Subjective visual experiences of colour and form induced by temporally modulated light

Cordula Becker

München 2005

Subjective visual experiences of colour and form induced by temporally modulated light

Cordula Becker

Inaugural-Dissertation

zur Erlangung des

Doktorgrades der Philosophie an der

Ludwig–Maximilians–Universität

München

vorgelegt von

Cordula Becker

aus Magdeburg

München, den 21.03.2005

Erstgutachter: Prof. Hermann J. Müller

Zweitgutachter: Prof. Heiner Deubel

Tag der mündlichen Prüfung: 29.06.2005

Ich hatte die Gabe, wenn ich die Augen schloß und mit niedergesenktem Haupte mir in die Mitte des Sehorgans eine Blume dachte, so verharrte sie nicht einen Augenblick in ihrer ersten Gestalt, sondern sie legte sich auseinander, und aus ihrem Inneren entfalteten sich wieder neue Blumen aus farbigen, auch wohl grünen Blättern; es waren keine natürlichen Blumen, sondern phantastische, jedoch regelmäßig wie die Rosetten der Bildhauer. Es war unmöglich, die hervorsprossende Schöpfung zu fixieren, hingegen dauerte sie so lange, als mir beliebte, ermattete nicht und verstärkte sich nicht. Dasselbe konnte ich hervorbringen, wenn ich mir den Zierrat einer buntgemalten Scheibe dachte, welche dann ebenfalls aus der Mitte gegen die Peripherie hin sich immerfort veränderte, völlig wie die in unseren Tagen erst erfundenen Kaleidoskope.

Johann Wolfgang von Goethe
Studien zur Morphologie

I wish to express my thanks to everyone who helped me during the various phases of writing this dissertation.

I am thankful to Hermann Müller for the opportunity to do research and write a thesis in his group in Munich. I also wish to thank him and Heiner Deubel for their willingness to act as reviewers of this thesis.

I am especially grateful to Mark Elliott for accepting me into his Psychophysics and Temporal Factors lab, introducing me to the paradigms employed in this thesis, his openness for discussions and support during all stages of experimentation, analysis, and writing of the thesis.

My thanks go to Andreas Schiegg for his help on the electronic interface of the experimental apparatus, as well as to Sven Garbade for sharing his expertise on the statistical programming language R.

For the revealing insights into electroencephalographic experiments, as well as for practical help concerning EEG experiments and analyses, I wish to thank Klaus Gramann.

This work could not have been realized without the help of my student helpers Christine Falter, Marieluise Hupfauer, Katerina Obermeier, and Bernhard Ostler. Many thanks to them and to all brave and patient volunteers who participated in my experiments.

Many thanks for proofreading the German summary to Stefanie Arndt.

Special thanks go to to my Bavarian colleagues for their introduction to Bavarian life and civilisation, in particular a primer to the Bavarian language and induction to the "Biergarten" culture.

I thank Johannes for proofreading and support throughout.

Contents

1 Introduction **1**

1.1 An overview of subjective visual experiences 4

1.1.1 Historical and religious reports of subjective visual experiences 4

1.1.2 Clinical descriptions of subjective visual experiences 6

1.1.3 Magnetically and electrically induced subjective visual experiences 9

1.2 Subjective visual experiences induced by visual stimulation 12

1.2.1 Benham's Top and Benham-like stimulation regimes 14

1.2.2 Stimulation of the visual ganzfeld 19

1.3 Physiological mechanisms of visual perception related to subjective experiences 24

1.3.1 Mechanisms of colour perception 24

1.3.2 Mechanisms of form perception 30

1.3.3 Physiological models of subjective visual experiences . . . 33

1.4 Overview of the thesis 39

2 Descriptive analysis of visually induced subjective experiences **43**

2.1 Rationale 44

2.2 Methods 44

2.3 Results 46

2.3.1 Reported categories of colour and form 46

2.3.2 Analysis of the distribution of subjective experiences over frequency 48
2.4 Discussion 51

3 Interdependencies in the appearance of subjective visual experiences 54
3.1 A multidimensional model of co-occurrent subjective visual experiences 55
3.1.1 Rationale 55
3.1.2 Methods of analysis 55
3.1.3 Results 58
3.1.4 Discussion 62
3.2 Progression of subjective visual experiences over time 63
3.2.1 Rationale 63
3.2.2 Methods of analysis 63
3.2.3 Results 64
3.2.4 Discussion 67

4 Relation of subjective visual experiences to the temporal characteristics of the stimulation 68
4.1 Rationale 69
4.2 Methods 70
4.3 Results 71
4.3.1 Analysis of the distributions of subjective experiences over frequency 71
4.3.2 Response time analysis 72
4.3.3 Analysis of response times over phase 73
4.4 Discussion 76

5 Spontaneous visual experiences during constant ganzfeld stimulation 77

5.1 Rationale 78
5.2 Methods 78
5.3 Results 80
5.3.1 Descriptive analysis of spontaneous visual experiences in free report 80
5.3.2 Impact of the results of Experiment 4 and 5 on the findings of Experiment 1 81
5.3.3 Descriptive analysis of spontaneous visual experiences in a forced-choice paradigm 85
5.3.4 Impact of the results of Experiment 4 and 5 on the findings of Experiment 2 and 3 87
5.4 Discussion 89

6 Phenomenology of subjective visual experiences 91

6.1 Description of subjective colours 92
6.1.1 Rationale 92
6.1.2 Methods 92
6.1.3 Results 99
6.1.4 Discussion 105
6.2 Description of subjective forms 107
6.2.1 Rationale 107
6.2.2 Methods 107
6.2.3 Results 108
6.2.4 Discussion 112

7 Electrophysiological correlates of subjective colour 114

7.1 Rationale 115
7.2 Methods 118

7.3 Results 123
7.4 Discussion 126

8 General Discussion **130**
8.1 Summary of the experimental evidence 131
8.2 A theoretical model of subjective colour 133
8.3 Mechanisms of subjective form and the relation between subjective colour and form 137
8.4 Future prospects 139

A Form of consentment **141**

B Instructions **143**

C Experiment 1 - Sizer plots **162**

D Experiment 1 - Kolmogorov-Smirnov-tests **165**

E Experiment 1 - Multidimensional scaling **167**

F Experiment 2 and 3 - Circular plots **195**

G Experiment 4 and 5 - SiZer plots **198**

H Experiment 7 - Drawings of subjective forms **201**

I Experiment 8 - EEG regression formulas **241**

German summary/Deutsche Zusammenfassung **257**

Bibliography **272**

Curriculum Vitae **289**

Chapter 1

Introduction

Conscious visual experience relies on the interaction of our nervous system with light reflected from spatial structures in the environment. It is often assumed that the visual experiences resulting from this interaction are *directly* related to the characteristics of the external stimulus, so that for example spatial properties of the external stimulus are directly mapped onto spatial properties of the internal experience. This approach already fails when considering colour perception, where the internal visual experience cannot be mapped directly onto the external physical properties in terms of light reflectance and light absorbance of objects. Colour metamers, for example, are pairs of perceptually indistinguishable colours based on the interaction of the visual system with light of different physical properties, i.e. spectral distributions [2]. Some recent philosophical-psychological debates on the subjectivity of colour experiences (see [3] and [4] and the related discussions) shed some light on the controversial potential of this mapping problem. While some philosophers believe in the absolute subjectivity of colour experience (e.g. Hardin [5]), that is the impossibility to describe colour in physical terms, Ross [3, 6], as well as Byrne and Hilbert [4] argue that subjectivism is not tenable on philosophical grounds and therefore colours have to be seen as objective physical properties of the external world. In contrast, some psychological perspectives on the problem [7, 8] follow a causal theory of perception. This approach states that colours are located at the end of a causal chain from (i) the distal external stimulus (i.e. the physical object with its physical properties), via (ii) the proximal stimulus (i.e. the stimulus on the retina), and (iii) the direct neural correlates of colour (i.e. the states of the nervous system) to (iv) the experience of colour (residing in the conscious visual experience). While the stages (ii) and (iii) clearly involve interactions between the external stimulus properties and the nervous system, the transition from (iii) to (iv) relates to the so-called and yet unsolved hard problem of consciousness. This problem relates to the question of how the neural states of the brain 'transform' into conscious experiences (see for example [9] and [10]). How and why does seeing the blue sky or imagining a green horse feels as blue or green as it does? In this work, I will adopt a perspective which assumes the stages (iii) and (iv) to be equivalent, therefore questioning the existence of a hard problem of consciousness [11, 12]. This perspective allows the investigation of subjective conscious experiences in relation to the external stimulation, looking for potential explanations of these conscious experiences in the causal chain outlined above [10, 12].

The present work will consider flicker-induced subjective visual experiences of colour and form. Even though these visual experiences cannot be *directly* mapped onto the physical properties (i.e. wavelength and spatial composition) of the external stimulation, I will show that subjective visual experiences indeed relate to certain characteristics of the stimulation following physiologically well-founded laws. This work will demonstrate that subjective visual experiences are 'subjective' in the sense that they do not relate to the external stimulation *directly* and therefore seem to exist only in the internal representations of the observers. However, I will show that the formation of these subjective visual experiences is well and objectively attributable to processes in the causal chain of normal visual perception. Subjective visual experiences usually do not appear under ordinary every day life conditions, but necessitate specific conditions of external stimulation, usually generated in experimental settings. Possibly the visual nervous system is driven to its borderline conditions of operation in this laboratory context. The subjective visual experiences might be expressions of a breakdown of proper functioning of the nervous system and their study therefore promises to be a valuable tool for the understanding of the basic mechanisms involved in information processing in the brain.

It is the aim of this introductory chapter to present a variety of reports of subjective experiences from a historical, clinical, and experimental perspective and to give an introduction to the mechanisms of normal colour and form perception which are of relevance for the understanding of subjective visual experiences. Finally, I will consider models that attempt to explain subjective visual experiences.

