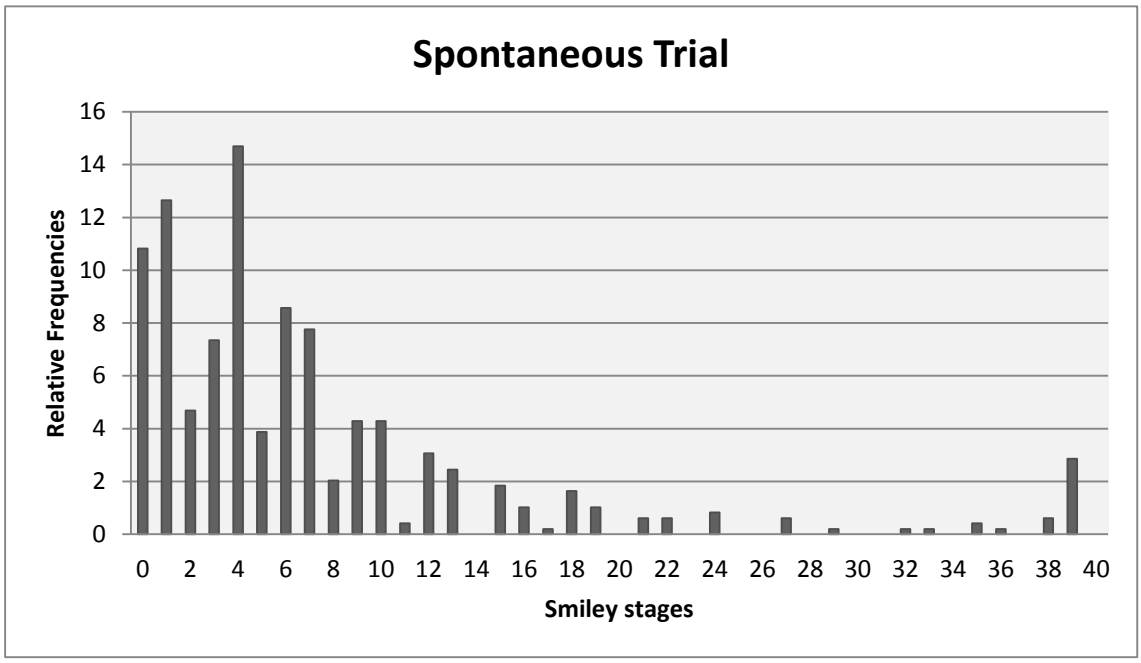

Figure 13.12: Spontaneous Trial: Achieved smiley stages over all participants

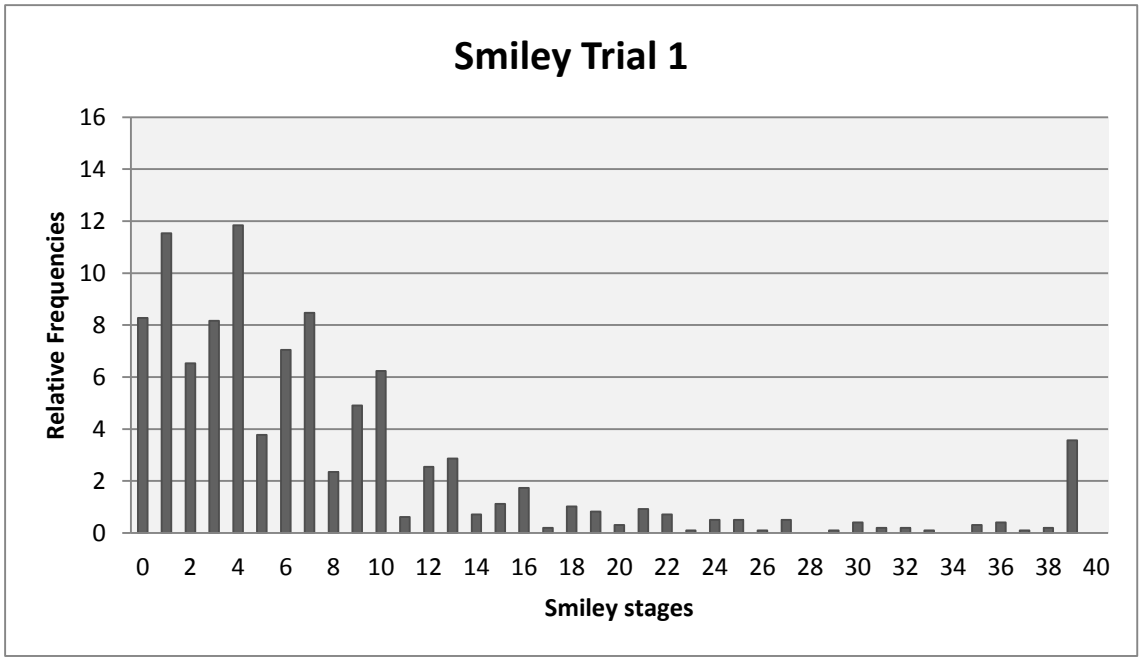

Figure 13.13: Smiley Trial 1: Achieved smiley stages over all participants

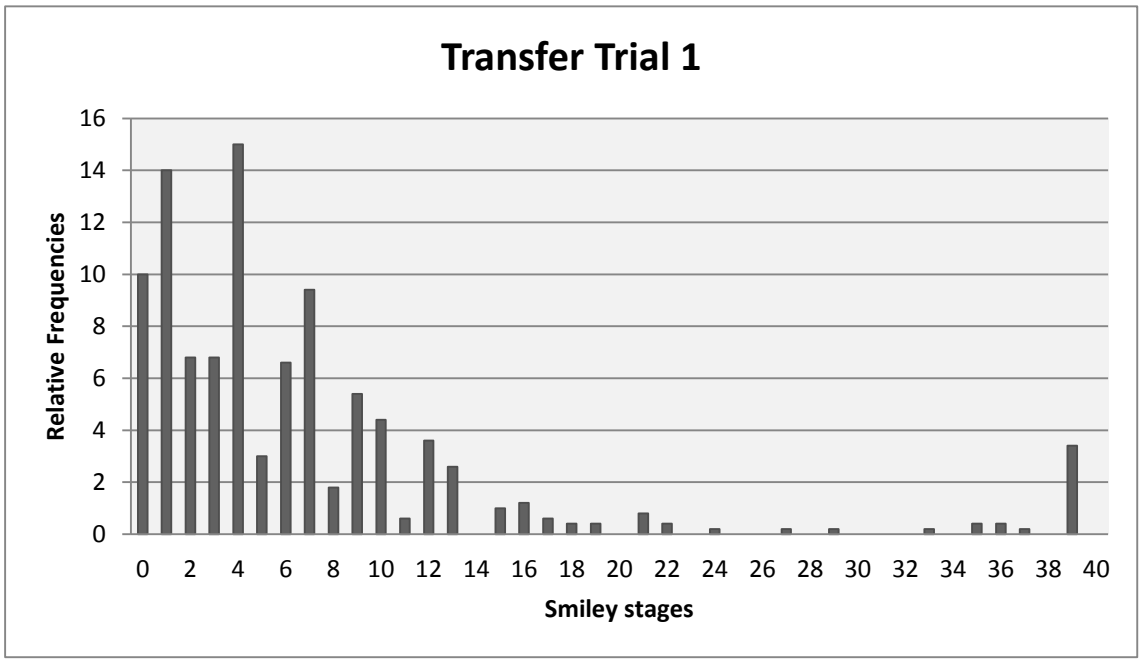

Figure 13.14: Transfer Trial 1: Achieved smiley stages over all participants

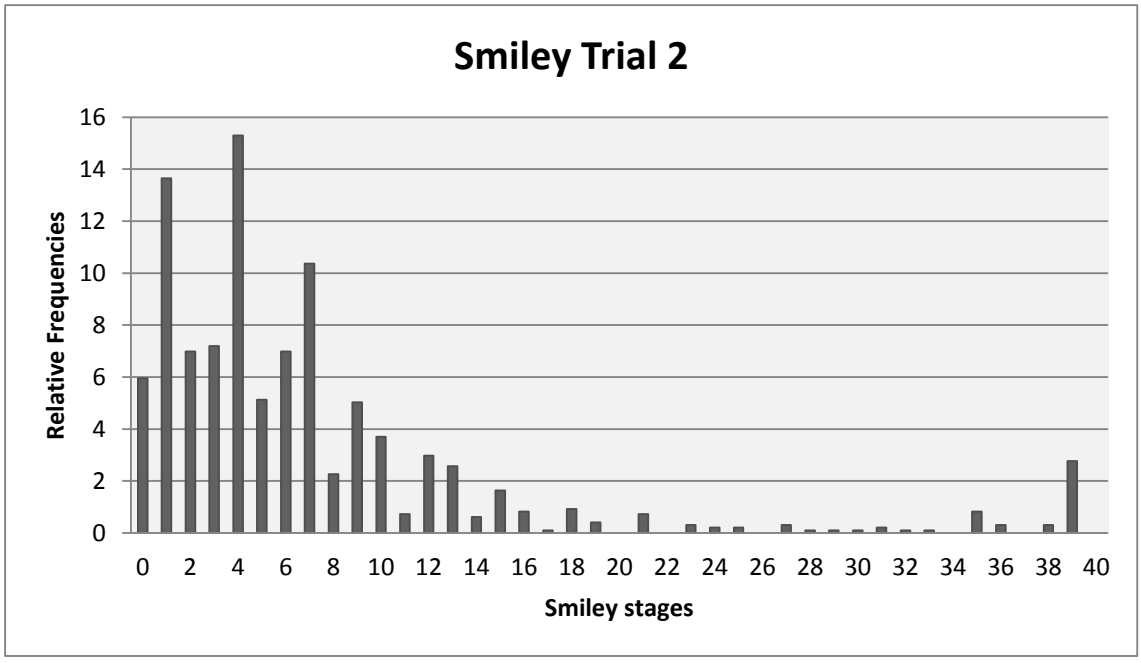

Figure 13.15: Smiley Trial 2: Achieved smiley stages over all participants

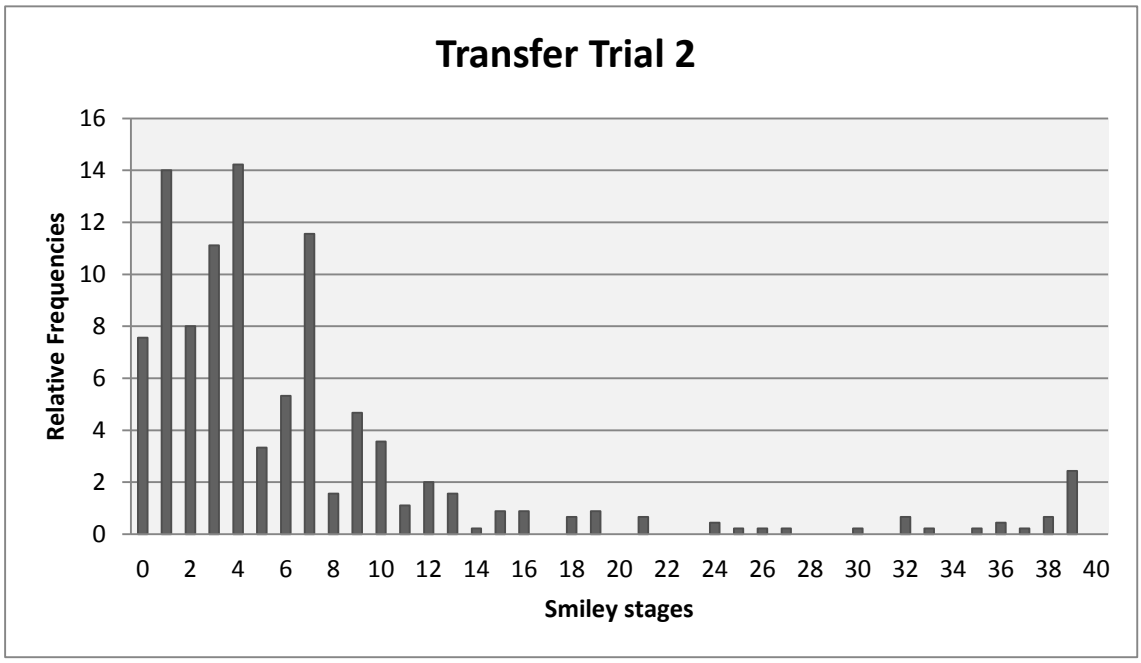

Figure 13.16: Transfer Trial 2: Achieved smiley stages over all participants

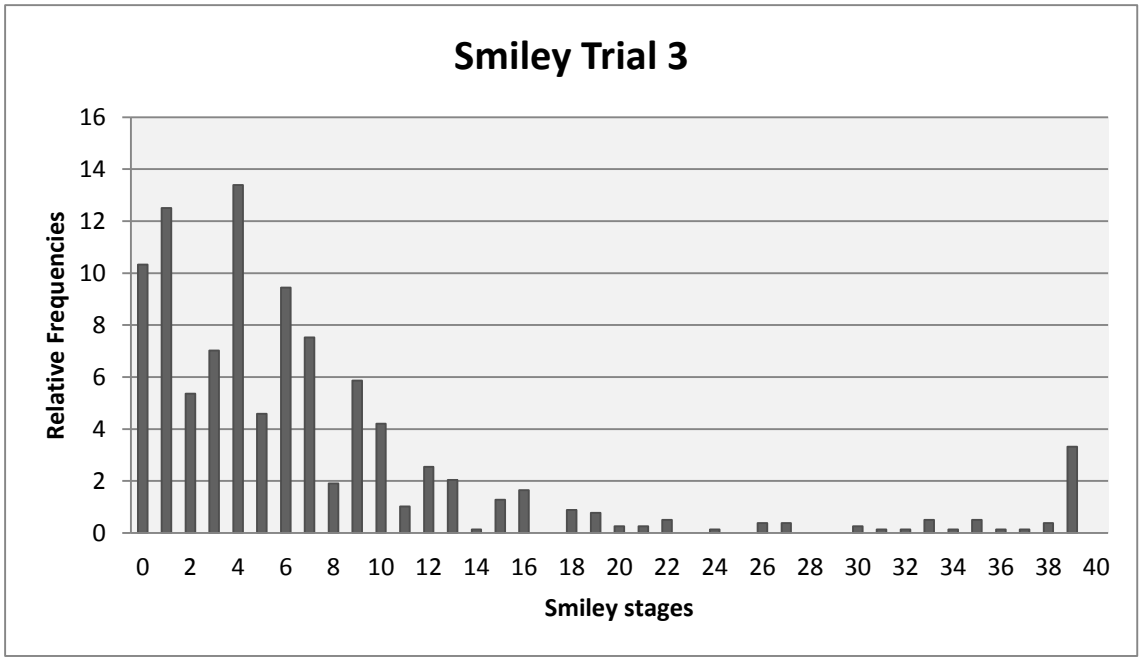