1.1 An overview of subjective visual experiences

As a first definition, I call visual experiences 'subjective' when they concern the perception of a structure or quality in the absence of structure- or quality-related information in the visual field. The term apperception will be used throughout this thesis to refer to the experience of a subjective colour or form. In this sense apperception is the conscious mental perception of something which cannot be mapped directly onto the external stimulation. A twofold differentiation between types of subjective experiences will be used in the following [13]: (i) related to causation, *endogenous* subjective experiences refer to experiences which arise independently from any exogenous or toxic influences on the person being subject to these experiences. While *toxically induced* subjective experiences are the result of an interaction of the nervous system with a psychoactive substance, *exogenous* subjective experiences are induced by external stimulation of the nervous system, such as pressure on the eyes. These causally different types of subjective experiences can be manifest in a number of (ii) forms: experiences may be *unspecified* (round, angular, coloured), *specific*, i.e. describable (circle, wave, red, blue) or *representational* (animals, humans, 'real world' objects).

1.1.1 Historical and religious reports of subjective visual experiences

This section aims to give some insight into the fascinating variety of reported subjective experiences related to religious activities in humans. In some instances subjective experiences of this kind are thought to be the basis for art dating back as far as to the palaeolithic times.

Subjective experiences were described to appear in humans who practise shamanistic activities [14]. While these experiences may be endogenous and induced by internal mental activity and emotional states, shamans also use toxic substances for the generation of such experiences [14, 15, 16]. Bednarik [17] developed a phosphene theory[1] of the lower palaeolithic art and proposed that simple geometric motifs marked on the rocks by hominids are an externalization of subjective visual experiences. Subjective visual experiences were also suggested as the underlying process for the abstract forms in neolithic art [18, 19]. While Lewis-Williams et al. [19] emphasized the possibility of inducing such subjective experiences in trance states related to shamanistic activities, others [17, 20, 21] criticized that geometric art cannot only be found in cultures practising shamanism, and emphasized the fact that subjective experiences can be induced in all humans independently of trance states, for example by boredom, sleep deprivation, or drowsiness (see also [22]).

Hodgson [22] pointed out the similarity between early palaeolithic art and infant drawings. He suggested that the results of these artistic activities are not only phenomenologically similar, but also relate to similar neurophysiological mechanisms of the primary visual cortex. Interestingly, the suggested relation between subjective experiences, palaeolithic art and infant drawing is also in agreement with findings of Kellog et al. [20] about the high similarity between infant drawings and phosphenes in adult humans.

Eichmeier and Höfer [13] suggested that a variety of religious reports might be based on the experiences of subjective phenomena, especially in the visual domain. Visions from the Christian middle ages [23] are often defined by geometric patterns which develop into more complex representational associations. Similar subjective experiences are reported in the Middle East [13] and in cultures from the Far East. In the Indian practice of meditation and yoga, subjective visual experiences may be seen as a disturbing factor [13]. However, in hinduistic yantra meditation, perception or imagination of a picture is the focus of the meditation practice; different subjective visual experiences are thought to represent the different degrees of contemplation [24].

[1] Subjective visual experiences are also referred to as phosphenes in the literature.

1.1.2 Clinical descriptions of subjective visual experiences

Toxically induced subjective visual experiences

Subjective visual experiences can be induced by a number of hallucinogenic substances, such as LSD [25] and mescaline [26]. Often, these visual experiences coincide with specific emotional conditions, the toxic psychoses, and are therefore rarely described with scientific precision. However, anecdotal reports, such as by Aldous Huxley [27], shed some light on the nature of these subjective experiences. Experimental studies evaluating the effects of LSD, mescaline, and psilocybin showed that these drugs elicit experiences of nonspecific or geometric nature when applied in sufficiently small toxic doses, while larger doses lead to the experience of representational figures or scenes [28].

Klüver [29, 30] noticed that toxically (in this case mescaline) induced subjective visual experiences resemble relaxation-induced experiences (in light sleep), insulin-induced hypoglycaemic visual experiences, and experiences during fever. He realized that the first stages of intoxication are accompanied by geometric patterns of a variety of forms: gratings, nets, honeycombs, spider webs, tunnels and avenues, and spirals. While these patterns varied in number, size, and shape, they were also subject to changes in the spatiotemporal relations: they were often repeated and combined to form more complex mosaic patterns. This suggests that the visual system responds to different conditions of stimulation with just a restricted number of shape and form constants ([29] cited from [13]). These may be combined to build more complex representations.

Mechanically induced subjective visual experiences

A first description of exogenous subjective experiences are the reports by Purkinje [31] describing geometric patterns which are seen when pressure is applied to the closed eyes. The appearance of pressure-induced visual experiences depends not only on the locus of pressure on the eye, but also on the degree of pressure applied

[13, 32]. Pressure in the middle of the eye produces rhombus-shaped patterns, while pressure at the outer corner of the eye results in the experience of circular forms. With increasing pressure, the patterns lighten and chessboard-like or web-like structures become visible [32].

Subjective visual experiences as symptoms of neuropsychological and psychiatric disorders

Subjective visual experiences of very different kinds have been described in a variety of neuropsychological and psychiatric disorders, such as epilepsy, migraine, psychoses, or brain damage.

An examination of patients with degenerative eye diseases [33] revealed a variety of subjective visual experiences. These experiences ranged from changes of the input information in partially blind patients (by perseveration, micro- and macropsia, and illusory visual spread) to visual phenomena that appeared independently of any sensory input in blind patients. Patients described patterns of tesselopsia (regular, repeating patterns, such as brickworks, lattices, mosaics), hyperchromatopsia (hyperintense, vivid and brilliant colours) and dendropsia (irregular branching forms, such as trees).

Similar visual experiences were described in a study of patients with a vascular lesion [34]. The reported patterns appeared in the four basic colours (red, green, blue, and yellow) and were usually horizontally and vertically oriented geometric patterns. Patients experiencing the coloured patterns constituted a homogeneous group with a hemianopia following a sustained cerebral infarction in small circumscribed regions in the striate area of the interhemispheric fissure and the adjacent white matter in the occipital lobes. As the visual defects mainly resolved after some time, the authors suggested that the experience of coloured patterns is due to a functional disorder rather than to tissue loss.

Epileptic episodes are often preceded by a so-called aura, a state in which the epileptic person may have a variety of sensory experiences. Visual aura symptoms that have been described in the literature comprise everything from nonspecific (e.g. lights, flashes [35]), over specific (e.g. circles, spirals [36]) to representational patterns (e.g. faces, scenes [37]).

A further visual experience which is not directly related to the external stimulation is the scintillating scotoma, which has predominantly been reported in migraine patients [38]. It is often composed of a scotoma in the form of a light point developing into a zigzag half circle with a growing radius until the scotoma disappears at the borders of the visual field [39, 40]. Phenomena of colour and light experiences within the scotoma area have been reported [41, 42]. Usually, the scintillating scotoma is seen binocularly, and with both closed or open eyes [43]. The scintillating scotoma is generally characterized by a modulation of shape (from the center outwards to the borders of the visual field) and by a temporal modulation (e.g. flickering). An investigation of the rate of flicker perceived in such a scintillating scotoma in migraine [44] revealed a mean perceived scotoma frequency of 18 Hz, while the reported frequencies ranged from 3 to 42 Hz and the variability between different patients was larger than the within-patient variability over different migraine episodes. This finding is very well in agreement with evidence by Klimesch [45] showing large interindividual differences in the EEG frequency spectrum, especially in the individual alpha frequency range.

In psychoses most subjective visual experiences of the non-representational type are reported in toxically induced psychoses described in Section 1.1.2. In manic-depressive patients [46, 47] and in schizophrenic patients [48] the reported visual experiences are mainly representational hallucinations. In addition, only a very few of all patients with endogenous psychoses are subject to visual hallucinations, while acoustic hallucinations are far more frequent [47]. Visual hallucinations might also develop in cases of dementia [47], even though the different possible sources of dementia (e.g. degenerative processes, traumatic injuries of the brain, toxic influences, metabolic malfunction) make it difficult to estimate the true triggers of such hallucinations.

Other subjective visual experiences

Almost 200 years ago, Johannes Müller [49] reported diverse patterns of visual experiences occurring in the state of relaxation preceding sleep. Beginning with nonspecific appearances of light, these experiences developed into a variety of representational, but often unfamiliar figures. Müller reported that the appearance of the visual impressions is much facilitated by a general relaxation without any part of the body or brain being specifically aroused. In addition, the effects were especially likely to appear during a period of fast.

The phenomena of subjective visual experiences and hallucinations are also tightly linked to the effects of sensory deprivation [50, 51]. Surprisingly, the shapes of visual experiences found during sensory deprivation in an almost completely darkened room [52] corresponded to experiences found under toxic stimulation [26], in cases of cerebral pathology [34], migraine [42], or degenerative eye diseases [33]. However, a minimal sensory input seems to be necessary for the generation of subjective experiences under sensory deprivation: Vernon [53] showed a decreasing number of subjective visual experiences under complete visual sensory deprivation in a dark room.

A fascinating phenomenon of subjective perception is synaesthesia [54], which is defined as a perception in one sensory modality during the stimulation of another sensory modality [55], e.g. the perception of colour while listening to music. However, the relation of these perceptions to other subjective visual experiences described above remains obscure.

1.1.3 Magnetically and electrically induced subjective visual experiences

A multitude of recent studies has shown the reliable possibility to induce subjective visual experiences (phosphenes) by transcranial magnetic stimulation (TMS). Kammer et al. [56] reported and described phosphenes generated by single pulses of TMS. The phosphenes were reported to be white or grey, and to resemble clouds or bubbles, usually with a distinct contour. Generally, they were found in the lower part of the visual field. An increasing intensity of the magnetic stimulation increased not only the vividness of the impression, but also the size of the phosphenes. Kammer et al. strengthened the point that phosphene visibility might depend on the detection of the contours, thus large phosphenes with more peripheral contours being more difficult to detect. While in this study the observers were stimulated with single pulses of TMS, there are also investigations using short trains of magnetic stimuli [57] to induce subjective visual experiences. Although the functional origin of TMS induced visual experiences is yet unclear, Kammer et al. hypothesized that the phosphenes might reflect the excitatory effect of a TMS pulse, while the following inhibitory phase of cortical activity might be expressed by the observed transient scotoma.

The major part of the literature on magnetically induced subjective visual experiences describes the experience of rather shapeless, nonspecific impressions of light [13, 58, 59]. Thompson [60] reported a light blueish flicker over the entire visual field during magnetic stimulation. While most studies used 50 Hz stimulation, Magnusson and Stevens [61] found magnetic stimulation between 20 and 30 Hz to be optimal for the generation of subjective visual experiences.

A systematic study of magnetically induced phosphenes that were distinctively formed and specific was presented by Seidel et al. [62, 63]. The authors stimulated the heads of blind-folded participants with a square-wave magnetic stimulation in the frequency range between 10 and 60 Hz. The participants were asked to describe their impressions during the experimental session and to draw these impressions afterwards from memory. From this data it was possible to distinguish between 16 classes of shapes: lines, curves, circles, waves, radial patterns, multiple patterns, nonspecific forms and rays, gratings, points, unclassified shapes, poles, zigzags, rectangles, spirals, triangles, and winding shapes. Although the stimulating frequency was varied during the experiment, no direct relation between the observed shapes and the frequency was found. However, taking all different subjective experiences together, the optimal frequency of stimulation was found to lie between 10 and 50 Hz (however, the lower border of this range coincides with the lowest stimulation frequency; no evidence is therefore available for stimulation frequencies below 10 Hz from this study).

Early reports of electrically induced subjective visual experiences suffer from the same drawbacks as described for magnetic stimulation - mostly, the reported impressions are rather nonspecific flicker experiences (see for example [64, 65]).

Knoll and colleagues investigated geometric and specific subjective visual experiences induced by electric stimulation in great detail ([66, 67]; see also [13] for a review of this work). Similarly to the studies of Seidel et al. [62, 63] on magnetic stimulation, observers were blind-folded and presented with square-wave electric stimulation in the frequency range from 5 to 40 Hz. An electric current of 1 mA was administered at two electrodes fixed at the temples of the observer. Again, the experienced phenomena were verbally reported during and drawn after the experiment by the participants. Besides nonspecific flickering impressions, observers reported well-defined, mostly geometric patterns. Although more experiences were reported during electrical stimulation as compared to magnetic stimulation, the electrically induced experiences could be classified into the same 16 categories as described for the magnetically induced phosphenes. Mostly, the patterns were said to be light on a darker background, while colour impressions were only rarely reported. Although the appearance of electrically induced subjective visual experiences was related to specific frequency ranges (an experience usually had a lower frequency at which it appeared and an upper frequency at which it disappeared), no correlation between the stimulation frequency and the different types of experiences was found. While the experiences had to be reproducible within an experimental session to be assumed to be reliable, the authors also showed that in a given observer the same experiences could be induced by electric stimulation with similar frequencies during repeated experimental sessions over a longer period of time (up to 200 days). Interestingly, electrically induced as well as magnetically induced subjective experiences highly resemble the ones reported during meditation (see Section 1.1.1), toxic stimulation, induced by pressure on the eyes, or found in clinical and related settings (see Section 1.1.2).

Young [68] electrically stimulated the eye with sequences of electric pulses modulated in sign and magnitude. Stimuli consisted of only corneo-negative pulses (stimuli 1 and 3 in Figure 1.1) or a combination of corneo-positive and corneo-negative pulses (stimuli 2 and 4 in Figure 1.1), and stimuli differed in the phases of the maximum stimulus magnitude in terms of the number of pulses (stimulus 1 vs. 3 and stimulus 2 vs. 4). Interestingly, phase was shown to be a critical factor in the generation of subjective colour. However, this was only the case when a combination of positive and negative electric pulses was delivered to the eye. In the case of mixed positive and negative stimulation, an early stimulus maximum (stimulus 2) was related to seeing yellow, while a late stimulus maximum (stimulus 4) was related to seeing red (and partly blue). The experience of green was independent of the phase of the stimulus maximum. These results seem to suggest that temporal factors, and especially the phase information in the temporal stimulation sequence, are of relevance for the formation of electrically induced subjective colour.

1.2 Subjective visual experiences induced by visual stimulation

Subjective visual experiences may not only be brought about by electric or magnetic stimulation, but can also be produced by appropriately stimulating the visual system with temporally modulated light. One very early description of such optically induced subjective visual experiences dates back to Purkinje in 1819 [31]. Purkinje described the experience of colours and forms which followed waving his

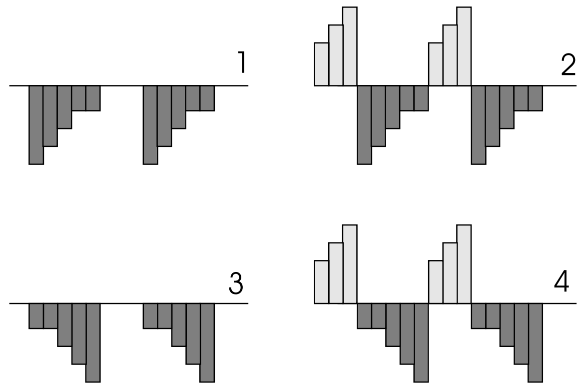


Figure 1.1: Example stimulus configurations of Young, reproduced after [68]. Time is plotted on the abscissa, the ordinate shows pulse counts per time bin. Light and dark grey bars represent positive and negative pulses, respectively. Further information is given in the text.

hand vigorously across his closed eyes while facing direct and bright sunlight.

In the following I will concentrate on three main types of stimulation regimes used to induce subjective visual experiences: (i) the so-called Benham disk, (ii) paradigms which seek to mimic certain stimulation characteristics of the Benham disk, and (iii) periodic stimulations of the entire visual field (ganzfeld). While subjective colours are the experiences investigated with the Benham disk and related paradigms, visual ganzfeld stimulations usually result in the experience of both, colours and forms.

The experiments described in the literature span a wide range of different stimulation regimes. However, a set of results corroborated by the different experiments may be summarized as follows: (i) Subjective experiences of colour and form can be evoked by temporally modulated visual stimuli. (ii) Subjective visual experiences are restricted to specific frequency ranges of stimulation. (iii) Subjective visual experiences are sensitive to differential changes of stimulus magnitude over time: shape or phase of the stimulation are critical. (iv) The actual features of the percepts depend on a number of stimulation parameters, such as luminance or wavelength of the stimulation, and spatial extension of the stimulation.

1.2.1 Benham's Top and Benham-like stimulation regimes

More than a hundred years ago, in 1894, Benham presented a method for the generation of an 'artificial spectrum' in *Nature* [69]. Although not being the first to present this mechanism (Fechner already in 1838 reported subjective colours generated by a spinning disk [70]), Benham's device, which was later called the Benham disk or Benham's top is the most well-known. It is depicted in Figure 1.2. When the disk, which is half black and half white and with additional black lines on the white part, is spun at a certain speed, the lines at different locations on the disk form rings that appear to the observer in different colours. Anticlockwise spinning of the top results in the outer rings to appear reddish, the middle rings greenish and the inner rings blueish. Interestingly, when the direction of spinning is reversed (i.e. into clockwise movement) the colours of the rings are also reversed (blue, green, red from the outer to the inner rings). Benham [69] argued that the perception of colour is related to the vibrations of light (i.e. light waves) of different periodicities (i.e. wavelength). He supposed that the different line configurations on the Benham disk stimulate the eye with different periodicities of light due to an interaction between the image and afterimage generated by the spinning disk, and therefore generate the 'artificial' perception of colours. The appearance of colours on the Benham disk is especially fascinating as one would expect the lines to form grey rings of equal brightness on the spinning disk. The spectral distribution of each of these rings is equal, and neither is there any difference in the average luminance of the rings. However, there is a large body of evidence of reliable, intra- and interindividually stable experiences of colours on the spinning Benham disk (see [71, 72] for reviews). There are also a number of theoretical approaches trying to explain the problem of subjective colours on the Benham disk, which will be further explained in Section 1.3.3.

Roelofs and Zeeman [73] investigated a number of interesting variations of the Benham disk in great detail (even though their reports remained at a purely de-

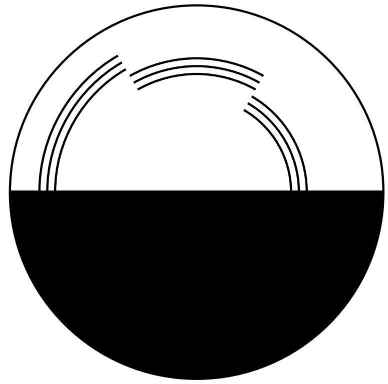


Figure 1.2: Example of a Benham-like disk, which is characterized by having a black and a white half and a number of lines in different sectors of the white part of the disk. When spun at frequencies between 5 and 10 Hz, the lines fuse and give the impression of coloured rings. Further details are given in the text.

scriptive and subjective level without any statistical justifications of the findings). They showed that the background colour of a Benham-like disk (which was a disk split up into four sectors and each sector being differentially coloured in black or white) is a critical factor for the experience of subjective colour. A black line in front of a white background (where the line is seen as the figure in a figure-ground configuration) yielded the percepts of blue, green, and purple; a white line against a black background resulted in the experience of red and yellow. This finding was taken to indicate that a dominance (i.e. being the figure) of either the light or dark parts of the stimulation generates different subjective colours. In addition, the authors showed that the perceived colour depends on the frequency of the light stimuli on the Benham disk. On a disk with white lines on a black background colours changed from white to yellow, red and grey with increasing frequency. In the reverse disk with black lines on a white background, the colour developed from black to purple, blue, green and grey with increasing frequency.