Figure 13.17: Smiley Trial 3: Achieved smiley stages over all participants

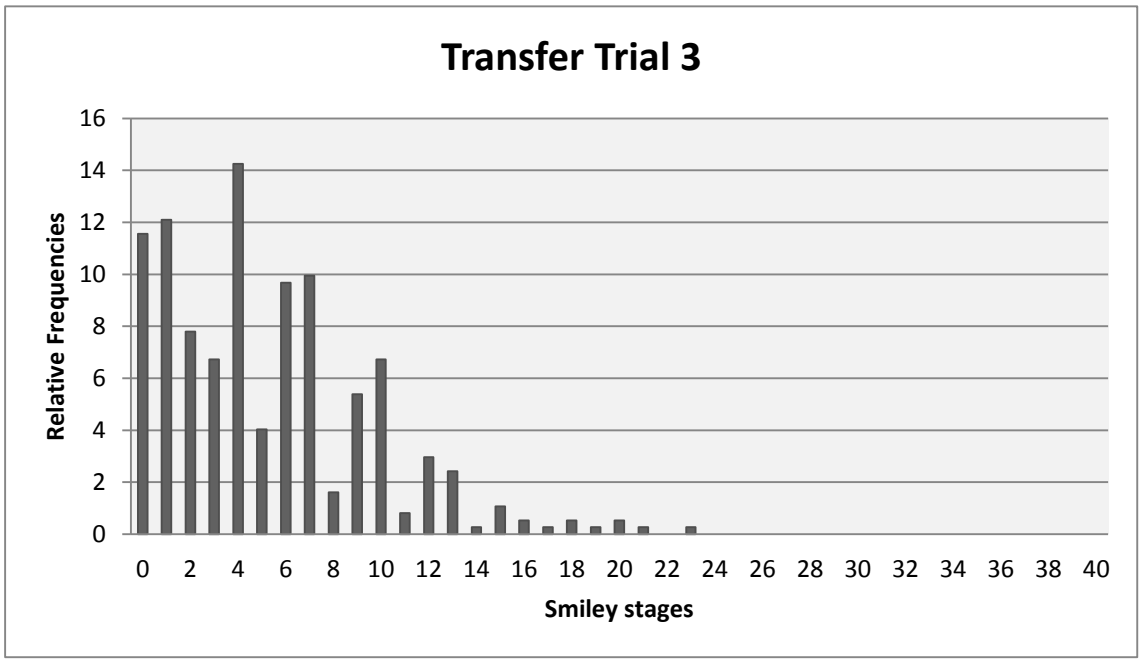

Figure 13.18: Transfer Trial 3: Achieved smiley stages over all participants

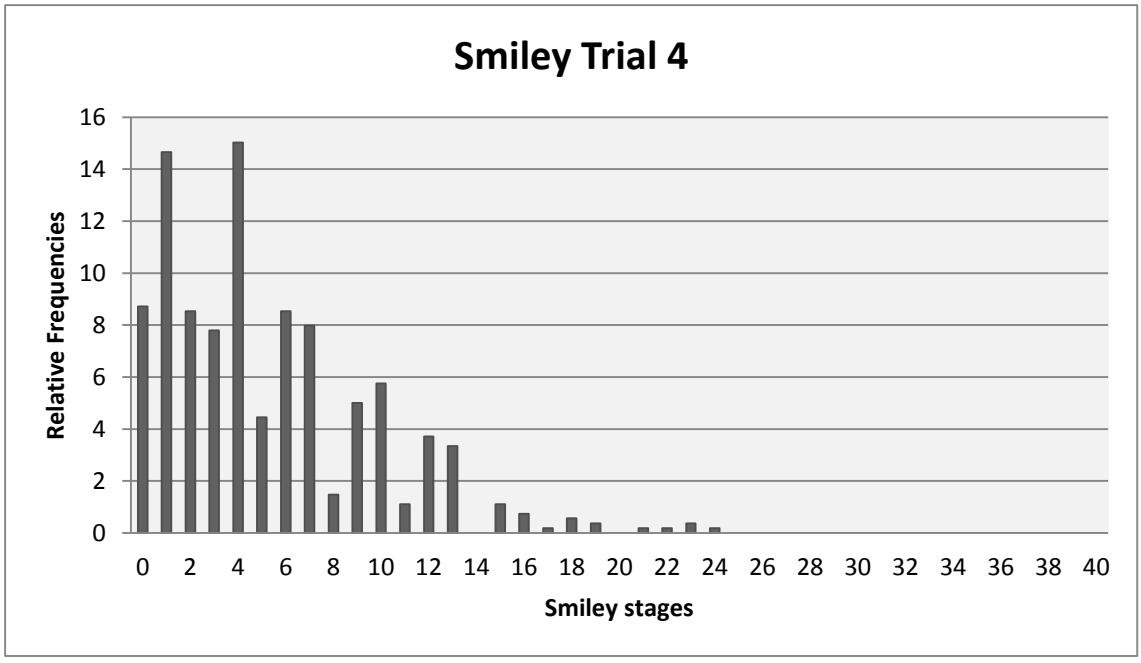

Figure 13.19: Smiley Trial 4: Achieved smiley stages over all participants

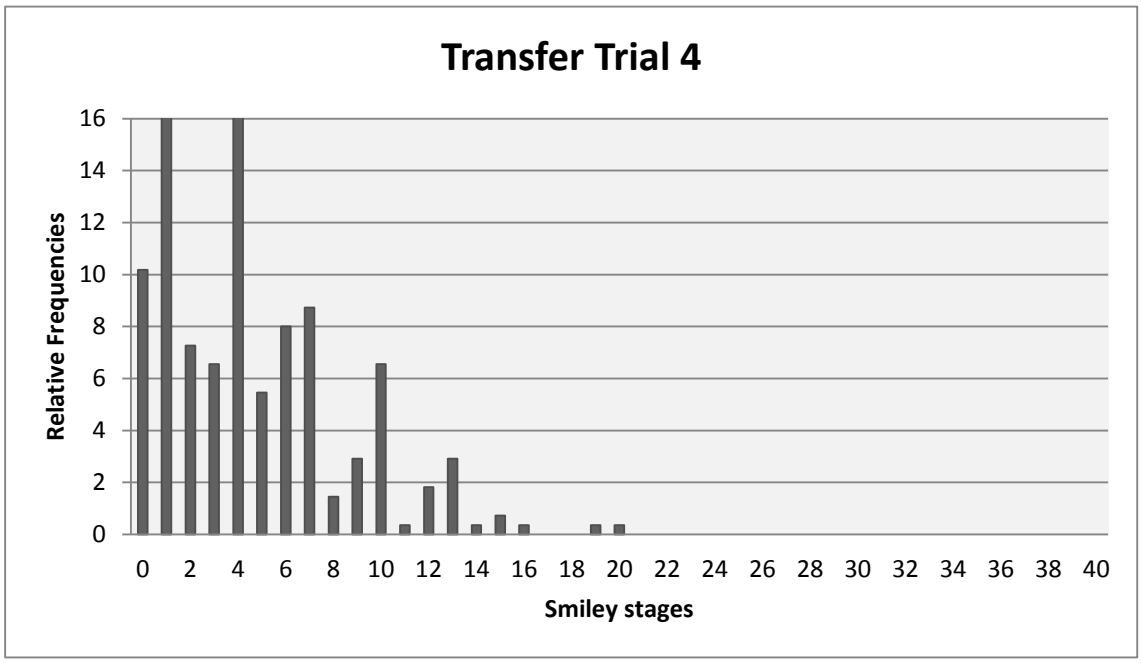

Figure 13.20: Transfer Trial 4: Achieved smiley stages over all participants

A repeated measure ANOVA will help to evaluate hypothesis 4. The Kolmogorov-Smirnov test revealed some significant results. A visual inspection of the values showed