Roelofs and Zeeman also investigated the effects of differently coloured background illuminations on the experience of subjective colour [73, 74]. They reported the personal observation that a given background colour always induced subjective experiences of the complementary colour in a given ring on a Benham-like disk. However, these experiments did not investigate the effects of illumination colour on the perceived colours of different rings on the Benham disk. Recently, Vienot and Le Rohellec [75] showed that illuminating the Benham disk with light of different wavelengths leads to a shift of the sequence of colours between the rings of the disk. Vienot and Le Rohellec used a Benham disk with four single ring sectors instead of three triple ring sectors as in the traditional disk of Figure 1.2 and asked the observers to name the subjective colours. When illuminated with light of a wavelength of 534 nm, the sequence of colours from the outer to the inner rings was red, yellow, green, blue. At around 557 - 566 nm (depending on the ring concerned) a reversal in subjective colours occurred and manifested itself more or less as the sequence blue, green, yellow, red.

The experience of subjective colours was shown to depend not only on the wavelength, but also on the level of illumination [76]. Additionally, an interaction between frequency and illumination can be observed: at lower levels of illumination the optimal stimulation frequency range is lower [71].

The optimal frequency of stimulation with the Benham disk or related paradigms was shown to lie between 5 and 10 Hz [71], the colour impressions being most vivid at these frequencies.

Subjective colours have also been observed when the different parts of the Benham disk are presented as stationary patterns with appropriate temporal modulations [77, 78]. In this context, Festinger et al. [77] stressed the role of temporal factors for the generation of subjective colours and developed a stimulation regime which allowed the quasi non-spatial representation of Benham-like stimuli. They used a spatially static (i.e. non-moving) stimulus consisting of a three bar grating displayed on a background. Critically, the illumination was experimentally varied over time in both the test bars, which were supposed to show the subjective colours, and in the background. The changes of illumination in the test bars were constructed such that they mimicked the changes of illumination on the retina

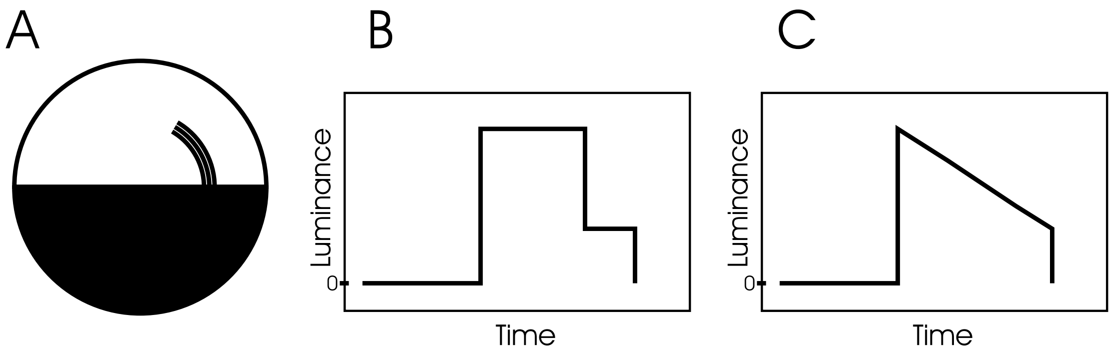


Figure 1.3: Different methods of stimulation for obtaining the subjective experience of the colour blue. (A) Benham disk [69]. (B) Time-luminance plot of the spatially stationary, but temporally modulated stimulation with flickering background used in [77, 78]. (C) Time-luminance plot of a smooth luminance modulation over time used to mimic the physiological response [77].

when stimulated with a Benham disk. Simulating the retinal stimulation for the subjective colour blue would for example consist of a 150 ms stimulus which is composed of 75 ms dark (representing the black half of the disk), 50 ms of full illumination magnitude (white part of the disk without lines), followed by 25 ms of intermediate illumination magnitude (the outer black lines on the white part of the disk, see Figure 1.3 (A) and (B)). With a dark or steadily illuminated background little or no subjective colours were observed independently from the Benham-like modulations in the test bars. However, when the background was made to flicker in a square wave and the test bars were modulated in simulation of a Benham disk the appropriate subjective colours were induced. These findings are in agreement with the work of Young [68] (see Section 1.1.3), who showed that electrically induced subjective colours are tightly related to the phase of the stimulation maximum. Young [68] related early and late stimulation maxima to the experience of yellow and red/blue, respectively. Using optical stimulation [77], early maxima seemed to generate experiences of blue, while late maxima induced experiences of red. Although both studies show qualitative evidence for phase-sensitive mechanisms, the drastic differences in the quantitative results (i.e.

phase-colour relations) demand further investigations.

Festinger at al. investigated the subjective colours induced by their stimulation at a single frequency, 7 Hz. Jarvis [78] tested a whole range of frequencies between 1 and 32 Hz with a similar stimulation and measured the purity (i.e. saturation) of the experienced colours, which were adjusted by the observers on a colourimeter. The perceived colours (red, green, and blue) were confined to narrow dominant wavelength bands and showed a very low intraindividual and interindividual variability. The dominant wavelength for the different colours varied between 587 - 594 nm (red), 582 - 584 nm (green) and 573 - 579 nm (complementary wavelength, purple/blue) for four different observers. For red, the maximum saturation occurred at about 6 Hz, and vivid colour impressions were confined to the frequency band of 4 - 14 Hz. Similar conclusions were drawn for the perception of green for three out of four observers, while the fourth participant perceived a saturated green even at higher stimulation frequencies. The subjective perception of blue was relatively unsaturated for all observers over the entire frequency range. Another experiment by Jarvis [78] varied the temporal relation between the background flicker (of a 75 ms period) and a short 15 ms pulse in the test bars. When the test pulse occurs near the onset of the background illumination, blue is obtained; whereas a test pulse temporally near the background offset results in the perception of red. This, as well as the fact that green is seen with pulses temporally in the middle of the background pulse, is in very good agreement with the finding obtained using standard Benham disks. Most interestingly, dichoptic viewing conditions, in which the test bars and the background were presented to different eyes and were fused by the observer did not result in the experience of subjective colour. This finding suggests that subjective (Benham) colours are generated in the visual system well before binocular fusion occurs (for further discussion of this problem see Section 1.3.3).

Festinger et al.[77] were puzzled by their finding that a background modulation was necessary for the experience of subjective colours in their study. They suggested to construct stimuli which perfectly mimic the physiological response to the two-partite stimulation with its inherent interactions [77]. Instead of using stepwise luminance modulation functions, as in the first experiments described above, the stimuli were constructed from ramped luminance on- and offsets with similar overall shapes as with stepwise stimulation (see Figure 1.3 (B) and (C)). As the physiological effect of the background flicker was supposed to be integrated into the test bar signal, no background modulation was applied. Nevertheless a constant illumination of the background was shown to be necessary for obtaining subjective colour. Using these 'physiologically meaningful' stimuli, which were supposed to circumvent and at the same time simulate the first visual processing stages, Festinger et al. [77] reliably produced the experience of subjective colours. However, it has to be noted that these findings could not be replicated by Jarvis [78], who attributed the effects of Festinger et al. to possible artifacts of the technical apparatus used.

The facts that the experience of Benham colours is restricted to optimal frequency ranges of stimulation, that the sequence of colours changes with reversal of the spinning direction, and that for the experience of subjective colours the movement of the stimuli on the retina as present in the Benham disk is not necessary, suggest a crucial role of temporal parameters for the generation of Benham subjective colours. These ideas will be investigated in further detail in Section 1.3.3, where attempts to explain the generation of subjective visual experiences will be examined.

1.2.2 Stimulation of the visual ganzfeld

The common ground of all studies presented in Section 1.2.1 is the presentation of luminance modulated stimuli to a small part of the visual field. However, early studies such as by Purkinje [31] showed that subjective experiences may also be induced by a temporally modulated stimulation of the whole visual field, the so-called ganzfeld. Interestingly, the subjective experiences in these stimulation regimes are not restricted to the experience of colour as in the Benham-like paradigms, but also extend to the experience of form and geometric pattern.

In a series of publications, Smythies [79, 80, 81] described the effects of stroboscopic ganzfeld stimulation on the experience of subjective experiences. In contrast to square-wave or sinusoidal flicker stimulations with equally long bright and dark periods, a stroboscopic light is characterized by a series of short luminance pulses separated by longer intervals of darkness. In a series of control experiments [81] Smythies verified that the waveform of the stimulation (i.e. stroboscopic, square-wave with a 1:3 period, or sine wave) did not have any substantial influence on the observed subjective experiences. In the studies of Smythies, participants were stimulated with a stroboscopic light filling the entire visual field at rates of 6, 12, or 18 Hz with binocular or monocular view of the stimulus. Smythies distinguished a number of different effects while viewing this stimulation: (i) effects of the dark phase [79], (ii) effects of the bright phase and afterimages [80], and (iii) further effects [81]. Under monocular (and only under monocular) viewing conditions, two states of subjective experiences were reported, which alternated in a way comparable to binocular rivalry. The idea was that one state (the bright phase) is related to activity from the stimulated (bright) eye, while the other state (the dark phase) represents effects generated by activity in the non-stimulated (dark) eye. The bright phase patterns were predominantly geometrical and flickered whereas the dark phase patterns mostly showed no geometrical forms and never flickered. Dark phase pattern were described in detail in [79], but shall not be further developed here as they never occurred during binocular stimulation as investigated in the studies of this thesis. Bright phase patterns have been observed during monocular as well as during binocular stimulation [80]. For reasons mentioned above, we will concentrate on effects obtained during a binocular stimulation preceded by a period of binocular non-stimulation (i.e. dark adaptation). The reports of a given participant tended to remain constant for that participant for years, even though some amount of interindividual variation was observed. Unfortunately, in the paper of Smythies [80] no clear distinction between monocular and binocular patterns was undertaken (although it was stated that binocularly more patterns were reported), but among the patterns occurring at binocular stroboscopic stimulation were circles, grids and checker-boards, cobwebs, wheels and flowers, mosaics, clovers, pattern of squares, central vortices and spots, suns, stars and radiation patterns, spirals, diffraction patterns, mazes, chains, herring-bone patterns, diamonds, and honeycombs. The patterns were classified into the following groups: unformed elements (i.e. blobs, dots), single lines, patterns of parallel straight lines, patterns of radially arranged straight lines, complex patterns based on straight lines (i.e. honeycomb), patterns of curved lines, designs and formed images. Smythies [80] stressed the fact that only very rarely patterns were composed of straight and curved lines as connected elements, these two configurations seemed to exclude their mutual appearance. During a given stimulation epoch patterns could change into another by continuous transformation, a sudden change, breaking up of the first pattern and formation of the next out of these broken elements, or intervened periods of no pattern between the two patterns. The colours of the observed patterns varied widely between subjects. While some observers reported only achromatic colours, others saw pastel shades and others again brilliant and saturated colours. The amount of experiences depended on the colour and luminance of the stimulation, white light and brighter stimulation being more effective than red light and less bright stimulation. An influence of stimulation frequency on the generation of subjective experiences was found: more patterns were described for 12 or 18 Hz than for stimulation at 6 Hz. In addition, with increasing frequency the reported patterns became finer and made up of smaller elements.

Piggins et al. [82] aimed to identify the frequency ranges of stroboscopic binocular stimulation in which subjective experiences of colour, saturated colour, and pattern appeared. Colours were reported between 3.99 and 15.69 Hz (mean frequency of experience onset and offset for 16 observers), saturated colours were found between 8.72 and 11.62 Hz and patterns appeared between 3.52 and 17.26 Hz of stimulation frequency. When looking at the minimum and maximum frequency at which experiences could be induced, colours were found between 1 and 24.7 Hz, saturated colours between 5 and 17 Hz, and patterns between 1 and 40 Hz. That is, the frequency range at which patterns could be elicited was larger than the effective frequency ranges for colour or saturated colour. Piggins et al. [82] classified the observed patterns into the categories given by Smythies [79] for dark phase patterns. Dark phase patterns can only be observed during monocular stimulation [79], whereas the stimulation in the study by Piggins et al. was described as being binocular. Smythies in [79] and [80] clearly stated the differences between dark and bright phase patterns; ideally the patterns observed by Piggins et al. should have been classified into the categories given by Smythies in [80] for bright phase patterns. Hence, unfortunately, the classification of subjective patterns given by Piggins et al. in [82] can hardly be interpreted in a meaningful way.

The influence of the degree of illumination on subjective experiences was demonstrated by Knoll and Welpe ([83], cited in [13]). The observers were stimulated with a ganzfeld of flickering light, characterized by a temporal ratio of light to dark periods of 1:4. A low illumination ($< 30cd/m^2$) generated subjective visual experiences highly similar to the ones found during electrical stimulation [62, 63]. The observed experiences were mostly simple geometric forms, which were classified into 20 categories, 12 of which were equivalent to the categories formed for electrically induced visual experiences. A very high brightness of the stimulation ($> 3000cd/m^2$) induced a variety of highly differentiated visual experiences, which usually were only observed under toxic stimulation [28]. The subjective visual patterns were described to be formed on a bright background and could be brighter or darker than the background. The stimulation frequency range optimal for the generation of subjective visual experiences was shown to lie between 5 and 30 Hz, while higher stimulation frequencies resulted in the perception of constant light. The range of frequencies which was appropriate for inducing a certain visual experience was usually larger for optic stimulation than for electric stimulation [13].

More recently, during an electroencephalographic (EEG) study of the cortical response to square-wave modulated flickering light, Herrmann [84] observed that most of his participants reported forms (stars or stripes) and colours (blue, red, or purple) at stimulation frequencies around 10 - 15 Hz. From a reexamination of Hermann's data, Herrmann and Elliott [85] described a range of colour (red, blue, and purple) and form (lines, honeycombs, tunnels) experiences which appeared to be confined to certain ranges of flicker frequencies within approximately the lower 40% of 1 - 100 Hz stimulation frequencies examined by Herrmann [84]. Reports of colour were approximately normally distributed around the stimulation frequency of 12 Hz with the frequency range covered by one standard deviation around this mean being 6.75 to 16.6 Hz. Subjective forms were observed with stimulation frequencies between 5 and 39 Hz, the center of this distribution lying at 22 Hz.

In another electroencephalographic study, Shevelev et al. [86] reported subjective visual experiences when observers were presented with stroboscopic luminance stimulations through closed eye lids in their individual alpha frequency range. Shevelev et al. tested not only the individual dominant frequency in the alpha range, but also adjacent frequencies up to 5 Hz around the individual alpha frequency. Observers reported seeing subjective rings and circles (35.4% of all reports), spirals (33.9%), and grids (26.8%). The optimal frequency to obtain these experiences was correlated ($r = 0.86$) with the dominant alpha-rhythm frequency with rings and spirals most frequently appearing at this frequency, and grids being related to frequencies 1 Hz below or above this individual dominant frequency. Shevelev et al. [86] compared the generation of subjective experiences in this study where the stroboscopic stimulation was synchronized with the individual alpha frequency with a study without synchronization of flashes with the individual alpha rhythm [87]. Very interestingly, both stimulation regimes induced the same subjective experiences. However, with synchronized presentation the subjective experiences appeared already 2 - 5 seconds following stimulation onset, compared to 10 - 15 seconds until subjective experiences developed in non-synchronized stimulation. Registering the EEG activity on the scalp, Shevelev et al. [86] observed typical trajectories of travelling EEG alpha-waves. This led them to argue that the observed subjective form experiences are a conscious experience of the spreading waves of activity scanning and reading information on the visual cortex.

1.3 Physiological mechanisms of visual perception related to subjective experiences

Sections 1.1 and 1.2 aimed to give an overview of existing reports of subjective visual experiences appearing under a variety of circumstances. The objective of this section is to introduce mechanisms of colour and form perception which might be related to the apperception of subjective visual experiences described above. In addition, existing theoretical models attempting to explain subjective visual experiences will be discussed.

1.3.1 Mechanisms of colour perception

The perception of colour very strongly depends on the interaction of our nervous system with the physical properties of the external world. Colours do not exist in the environment, but it is the qualities of the external objects such as reflectance and absorbance of light that in interaction with the specific properties of the visual system of the observer determine the perceived colour. Therefore, with identical physical stimulation the perceived colour may differ for observers with different properties of the visual system. Revealing examples of this fact are observers suffering from a colour deficiency. Dichromats with a protanopia or deuteranopia are missing certain visual pigments and therefore fail to perceive the colours red and green [88], although the physical stimulation meeting their retinae is equivalent to the stimulation of a colour normal observer.

To understand colour vision it is necessary to have some knowledge about the physical properties of light. Light consists of small units, the photons, which behave like particles in some respect or like waves in others. For colour perception the wave behaviour of the photons is most important. A photon is a packet of electromagnetic energy which may be characterized by the wavelength of its vibration. The photons which our visual system is able to process stem from only a small portion of the entire electromagnetic spectrum: the visible spectrum covers wavelength from about 400 nanometers (nm) to 700 nm. Monochromatic light contains only one wavelength, but usually light is polychromatic and composed of a band of wavelengths [2].

The light hitting the retina is recorded by the retinal receptors, rods and cones, and is transformed into neuronal signals. In simplification, these signals are then transmitted via retinal ganglion cells (see [89] for an extensive review on colour coding in the retina) to the lateral geniculate nucleus (LGN) in the thalamus [90] and the primary visual cortex (V1). Following V1, information is transmitted to area V2 and higher cortical areas. The existence of two separate higher cortical visual systems has been suggested by Ungerleider and Mishkin [91]. The ventral stream, comprising parts of area V2, area V4, and the inferotemporal cortex (IT) is thought to be the 'What' path of the visual nervous system processing object form, size, and colour. The dorsal stream, or 'Where' path, comprising areas V3, MT, and MST is attributed to the processing of object location and motion.

In the following, two basic theories of colour perception, which seem contradictory at first inspection, but have been shown to complement each other, and their physiological bases will be discussed.

The trichromatic theory of colour vision was proposed by Thomas Young [92] and Hermann von Helmholtz [93] following the discovery that people with normal colour vision need at least three lights of different wavelengths to match any given wavelength. The theory proposed that colour perception is based on three receptor mechanisms with different spectral sensitivities. Light of a given wavelength would stimulate these three receptor mechanisms to a different degree, and this specific pattern of activities leads to the perception of a colour [2, 88]. The trichromatic theory can be verified at a physiological level, where the existence of three types of cones with different absorption spectra has been demonstrated [94]. The peaks of activity of these cone types are found at around 440 nm (short wavelength, S-cones), 530 nm (middle wavelength, M-cones) and 560 nm (long wavelength, L-cones) [95]. Even though the proportions of the three cone photoreceptors vary largely between individuals, these variations do not seem to affect proper colour vision [96].

The opponent process theory of colour vision was suggested by Ewald Hering [97] based on his observation on colour afterimages and colour deficiencies. The theory states that the perception of colour is caused by opposing responses generated by blue and yellow and by red and green, and by an additional mechanism for black and white. Physiological evidence for the opponent process theory comes from findings of opponent neurons in the retina and the lateral geniculate nucleus (LGN). DeValois and Jacobs [98, 99] found different types of cells in the monkey's lateral geniculate nucleus. B+Y- cells increased and decreased their firing rates under stimulation of 450 nm (blue) or 580 nm (yellow), respectively. Accordingly, Y+B- and G+R- (firing rate increase at 510 nm (green) and decrease at 660 nm (red)) and R+G- cells were found, as well as Wh+Bl- and Bl+Wh- cells responding differentially to the presence and absence of light.

While in the 19th century these two theories of colour vision were thought to be contradictory, it became clear later that they both represent features of the visual colour system in a valid manner. However, they apply to different stages of visual processing. Trichromacy holds for the receptor stage of visual processing, whereas opponent neurons play a role later in the visual system [88]. Most reports of opponent cells exist for the LGN (for example, [98]), but opponent response patterns have also been found in bipolar and ganglion cells of the retina [2]. The information represented in the opponent cells can be calculated from patterns of excitatory and inhibitory interactions of the three cone types. For example, a R+G- opponent cell receives excitatory and inhibitory input from L-cones (red) and M-cones (green), respectively. A B+Y- cell however, is excited by S-cone (blue) activity and inhibited by activity from a cell that sums excitatory inputs from M- (green) and L-cones (red), thus representing the colour yellow [2, 88, 100].