that participant 15 runs away from other participants, having much higher values (for all trials) than the others. Thus, to receive Gaussian distribution of the data, I excluded this participant from further calculation. Moreover, Mauchly`s test of sphericity displayed a significant result ($p = 0.000$) so that I had to use the Greenhouse-Geisser correction. The outcome of the repeated measure ANOVA showed no differences between the trials, $F = 1.270$, $df = 1,538$, $p < 0.299$. Table 13.3 as well as figure 13.21 finally display the mean smiley stages over all participants and trials.

Trials	Smiley stages
Spontan	7.23
Smiley 1	8.01
Smiley 2	7.20
Smiley 3	7.40
Smiley 4	5.29
Transfer 1	6.95
Transfer 2	6.86
Transfer 3	5.24
Transfer 4	4.64

Table 13.3: Mean achieved smiley stages over all participants and trials

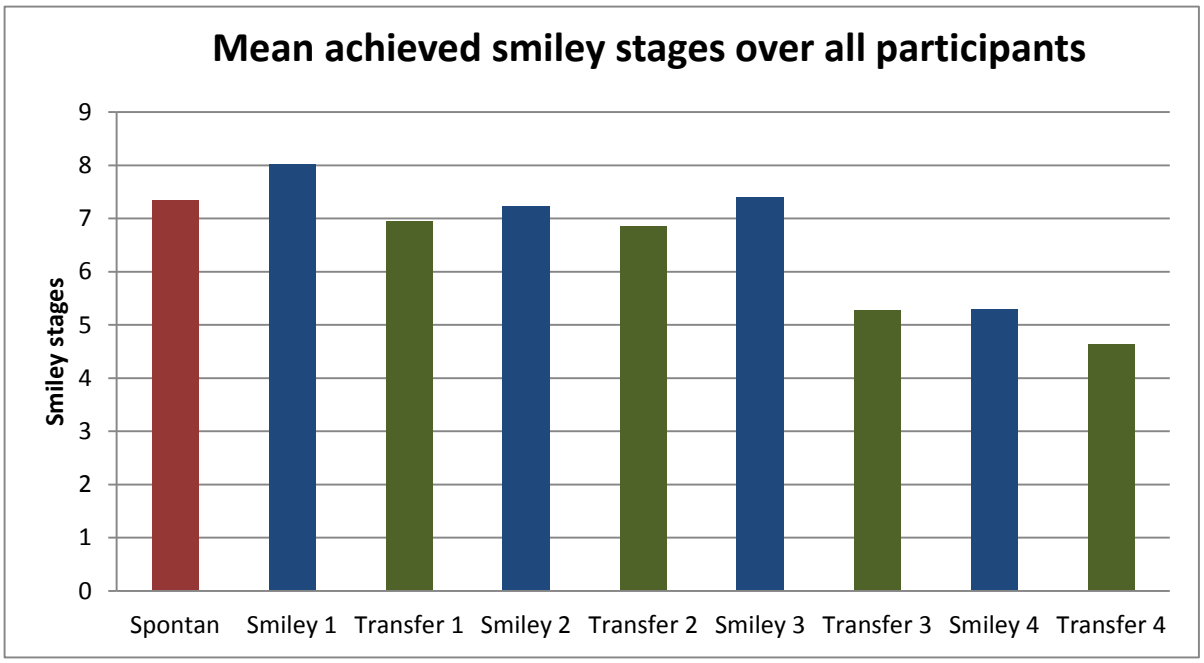

Figure 13.21: Mean achieved smiley stages over all participants and trials

The values and the histogram reflect the result of the correlations but both are far from expectation. Thus, hypothesis 4 is not confirmed, too. The arithmetic mean of the smiley stages does not differ between the trials nor does the graphical depiction display any trend toward higher values.

For the sake of completion, figure 13.22 shows the temporal trend of the achieved smiley stages over the experiment. Clearly, it does not illustrate the expected increase of the values. Contrary, a slightly decrease is visible. Hypothesis 5 as well has to be rejected.

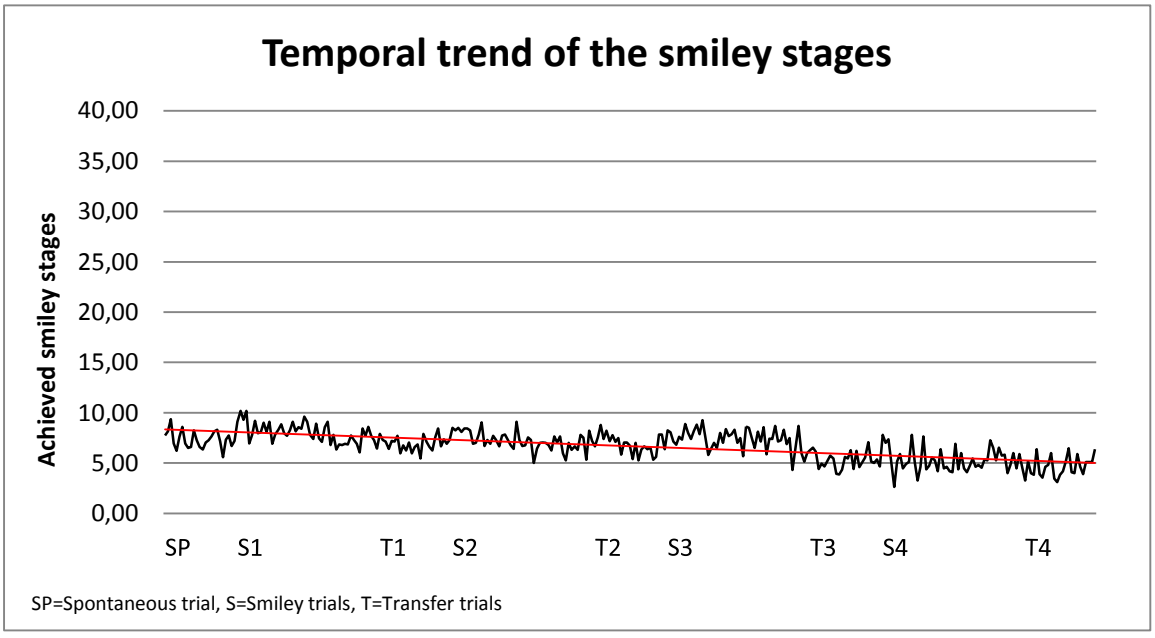

Figure 13.22: Temporal trend of the smiley stages

13.4 Result of the APM scores

Two people, namely participant 5 and 7, did not finish the APM after the experiment. Thus, for only 18 participants are data on the APM scores fully available. Table 13.4 shows the scores of them, before and after the training for each participant.

Participant	Before EEG	After EEG
01	19	18
02	19	17
03	17	16
04	23	18
05	20	m.v.
06	14	15
07	16	m.v.
08	17	13
09	18	14
10	20	17
11	22	19
12	22	21
13	20	21
14	10	8
15	23	23
16	18	18
17	19	20
18	22	23
19	15	12
20	15	19

m.v.=missing values

Table 13.4: Scores of the APM before and after the experiment

The Kolmogorov-Smirnov Test showed no significant result. Thus, Gaussian distribution of the data and the difference can be assumed. The outcome of the one-way paired t-test does not correspond with the expected one. The result shows a significant difference between the two measurements, $t = 2.145$, $df = 17$, $p = 0.0235$, mean (M) (before) = 18.50, M (after) = 17.33, standard error of the mean (SE) (before) = 0.817, SE (after) = 0.981. The results are therefore better before the training than after the training. I suggest that people became tired after a long day and that they already had some problems to focus on the task. Anyway, hypothesis 6 clearly has to be rejected.

13.5 Result of the verbal feedback of the participants

Following the results of the correlations and achieved smileys as well as the APM scores, the analysis of the verbal feedback of the participants does not include any surprise.

Generally, most of the participants rated the design a bit strenuous. All together 4 participants break the experiment after transfer trial 3. These people argued with another appointment, although it could have motivational reasons, too. No participant had problems to understand the task. In summary and under consideration of the rather long duration, most of them were in a good mood after the experiment and quite curious about the real aim of this study.

The participants reported various strategies to gain control over the smiley happiness. For instance, some tried to imagine scenes, other tried to relax, whereas other reported to focus directly on the smiley to make him smile. Others also mentioned some aggressive feelings after a couple of time without success. The different strategies range from ideas, memories, emotions, imaginations up to total relaxation. But none of the participants managed this or felt successful to manage, respectively. Most of them reported to stop with their efforts after trial 3 as they felt totally unable to do. They had not the impression to have any chance to make them smile. Whenever the smiley happiness increased, the participants had no idea why. Notably, the feedback of most of the participants to stop with their efforts after trial 3 further corresponds with the slightly decreasing correlations during that time.

In conclusion, hypothesis 7 is not supported by this feedback and has to be rejected, too. The verbal self-rating and reported feedback does correspond with the results of the correlations and the achieved smiley stages.