The information of the three opponent channels is transmitted from the retina to the LGN and further to the cortical area V1 in anatomically distinct pathways [90, 101, 102]: the magnocellular layers are sensitive to luminance (the L+M information), cells in the parvocellular layers to red-green (L-M) information and cells in the koniocellular layers to blue-yellow (S-(L+M)) information.

Most ganglion cells in the retina show a center-surround organization which is accomplished by mechanisms of lateral inhibition [2]. For example, a ganglion cell with a receptive field with excitatory center and inhibitory surround organization will best respond when the excitatory center is stimulated with light and the inhibitory surround remains dark. When the whole receptive field is stimulated by light, the inhibitory effects from the surround will suppress the excitatory responses of the center. Similarly, colour coding ganglion cells may be equipped with a receptive field of center-surround organization, with for example an excitatory response to red in the center and an inhibitory response to green in the surround. This ganglion cell would be best stimulated by a small red spot, while any larger stimulus containing light of a medium wavelength (green) would inhibit the cell [103]. Interestingly, and related to colour vision, double opponent cells were found in the primary visual cortex [104] and V2 [105]. These cells do not only have a spatially opponent center-surround organization, but also a chromatically opponent structure. The centers and surrounds both have opponent colour coding with the surround colours being opponent to the center colours. For example, a red/green double opponent cell might be excitatory to red and inhibitory to green in the center, and excitatory to green and inhibitory to red in the surround, or vice versa [2].

The processing of colour in the cortex seems to be less clear. The existence of patients with cortical colour blindness who are perfectly able to perceive form and movement with good visual acuity have led to the idea of a specialized colour center in the brain [106, 107]. However, neurons responding to wavelength and colour or showing colour opponent responses have been found in many areas of the cortex. About 50% of the neurons in the early visual areas V1 to V4 are known to be colour selective cells [90, 102]. Findings of colour selective cells and colour coding mechanisms from area V1 [104], V2 [105, 108], and V4 [109] suggest that colour processing might be a distributed process in the entire ventral processing stream [88]. However, colour selective cells were even found in area V3 of the macaque monkey [110] and in area MT [111], which is inconsistent with the functional ventral-dorsal segregation. Interestingly, while most cells in the LGN are tuned to stimuli along the cardinal red-green and yellow-blue axes [112], cortical colour cells can have preferences to far many other hues [105, 113], suggesting that at this stage information from the different colour coding streams has been integrated to represent the natural diversity of colours [102]. Additionally, rather than being restricted to responding to colour, colour selective cells in the cortex have also been shown to be responsive to specific forms and orientations [113, 114, 115].

Little is known so far about the temporal characteristics of colour vision. However, in relation to flicker-induced subjective colours, these temporal aspects of the visual colour coding system are especially important. Fiorentini et al. [116] investigated the temporal characteristics of luminance and colour mechanisms and found chromatic processing to be more sustained than the processing of luminance. Basically, these results may be explained by the different processing streams of the visual system. Luminance information is mainly transmitted via the magnocellular (i.e. the fast) pathway, while chromatic information travels along the parvocellular and koniocellular pathways, which are known to show slower transmission rates. While Fiorentini et al. did not consider the two different chromatic systems, Cottaris and De Valois [117] later showed that indeed there are temporal processing differences between the different colour mechanisms. Single cell recordings in the macaque area V1 aimed to investigate the temporal delays with which information is transmitted from the retina to the cortex. A substantial temporal difference was found between the L/M-opponent inputs, signalling about 68 - 95 ms after stimulation and the S-opponent inputs, signalling only after 96 - 135 ms. It is known that only about 8% of the cones in the retina are S-cones [94, 96]. Cottaris and De Valois propose that these sparse S-cone signals are amplified in area V1, possibly through recurrent excitatory networks, resulting in a delayed and sluggish S-cone signal. A psychophysical investigation of processing latencies for the different chromatic subsystems [118] demonstrated the temporal difference between the L/M-opponent and the S-opponent system to vary between subjects and to be at most 20 - 30 ms. Although the authors claim a difference between their results and Cottaris and De Valois's findings, the results are rather well in accordance. The single cell recordings were only attributed to two classes of temporal latencies. Even though the maximal difference between the two classes was large (from 68 ms to 135 ms), a mean difference between the two classes can be assumed to lie around 30 ms (but no statistical evaluation of this kind was given in [117]). Evidence for a slower S-cone system also comes from a reaction time (RT) study by McKeefry et al. [119]. Simple RTs generated in response to S-cone isolating stimuli were longest, whereas the shortest RTs were generated by (L-M)-cone isolating stimuli. Similarly to studies above, the authors concluded that the visual system has a faster processing capability for information encoded by the (L-M) system than that encoded by the S-(L+M) system. In addition, using chromatic stimuli intermediate to the cardinal chromatic axes allowed them to conclude that the response time differentiation is best at the cardinal axes (i.e. red-green, blue-yellow) of chromatic space. The known temporal characteristics can therefore be summarized as follows: (i) luminance information is encoded faster than chromatic information and (ii) the L/M-opponent colour system exhibits faster processing than the S-opponent system in both physiological and psychophysical investigations.

1.3.2 Mechanisms of form perception

The perception of shape, pattern or form is based on the same processing streams as outlined above for the perception of colour: the light meeting the retina is transmitted via retinal ganglion cells to the LGN and the cortex [103].

A spatially structured stimulus, for example a black square on a white background, stimulates the different parts of the retina differentially according to its light reflectance properties. Interestingly, these differential patterns of stimulation persist over the different stages of visual processing and are evident as so-called retinotopic maps in the LGN and the cortex. Retinotopy means that each location in the LGN or cortex corresponds to a location on the retina with preservation of neighboring relations [2, 88].

Naturally, the center-surround organization and the process of lateral inhibition at the level of retinal ganglion cells is critical for the perception of form [2, 103]. For example, an on-center/off-surround ganglion cell would respond best to a spatially distinct small spot of light with the size of its on-center, while any smaller or larger stimulus would only exhibit relatively low responses of this cell.

As for colour, a distinction between different pathways from the retina to the LGN and the cortex exists for the perception of form. Fine textures and pattern with high spatial frequency are mainly transmitted via the parvocellular pathway, which has been shown to carry chromatic signals [90]. The magnocellular pathway, on the other hand, is more suitable for the transmission of motion information and signals with high temporal resolution [88]. Additionally, receptive field size differentiates between these two pathways: parvocellular receptive fields are smaller than magnocellular ones [2].

In the striate cortex (V1) neurons specialized to specific features of visual stimuli, such as orientation, movement and size are found [2, 88, 103]. Hubel and Wiesel [120] distinguished three types of neurons based on the stimuli to which the neurons responded best: (i) simple cortical cells, (ii) complex cortical cells, and (iii) end-stopped cells. (i) Simple cells have excitatory and inhibitory areas, which are arranged in a side-by-side manner and make these cells to respond best to bars of light with a particular orientation. While each cell shows a more or less sharp tuning to a specific orientation, different cells are tuned to the different possible orientations [88]. (ii) Complex cells respond best when a light bar with a particular orientation is moving across their receptive field. Many complex cells also respond best to certain directions of movement. (iii) End-stopped cells, finally, respond best to moving lines of a specific length or to moving corners and angles.

The primary visual cortex (V1) is not only retinotopically organized, but exhibits a general columnar organization [88, 103] of the cells discovered by Hubel and Wiesel [120]. V1 is composed of columns of neurons processing similar features of a visual stimulus. The largest organizational unit is the hypercolumn, which is equivalent to a location column relating to a specific retinal location. The location column consists of two types of right and left ocular dominance columns coding the preferential responses to one of the eyes. These ocular dominance columns again are composed of a set of orientation columns for orientations from 0 to 180 degrees.

In humans the processing of orientation does not work equally well for all possible orientations: humans are more sensitive to horizontally and vertically oriented gratings than to other oblique orientations [121]. This effect directly relates to the number of neurons coding different orientations in the brain. In the macaque visual cortex the majority of cells have been found to be horizontal and vertical coding cells [122].

Another important feature of visual stimuli besides orientation and size is the spatial frequency, that is the density of elements making up the stimulus [2, 88, 103]. Using physiological [123] as well as psychophysical [124] studies, the existence of spatial frequency analyzers, i.e. cells tuned to respond to a specific spatial frequency, have been revealed in area V1.

When considering form information processing in higher cortical areas, the distinction between ventral and dorsal pathways becomes again critical [88, 91]. While the dorsal or 'Where' pathway codes information about the stimulus location, the ventral or 'What' pathway is assumed to code the features of the object, such as form, size, and colour. Importantly, the two pathways are not entirely separate, but a number of cross-connections between the cortical areas comprised by them have been established [88, 125].

Of special relevance to the problem of form processing is the inferotemporal cortex (IT) in the ventral processing stream. Tanaka and colleagues [126, 127] differentiated primary and elaborate cells in IT. While primary cells responded best to fairly simple stimuli, such as slits, spots, ellipses, and squares, the elaborate cells responded to more complex stimuli, such as specific forms or forms combined with a colour or texture [128]. Tanaka proposed that a complex form stimulates a number of neurons sensitive to specific form features and that perception of a particular form arises from the combination of the information of all stimulated cells [88].

A variety of further higher level processing mechanisms are concerned with the perception of real objects [2, 88, 103]. Among these are attentional mechanisms, mechanisms of gestalt perception, and binding mechanisms. Although these processes are of indispensable importance for the perception of real objects and scenes, they will not be discussed in detail here, as their relevance to the perception of subjective form seems limited.