14 Discussion

The general idea of the present study was to train human subjects to gain control over synchronization in the gamma frequency range. However, the results clearly show that our attempt was not successful. None of the hypotheses could be confirmed - all of them had to be rejected. The correlations and the achieved smiley stages displayed the same results. Both are related to the underlying synchronization and thus have to be the same. Generally, the histograms showing the relative frequencies above all participants do not differ that much between the 9 trials. There is a slightly increase of the values between the spontaneous trial and the smiley trial 1 which corresponds our expectation. Anyway, it is not a significant difference. Contrary, the more detailed visual inspection of the 49 episodes in smiley trial 1 displayed a trend with decreasing values rather than the expected increasing values, although training took place. Furthermore, starting with transfer trial 3 a slightly decrease is visible. The most probable explanation for this is that participants became tired and resigned due to the lack of success to gain control on the smiley happiness. The histogram showing the mean correlations over all participants is in good accordance with the single histograms of the different trials. It clearly shows that there is no trend toward higher values from trial to trial. It rather looks like a result received by chance. Additionally, the repeated measure ANOVA revealed no differences between the 9 trials, either for the correlations or the smiley stages, respectively. The histogram showing the temporal trend does correspond with the negative results in a perfect way. It displays a slightly decreasing trend. Interestingly, the result of the APM revealed a significant difference between the measurements. Contrary to our expectation, the values are higher before than after the experiment. This looks like a confirmation for the supposition that participants became tired. Finally, the analysis of the verbal feedback is in good agreement with the achieved results. None of the participants was able to report a successful strategy. Contrary, they had the feeling to have absolutely no influence on the smiley happiness. Clearly, this results more or less in resignation. However, this as well is in accordance with the slightly decrease of the correlations from transfer trial 3 up to the end of the experiment. All in all, we have not been able to train people to gain control over synchronization in the gamma frequency range. In other words, our attempt was not successful. This null finding could have various reasons:

- The chosen design was simply too strenuous for the participants. Considering the additional rather long time needed for electrode application, lacks in motivation are likely to appear.

- Another reason could be the amount of training. Normally, biofeedback designs need more settings to be successful. Only one day simply could be to less to gain control over gamma synchronization (e.g. Heinrich et al., 2007).

- The given feedback was not ideal. We provided them only in one direction, i.e. the smiley faces became only happier, but not sad in case of decreasing correlations. A two directed feedback might have worked better.

- Another improvement might be a more accurate feedback. We have chosen to change the smiley happiness with correlations above 0.90. Giving feedback for any correlation would offer a much better training possibility, but also results in flickering feedback.

- Another reason could be the chosen frequency at the beginning of the experiment. Remember, we measured alpha and calculated with three in order to have a frequency in the gamma range. Usually, this resulted in a frequency around 33 Hz, whereas in most of the reported support the synchrony occurred in a much higher gamma frequency range. We thus possibly choose the wrong frequency.

- The selected areas for which we measured synchronization (F3 and P4) are not involved in thoughts and images. Choosing different areas might have a positive effect.

- Correlation was the wrong type of measurement. Maybe another method would have worked better.

- The measurement of gamma synchronization with scalp electrodes involves another possible problem. Generally, gamma synchrony can be measured from the scalp. But it could also be that gamma synchrony occurred but actually too small to measure. Additionally, volume conduction is another problem which might affected our results.

- The chosen electrode positions involve areas which are not suited to a biofeedback experiment. Other areas might have worked.

- Gamma synchronization was central to this study, not only the occurrence of gamma oscillations. We expected them also during thoughts and imagination. And, on the other hand, that thoughts and images should have influences on gamma synchrony, too. But it could be that gamma synchronization is not involved in thinking and imagination. It could also be that gamma synchrony occurred but too short to result in significant measures.

- Finally, the distance of the chosen electrodes is quite big. Actually, this constitutes one of the most difficult cases to achieve synchronization, as the hemispheres are crossed, too. Having two electrodes more close could have worked better.

In summary, the basic idea behind the design was that people gain control through their thoughts and imaginations and that these processes require the coherent activity of cortical neurons. If the theory of gamma synchronization holds true, this process should have resulted in neuronal assemblies which fire their action potentials in temporal synchrony. And we expected to measure them with scalp EEG and give the participants feedback to train the active influence. Anyway, it did not work. This might be due to one of the above mentioned reasons but could also mean that gamma synchronization is not the underlying mechanism for binding in the brain. However, as a matter of fact, further research is much needed. The given knowledge does not allow accepting or rejecting this still controversially discussed theory at this time. A more direct proof in an experimental setting would lead to causal results, but requires other technical devices, currently not available. Anyway, although our design did not work, I would rate it as a step forward. For sure, the basic approach is an interesting idea. It might be of further interest to use them again, this time having not that much participants, but train less of them in more sessions and on different days. This most likely will increase the chance of a learning process through biofeedback. Additionally, the variation of the chosen target frequency in the gamma range might be a good idea. And the provided feedback should be at least in two directions, ideally reflect the actual correlations in real-time. Adding such adaptations in the design might reveal totally new and interesting insights on human control over gamma synchronization. However, the EEG measurement and theoretical work on this interesting topic was very exciting. Although the design did not work and the hypotheses were not confirmed, it should be another step having new insights and profit. Of course, the knowledge how the brain definitely manages to combine and integrate its distributed activities would implicate much advantages, not only of theoretical nature. Anyway, it seems that we are far from having an answer.

15 Summary

Synchronization of neuronal activity in the gamma frequency range is up to date the most likely solution to the binding problem, but still in controversially discussion. In short, the theory states the formation of assemblies through synchronous (in-cycle) firing of cortical neurons. Those neurons, coding for one object, fire their action potentials in temporal synchrony with a precision in the millisecond range whereas no temporal synchrony takes place between neurons coding for different objects (e.g. Singer, 1993).

The goal of the present study was to examine if human subjects are able to gain control on synchronization in the gamma frequency range. To test this, EEG signals from the scalp were recorded from 20 healthy subjects in the age from 21 to 36 years. From two electrodes, namely F3 and P4, synchronization was calculated online and reported back to the clients in real-time. Thus, an EEG biofeedback paradigm was applied. Synchronization was calculated with a simple correlation. Feedback was presented through a smiley on a screen and the participants were instructed to make them as happy as possible.

Three different trials have been applied. At the beginning, a baseline trial was used to measure the spontaneous synchronization. This was followed by the feedback condition. During that, the participants received feedback about their success in order to gain control over the smiley happiness and thus, over synchronization between the two electrodes. This trial consisted of 49 episodes, each lasting 5 seconds. For any of the 49 episodes, 7-8 correlations have been calculated each second. In case of correlations of 0.90 and above, the smiley started to become happier. The transfer trial finally followed the feedback condition. The correlation still was calculated, but no feedback given. The screen showed a white circle only. This trial consisted of 25 episodes. Feedback condition and transfer trial have been presented all together 4 times in alternated order.

The obtained results clearly show that participants have not been able to gain control over the smiley happiness. In other words, participants could not control synchronization. The histograms of the correlations do not show any trend toward higher correlations during the experiment, which would have been expected if the subjects were able to gain control. In general, no significant difference between the correlations was evident - they have been quite similar throughout the study. Furthermore, the amount of achieved smiley happiness stayed constant throughout the experiment. Additionally, the participants explained their experiences at the end of the study. In accordance with

the obtained results, all participants reported various strategies to control the smiley happiness, but finally no one could manage.

In summary, this study could not provide support for the theory of gamma synchronization. Although, on a critical view, some major points need to be considered. The chosen design was very strenuous as the participants had to spend around four hours for the experiment and another three hours for application of the electrodes, suggesting some problems in motivation. EEG biofeedback is known to need around 25 sessions to achieve success whereas the present design consisted of one session only. Further questions arise with the chosen frequency and calculation. Is correlation the ideal method or would have coherence been the better one? In addition, the chosen electrodes constitute an extreme case with crossing hemispheres. In conclusion, then, the outcome of this study does not disprove the theory of gamma synchronization as possible solution to the binding problem. It is just another small step in finding the way how our brain solves the integration of its distributed network activities. As synchronization is a ubiquitous phenomenon, further research is needed before this still controversially discussed theory can be either accepted or rejected.

III APPENDIX

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SPSS Output

I: Repeated measure ANOVA for correlations

	Mean	Std. Deviation	N
Spontansynchronization	,166373964	,2378942226	11
Smiley 1	,235044676	,2718556320	11
Transfer 1	,162032040	,2321571137	11
Smiley 2	,162684331	,1562921851	11
Transfer 2	,115828174	,1265427653	11
Smiley 3	,147027447	,1652693518	11
Transfer 3	,147951044	,1485693786	11
Smiley 4	,161780844	,1259227486	11
Transfer 4	,119033512	,1590739681	11

Effect		Value	F	Hypothesis df	Error df	Sig.
Trials	Pillai's Trace	,781	1,341	8,000	3,000	,446
	Wilks' Lambda	,219	1,341	8,000	3,000	,446
	Hotelling's Trace	3,576	1,341	8,000	3,000	,446
	Roy's Largest Root	3,576	1,341	8,000	3,000	,446

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Trials	,000	70,803	35	,001	,239	,293	,125

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
Trials	Sphericity Assumed	,105	8	,013	,815	,591
	Greenhouse-Geisser	,105	1,908	,055	,815	,452
	Huynh-Feldt	,105	2,347	,045	,815	,472
	Lower-bound	,105	1,000	,105	,815	,388
Error(Trials)	Sphericity Assumed	1,292	80	,016		
	Greenhouse-Geisser	1,292	19,081	,068		
	Huynh-Feldt	1,292	23,467	,055		
	Lower-bound	1,292	10,000	,129		

Trials	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	,166	,072	,007	,326
2	,235	,082	,052	,418
3	,162	,070	,006	,318
4	,163	,047	,058	,268
5	,116	,038	,031	,201
6	,147	,050	,036	,258
7	,148	,045	,048	,248
8	,162	,038	,077	,246
9	,119	,048	,012	,226

II: Repeated measure ANOVA for achieved smiley stages

		Spontan	Smiley 1	Transfer 1	Smiley 2	Transfer 2	Smiley 3	Transfer 3	Smiley 4	Transfer 4
N		20	20	20	20	18	16	15	11	11
Normal Parameters	Mean	7,2300	8,0095	6,9480	7,1985	6,8578	7,3969	5,2447	5,2891	4,6364
	Std. Deviation	7,64326	8,01207	7,57256	7,23304	7,67000	7,95319	2,17143	1,86476	2,12930
Most Extreme Differences	Absolute	,277	,250	,289	,332	,344	,350	,103	,140	,219
	Positive	,277	,250	,289	,332	,344	,350	,088	,140	,219
	Negative	-,224	-,218	-,255	-,237	-,277	-,222	-,103	-,091	-,160
Kolmogorov-Smirnov Z		1,237	1,118	1,293	1,484	1,460	1,399	,398	,466	,727
Asymp. Sig. (2-tailed)		,094	,164	,071	,025	,028	,040	,997	,982	,667

		Spontan	Smiley 1	Transfer 1	Smiley 2	Transfer 2	Smiley 3	Transfer 3	Smiley 4	Transfer 4
N		19	19	19	19	17	15	15	11	11
Normal Parameters	Mean	5,6989	6,4526	5,3663	5,6805	5,1765	5,5387	5,2447	5,2891	4,6364
	Std. Deviation	3,48968	4,07303	2,77763	2,56479	2,90572	2,92883	2,17143	1,86476	2,12930
Most Extreme Differences	Absolute	,182	,184	,132	,155	,225	,153	,103	,140	,219
	Positive	,182	,184	,132	,155	,225	,153	,088	,140	,219
	Negative	-,111	-,144	-,110	-,127	-,163	-,109	-,103	-,091	-,160
Kolmogorov-Smirnov Z		,792	,804	,577	,675	,926	,591	,398	,466	,727
Asymp. Sig. (2-tailed)		,556	,538	,893	,753	,358	,876	,997	,982	,667

	Mean	Std. Deviation	N
Spontan	5,9164	4,05484	11
Smiley 1	6,9436	4,63758	11
Transfer 1	5,2582	3,12033	11
Smiley 2	5,4582	1,79533	11
Transfer 2	4,6473	1,41950	11
Smiley 3	5,2682	1,87215	11
Transfer 3	5,1127	1,82418	11
Smiley 4	5,2891	1,86476	11
Transfer 4	4,6364	2,12930	11

Effect		Value	F	Hypothesis df	Error df	Sig.
Trials	Pillai's Trace	,804	1,534	8,000	3,000	,396
	Wilks' Lambda	,196	1,534	8,000	3,000	,396
	Hotelling's Trace	4,090	1,534	8,000	3,000	,396
	Roy's Largest Root	4,090	1,534	8,000	3,000	,396

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Trials	,000	95,999	35	,000	,192	,220	,125

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
Trials	Sphericity Assumed	43,278	8	5,410	1,270	,271
	Greenhouse-Geisser	43,278	1,538	28,131	1,270	,299
	Huynh-Feldt	43,278	1,764	24,540	1,270	,301
	Lower-bound	43,278	1,000	43,278	1,270	,286
Error(Trials)	Sphericity Assumed	340,724	80	4,259		
	Greenhouse-Geisser	340,724	15,384	22,147		
	Huynh-Feldt	340,724	17,636	19,320		
	Lower-bound	340,724	10,000	34,072		

Trials	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
1	5,916	1,223	3,192	8,640
2	6,944	1,398	3,828	10,059
3	5,258	,941	3,162	7,354
4	5,458	,541	4,252	6,664
5	4,647	,428	3,694	5,601
6	5,268	,564	4,010	6,526
7	5,113	,550	3,887	6,338
8	5,289	,562	4,036	6,542
9	4,636	,642	3,206	6,067