1.3.3 Physiological models of subjective visual experiences

In the following, I will present theoretical approaches that have been developed to explain the subjective visual phenomena described in Section 1.1. The majority of these models concerns the generation of subjective colour on the Benham disk or with Benham-like stimulations. In addition, some theoretical attempts to explain the generation of pattern in ganzfeld stimulation with stroboscopic light will be outlined.

The first attempt to explain subjective colours as seen on a rotating black-and-white disk was possibly by Fechner [70]. Fechner supposed that the perception of white light depends on a number of different receptor in the eye, and that each of these receptor types has a different rate of fall (i.e. time constant) in its activation. The red process was assumed to be the fastest, and the blue process to be the slowest. These different time constants were assumed to be the basis for the experience of the different colours on the rotating disk [72].

Benham [69] followed a more physical theory of colour perception to understand the generation of subjective colours with his disk. He proposed that light vibrates and that the visual system responds to these vibrations with internal vibrations of three different degrees that generate the perception of the primary colours red, green, and violet. Due to afterimages of the black half of the disk and the lines on the white sector, rotation of the disk changes the number of vibrations per second of the white light (i.e. the wavelength). That means that white light reflected by the Benham disk somehow contains modified wavelengths, therefore stimulating the visual system differentially and inducing the experience of colours corresponding to these specific wavelengths.

Although fascinating, these two theories of subjective colours are not satisfying when one takes into account the physiological knowledge about the visual system accumulated in the last century. Therefore, some modern and more promising approaches of explaining subjective colour will be outlined next.

Von Campenhausen and colleagues (see [71] for a review) suggested that subjective colours are based on phase-sensitive lateral interactions of modulated neural activity in the retina followed by additional spatial interactions in the visual cortex behind the locus of binocular fusion. Of special importance for this concept is the existence of spatially adjacent parts on the disk that show a temporally different behaviour of stimulation. The stimulation of each of the rings of the Benham disk stands in a specific relation to the background modulation (i.e. the half black, half white configuration) of the disk. On the standard Benham disk as depicted in Figure 1.2 the length of the black lines relative to the disk diameter at their position is the same. What differs for the different lines is their phase relation to the background black-white modulation. While the onset of light of the inner ring (blue) coincides with the onset of the background light, the light offset of the outer ring (red) occurs at the same time as the light offset of the background. Von Campenhausen et al. [71] suggested that there are lateral interactions connecting the parts of the retina which are differentially stimulated by the rings and by the background. In addition, and most important, these lateral interactions seem to be sensitive to the phase of activation of its two interacting parts. Based on experiments using stimulation with binocular fusion [129], it was concluded that no brain loci behind the sites of binocular fusion are involved in the generation of subjective colour. Phase-sensitive lateral interactions were thought to reside at the retinal level and at parts of the brain where visual information is retinotopically coded.

Phase relations between the different parts of the stimulation have also been suggested of importance by a number of other groups investigating subjective colour with optical or electrical stimulation [68, 78].

The exact role of of the lateral inhibitory processes suggested by von Campenhausen et al. [71] are unclear. Festinger et al. [77] tried to integrate the mechanisms of lateral inhibition into a more general model of subjective colour. They proposed that the stimulation with a Benham-disk in some way mimics the activity the the visual nervous system in response to light of different wavelengths (i.e. different ‘real’ colours). In a series of experiments they were able to show that the temporal code delivered by the rings of the Benham-disk alone is not sufficient to induce the experience of subjective colours. In contrast, a spatially adjacent stimulus modulation similar to the background modulation of the Benham disk was always necessary for the experience of subjective colours. Lateral inhibition due to the additional background stimulation was thought to change the neural activation induced by the rings in a way which mimicked the neural code in response to ‘real’ colour stimuli. By modelling the effect of lateral inhibition of the background on the rings, Festinger et al. designed stimuli which were assumed to approximate this neural code more directly (see Figure 1.3 (C)). Most interestingly, with these stimuli it was possible to induce subjective colours without the necessity of additional background modulation [77]. However, it has to be noted that these findings could not be replicated by Jarvis [78], which was later attributed to differences in contrast in both studies [130].

The novel stimuli with a stimulus amplitude modulation over time (Figure 1.3 (C)) suggested by Festinger et al. [77] were later used as the basis for a physiologically motivated model of subjective colours [130]. Courtney and Buchsbaum [130] based their model on the temporal differences of processing between the different colour pathways. They derived the impulse response functions and nonlinearities of the three most common wavelength selective on-center parvocellular ganglion cell types (L+M-, M+L-, and S+(L+M)-) from physiological data. A nonlinearity of the S+(L+M)- cells was taken into account as well as the different temporal characteristics of the cell types. Following a study of Schnapf et al. [131] the temporal properties of the M, L, and S-cones were determined (the M-cones being the fastest to peak (51 ms) and to have the shortest integration time (19 ms), followed by the L-cones (55 ms, 28 ms), and S-cones (61 ms, 34 ms)). The model demonstrated that the Festinger stimuli can create an imbalance in the responses of the different colour pathways when they are integrated over time.

In relation to the activation induced by a neutral stimulus, the Festinger stimuli clearly generated a response benefit for the appropriate colour-coding ganglion cell.

The input stimuli fed into the model of Courtney and Buchsbaum [130] did not directly correspond to the stimulation of a Benham-disk, but were the outcome of a theoretical interaction of the Benham-like stimulus with the first stages of the visual system [77]. Grunfeld and Spitzer [132] developed a model which is able to simulate the appropriate neural response to actual Benham-like stimulations. For this purpose the authors include spatial as well as temporal parameters of the spatially- and cone-opponent ganglion cells (L+M-, M+L-, and S-(L+M)) into their model. Besides the temporal parameters outlined for the Courtney and Buchsbaum model, the authors suggest the relevance of a so-called rebound response. The rebound response is a common excitatory response to the turning-off of an inhibitory stimulus. Related to the three types of ganglion cells the following pattern of responses to the Benham-disk were outlined: when the whole receptive field is stimulated with a diffuse black stimulation (black half of the disk), none of the ganglion cells changes its spontaneous activity. During white illumination, the L+M- and M+L- cells are excited due to the larger weight of their receptive fields' center regions. In contrast, S-(L+M) cells are inhibited due to the same imbalance in centre-surround mechanisms. When one of the rings of the Benham disk meets the center of the ganglion cell receptive fields, M+L- and L+M- cells are inhibited by the illuminated surround and S-(L+M) cells are excited by the illuminated surround. Altogether these patterns of inhibition and excitation, together with the assumed rebound response to turned-off inhibition, allowed Grunfeld and Spitzer to appropriately model the activity of the different ganglion cell types to corresponding Benham-like stimuli.

The theoretical approaches set out so far were all concerned with the experience of subjective colours during stimulation with a Benham disk or Benham-like stimulation. As has been detailed in Section 1.2.2, visual subjective appearances can also be brought about by appropriate stimulation of the visual ganzfeld. Only a very few approaches to explain these effects exist and shall be described in the following.

In the last paper of his series of publications on stroboscopic patterns [81], Smythies listed different hypotheses that might account for the perception of pattern and form during intermittent illumination. (i) A first hypothesis assumed that the observed patterns represent visualized retinal structures. However, the motion which is often observed in relation to the pattern makes this hypothesis quite improbable. Smythies mentioned two physiological factor that might determine the perception of subjective form. The fact that foveal neurons have shorter conduction latencies than peripheral neurons might lead to an intermittent light being represented by a series of expanding concentric circles. Further, the differential organization of the retina in terms of the number and relative proportion of rods and cones might explain subjective patterns observed under intermittent illumination. (ii) The second hypothesis stated that the stroboscopic patterns are interference phenomena produced in a scanning mechanisms attempting to deal with an intermittent signal. The form of such interference phenomena would always be related to the specific form of the scanning mechanism: linear scans might result in straight lines, a polar scan would give curved lines, and a radial scan radially arranged lines. Support for this hypothesis also comes from recent electrophysiological investigations [86] equating travelling alpha-waves of the EEG with visual impressions of circles, spirals and grids. However, the possibility of explaining the entire variety and complexity of subjective forms by these mechanisms seems limited. (iii) The third hypothesis developed by Smythies assumed that during intermittent visual stimulation the brain is presented with some totally unfamiliar kind of information and therefore starts building hypotheses of what this activity might actually represent. The testing and discarding of these hypotheses would be represented by the various different patterns following each other. While this idea seems valid and might prove to be a good general framework of brain functioning, it is far too unspecific to give any detailed ideas about the generation of subjective pattern and form. (iv) The fourth hypothesis adopts the perspective that the stroboscopic patterns represent a formation of corresponding domains among retinal and cortical neurons, that is the concurrent activation of neurons coding specific stimulus features. Smythies suggested that the successive waves of excitations induced by the intermittent stimulation might generate complex wave patterns in the brain which resemble standing wave patterns on vibrating metal plates or liquids (see for example [133]).

The last hypothesis was further developed by Stwertka [134]. He suggested the patterns observed during stroboscopic stimulation are so-called dissipative patterns, that is self-organizing macrostates of spatio-temporal coherence in the cortex. In general, dissipative structures appear to display certain preferred patterns of organization reflecting the dynamic properties of the system in which they arise. This means that the subjective experiences display the preferred patterns of cortical organization based on the specific dynamic properties of the nervous system. It was assumed by Stwertka that the structures emerge as a self-organizing phenomenon dependent on the continual input of photic driving energy. Specifically, and in relation to the anatomy of the human nervous system, the patterns were thought to represent the hypercolumnar organization of the visual cortical areas. Eckhorn [135] suggested that spatially distributed orientation columns in the cortex are linked by a transient synchronization of the local oscillations of individual cortical columns. Stwertka's model assumed that the stroboscopic patterns arise from a similar process, that is the phasic synchronization of sets of tuning columns corresponding to the perceptual features of the perceived patterns.