III: One-way paired t-test

		APM before EEG	APM after EEG	diff
N		20	18	18
Normal Parameters	Mean	18,45	17,33	1,1667
	Std. Deviation	3,348	3,896	2,30728
Most Extreme Differences	Absolute	,115	,133	,120
	Positive	,087	,073	,104
	Negative	-,115	-,133	-,120
Kolmogorov-Smirnov Z		,515	,562	,509
Asymp. Sig. (2-tailed)		,953	,910	,958

		Mean	N	Std. Deviation	Std. Error Mean
Pair 1	APM before EEG	18,50	18	3,468	,817
	APM after EEG	17,33	18	3,896	,918

		N	Correlation	Sig.
Pair 1	APM before EEG & APM after EEG	18	,810	,000

		Paired Differences					t	df	Sig. (2-tailed)
		Mean	Std. Deviation	Std. Error Mean	95% Confidence Interval of the Difference				
					Lower	Upper			
Pair 1	APM before EEG - APM after EEG	1,167	2,307	,544	,019	2,314	2,145	17	,047

Declaration

Ich versichere:

1.) Dass ich die Diplomarbeit selbstständig verfasst, keine anderen als die angegebenen Quellen und Hilfsmittel benutzt und mich auch sonst keiner unerlaubten Hilfe bedient habe.

2.) Dass ich diese Diplomarbeit bisher weder im In- noch im Ausland in irgendeiner Form als Prüfungsarbeit vorgelegt habe.

3.) Dass ich mich bemüht habe, sämtliche Inhaber der Bildrechte ausfindig zu machen und Ihre Zustimmung zur Verwendung der Bilder in dieser Arbeit eingeholt habe. Sollte dennoch eine Urheberrechtsverletzung bekannt werden, ersuche ich um Meldung bei mir.

Zusammenfassung

Das Bindungsproblem beschäftigt sich mit der Kombination und Integration der verteilten Netzwerke in unserem Gehirn. Neuronale Phasen-Synchronisation im Gamma-Frequenz-Bereich ist die vermutete zugrunde liegende Lösung dafür. Dieser Theorie nach entsteht die Bildung von neuronalen Zellgruppen durch das synchrone feuern der zugehörigen Neuronen. Dies geschieht in einem Zeitrahmen von wenigen Millisekunden. Die vorliegende Studie untersuchte, ob die teilnehmenden Versuchspersonen aktive Kontrolle über Synchronisation im Gamma-Frequenz-Bereich erlangen können. Um dies zu testen, wurde ein Biofeedback-Design verwendet. Mittels EEG wurden die Gehirnsignale von insgesamt 20 gesunden Probanden aufgezeichnet. Zwischen zwei Elektroden wurde die Synchronisation in Echtzeit gemessen und unmittelbar an die Teilnehmer rückgemeldet. Zur Berechnung der Synchronisation wurde eine Korrelation verwendet. Als Feedback an die Versuchsteilnehmer diente ein Smiley, präsentiert auf einem Bildschirm und die Teilnehmer wurden instruiert, diesen möglichst „glücklich“ zu machen. Die Ergebnisse zeigen relativ klar, dass die Teilnehmer keine Kontrolle über Synchronisation erzielen konnten. Die Korrelationen blieben während des gesamten Experiments unverändert. Keiner der Teilnehmer konnte eine Strategie zur Kontrolle der Smileys berichten. Kritisch ist allerdings anzumerken, dass das gewählte Design von langer Dauer und daher auch mit hoher Anstrengung verbunden war. Dies könnte zu Motivationsproblemen geführt haben. Zudem wurde das Training an einem einzigen Tag durchgeführt, wobei EEG-Biofeedback in der Regel deutlich mehr Zeit benötigt. Obwohl die vorliegende Studie die Theorie von Phasen-Synchronisation im Gamma-Frequenz-Bereich als Lösung für das Bindungsproblem nicht bestätigen konnte, ist die funktionelle Relevanz von diesem Phänomen weiterhin ungeklärt und erfordert zusätzliche Untersuchungen.

Curriculum Vitae

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Work Experience

December 2012 - Present	**Managing Director** Radreisefreunde GmbH, Neubaugasse 78/4, 1070 Vienna Responsible for organization, sales, evaluation, and calculation
October 2012 - November 2012	**Sales Manager** Donauradfreunde GmbH, Nibelungenstraße 68, 4090 Engelhartszell Responsible for sales and calculation
August 2005 - September 2012	**Business Manager** Donauradfreunde M. Lötsch GmbH, Ronthal 2, 4090 Engelhartszell Responsible for organization, sales, and calculation
April 1999 - September 1999	**Commercial Executive** Donauradfreunde M. Lötsch GmbH, Ronthal 2, 4090 Engelhartszell Responsible for bookings and logistics
August 1990 - August 1997	**Commercial Executive** Josef Heindl Handelsgesellschaft mbH, Linzer Tor 3, 4780 Schärding am Inn Responsible for invoicing, purchase, quotation, and inventory control

Education and Training

September 1999 - July 2005	**Diploma study of Psychology** University of Vienna, Universitätsring 1, 1010 Vienna Personal interest in Neuropsychology and Psychology in economy First part leaving with distinction
September 1997 - October 1998	**A-levels** Höhere Bundeslehranstalt für wirtschaftliche Berufe, Eybnerstraße 23, 3100 St. Pölten German, English, Mathematics, and Biology
July 1990 - August 1993	**Scholastic Profession** Berufsschule II, Max-Hirschenauer-Straße 250, 4780 Schärding am Inn Leaving with distinction
September 1986 - July 1990	**Secondary modern school** Hauptschule, Nr. 2, 4725 St. Aegidi

Languages

Mother tongue	**German**
Other languages	**English** Understanding B 2 / Speaking C 1 / Writing C 1 **Spanish** Understanding A 2 / Speaking A 2 / Writing A 1 **Russian** Understanding A 2 / Speaking A 2 / Writing A 1 **Chinese** Understanding A 1 / Speaking A 1 / Writing A 1

Levels: A1/2: Basic user - B1/2: Independent user - C1/2: Proficient user
Common European Framework of Reference for Languages

Personal Skills

Social skills	Good ability to work under pressure Concentrativeness Very good apprehension
Organizational skills	Leadership (currently responsible for a team of 3 people) Excellent organizational and prioritization skills
Artistic skills	Music (guitar and clarinet)
Computer skills	Proficient with Microsoft Office programs Basic knowledge with MAC OS
Other skills	Cross country skiing, cycling, and swimming
Driving license	Category A and B
Further interests	Philosophy, economy, and movie direction