While some promising accounts for the understanding of subjective Benham-colours [130, 132] and stroboscopic patterns [134] have been described in the literature, there is so far no theoretical model able to explain the appearance of colours in the homogeneous ganzfeld-stimulation (although reference might be drawn to the models described in [130] and [132]), or the co-appearance of colours and forms in temporally modulated visual stimulation. The models accounting for subjective colour usually assume the colours to be generated at very early levels in the visual processing stream. In comparison, subjective form rather seems to be related to cortical organization principles. The question arises, how exactly these two processes are combined to generate the experience of coloured forms as it was demonstrated for temporally modulated stimulation of the homogeneous ganzfeld [84, 85].

1.4 Overview of the thesis

The phenomenon of subjective experiences induced by temporally modulated visual stimulation is as fascinating as it is controversial. While the existence of visually induced subjective experiences has been confirmed by many studies (see Section 1.2 for a review), some reported results are at issue. For example, it is not yet clear whether subjective experiences can be reliably induced by a visual ganzfeld of temporally modulated light [71, 78, 132] and if so, what factors instead of spatial information determine the experiences. In addition, the relation between subjective colour and subjective form has never been explicitly examined, but always arose as a by-product of the investigation of one of the two (e.g. [79]). The aim of this thesis is to address these and a series of other questions, which will be outlined in the following.

In a first study, participants were presented with a ganzfeld of flickering light in the frequency range of 1 - 60 Hz. They were asked to freely report their subjective experiences of colour and form. Chapter 2 presents the descriptive analysis of the results of this first experiment. The reported colours and forms were classified into distinct categories, which are white, black, grey, blue, yellow, red, green, and purple for colour, and line, circle, radial, spiral, rectangle, grating, wave, zigzag, and point for form. It was shown that these experiences are reliably reported across the participants. The occurrence of subjective experiences was restricted to specific frequency ranges. In addition, the frequency ranges differed between different subjective experiences. Chapter 3 investigates the interdependencies in the occurrence of subjective experiences. The data of Experiment 1 is analyzed with the aim to (i) determine experiences which co-occur or exclude their mutual appearance within a stimulation epoch and (ii) to evaluate the sequences in which experiences are reported during a stimulation epoch. Analysis (i) revealed a complex pattern of interdependencies in the apperception of subjective experiences. The possible relation of these patterns to colour opponency and topographical principles of form perception is discussed. Analysis (ii) did not confirm any specific patterns in the succession of reported subjective experiences over time. This suggests that while certain experiences tend to co-occur, their progression is not based on a precise internal sequence of colour or form development.

Experiments 2 and 3, which are presented in Chapter 4, aimed to investigate the role of temporal characteristics of the stimulation besides frequency upon the perception of subjective experiences. In a number of previous studies inducing subjective colour by electrical stimulation [68] or through Benham-like stimulation regimes [71], the role of phase-sensitive mechanisms has been claimed. In the experimental paradigm used here, phase can be expressed as the relation between the periodic characteristics of the stimulation and the moment of appearance of a subjective experience. Consequently, in Experiments 2 and 3, a forced-choice paradigm was applied, in which participants were presented with flickering light, prompted verbally to respond to a particular type of subjective experience, and were asked to give an immediate manual response to the occurrence of that experience. Response time was then analyzed in relation to the phase of the flickering stimulation. The results of Experiment 2 and 3 clearly suggest that subjective colour and form are coded in a phase-specific manner. Most interestingly, the findings indicate that phase-specificity may represent a mechanisms for the coding of opponent colours.

Subjective visual experiences have also been described in the literature in the absence of temporally modulated stimulation, for example during sensory deprivation [50, 52]. Experiment 4 and 5 were designed to measure subjective experiences evolving during the stimulation with a constantly illuminated ganzfeld. It is the aim of Chapter 5 to rectify the findings of of Experiments 1 to 3 by the effects measured under constant stimulation. Participants reported a number of subjective experiences during constant stimulation. The frequency ranges in which subjective experiences were reported, and the pattern of interdependencies between the occurrences of subjective experiences in Experiment 1 were adjusted according to the reports under constant stimulation. Similarly, the frequency ranges were modified for Experiment 2 and 3. These corrections emphasized the frequency specificity of subjective experiences by generally reducing the frequency ranges, and helped to tighten the pattern of interdependencies between experiences described in Chapter 3. In addition, the data of Experiment 4 and 5 served as further evidence for the statistical validity of the phase specificity as described in Chapter 4.

Chapter 6 explores in detail the phenomenology of subjective colour and form reported during the stimulation with flickering light. In Experiment 6, participants matched colours based on red-green-blue (RGB) values on the computer screen with their subjective experiences. As a control, the ability to match real target colours with colours on a computer screen was assessed, and participants were shown to be able to accomplish this task very well. Subsequently, the RGB-colours matched to the subjective colours were represented by their dominant wavelength. The reported colour categories were clearly separable on the basis of the dominant wavelengths. While some colours exhibit small interindividual differences (for example, yellow or purple), others show larger interindividual variability (for example, blue, green, or red). It is suggested in Chapter 6 that this effect may be based on the physiological properties of the colour coding system. In addition, the dominant wavelength is positively correlated with the frequency of stimulation. Further analyses revealed that this effect relates to colour categories rather than to a colour continuum, suggesting that transitions from one colour category to another occur with changes in stimulation frequency.

In Experiment 7, the participants were asked to draw the subjective forms they experienced during the stimulation with flickering light. A detailed description of these drawings is given in Chapter 6, while the drawings themselves can be found in Appendix H. The reported forms show a certain degree of interindividual agreement, and they are also in accordance with reports in the literature (e.g. [80]). Furthermore, their resemblance to patterns produced in computational models [136] and in resonant systems [133] suggests possible mechanisms of subjective form generation.

While there have been some electroencephalographic (EEG) studies on the experience of subjective form, there have been no such attempts relating to subjective colour. Using EEG, Experiment 8 aimed to investigate the electrophysiological neural responses during the experience of subjective colour. The findings presented in Chapter 7 can be summarized as follows: the report of a subjective colour is preceded by a specific pattern of activity increases and decreases in the different EEG frequency bands. A decrease of activity in the alpha frequency bands suggests an increase in task related information processing during the time interval (2000 ms) directly preceding the response. In addition, the decreasing alpha activity may reflect processes related to a switch between different percepts (i.e. colours) and processes related to stimulus detection. While the observed increase in gamma band activation may also correlate with a perceptual switch, it may even indicate the formation of a coherent percept preceding the response.

Finally, Chapter 8 summarizes the findings reported in this thesis and attempts to give a theoretical, generalized account for the mechanisms underlying the perception of subjective colour and form. Future prospects of research in the area of subjective experiences and their role in experimental psychology and neuroscience are outlined.

Chapter 2

Descriptive analysis of visually induced subjective experiences

2.1 Rationale

The aim of Experiment 1 was to determine (i) the type of subjective experiences reported during the stimulation with flickering light, (ii) the range of flicker frequencies over which these experiences were reported, and (iii) the patterns of co-occurrence between those subjective experiences. Besides defining classes of subjective experiences, the exact ranges of frequencies over which these experiences were reported were derived. On the basis of Herrmann and Elliott's [85] observations, reports were expected to fall into restricted ranges of stimulation frequency while very specific subranges might be expected for particular experiences. Finally, the investigations described here aimed to explore whether these experiences were co-occurrent (i.e. appeared in the same stimulation epochs) or whether they appeared to be mutually exclusive. In the former case we were interested to assess any potential dependency relations between subjective experiences alongside the existence of possible patterns of mutual inhibition (see Chapter 3).

2.2 Methods

General methods

A PCI technology timer card (CIO-CTR05 with CTS9513 chip capable of temporal resolutions of up to 5 kHz) was mounted in a conventional IBM compatible PC running in MSDOS mode and was connected to four LEDs (light emitting diodes; Type WU-2-310SWC-UR, luminous intensity 900mcd, 3mm diameter, emission colour white, CIE 1931 Standard: x=0.29, y=0.30, Conrad Electronic GmbH, 92240 Hirschau, Germany, order number 153881-62) mounted in a specially constructed box with two diodes placed in both the upper and lower left and right of a single viewing aperture. The diodes were screened from view and projected onto a uniformly white screen (of 10 $\times$ 20 cm) mounted within the box, some 12 cm from the viewing aperture. Aside from the viewing aperture, which was molded to fit a standard facial physiognomy, there were no potential sources of external light in the box. During stimulation epochs, the screen was illuminated by rapid and intermittent square-wave light pulses of 13 cd/m^2 emitted simultaneously from each of the 4 diodes. Using the viewing aperture observers viewed the projection of intermittent diode illumination onto the white screen, which for a certain range of presentation frequencies (below flicker fusion frequency, FFF $< \approx 38$ Hz) was experienced as a ganzfeld of uniform (that is spatially homogeneous) flicker. In contrast, for higher frequencies (above FFF) observers viewed apparently constant illumination in an otherwise spatially homogeneous field. The experiment was run on custom software programmed in a combination of the C (DJGPP compiler) and generic MATLAB© programming routines. All experiments were conducted in accordance with the code of ethics of the World Medical Association (the Declaration of Helsinki, 1964), under the guidelines of the American Psychological Association, and following the approval of departmental ethics advisors. All observers gave written informed consent to their participation in the study following screening for neurological and in particular for neuroleptic disorders.

Participants

Nine paid observers (3 male, mean age 25 years, vision normal or corrected to normal) participated in Experiment 1. Observers were paid for their participation at a rate of 8 Euro per hour.

Design and Procedure

Experiment 1 was conducted over 2 sessions, each of which consisted of 30 trials which were divided into a 60 second epoch of stimulation with flickering light followed by a 30 seconds dark or resting period. The flickering light was presented at frequencies in integer multiples of between 1 and 60 Hz. Frequency was maintained as trial-wise constant (i.e. the light was presented at only one frequency during each epoch) but was varied between trials. In this way, each observer experienced each of 60 flicker frequencies once during 60 separate stimulation epochs. The presentation order of these epochs was pseudo-randomized across trials and subsequently divided across the two experimental sessions. Randomization was performed for each observer separately. Observers were asked to verbally describe as clearly and as specifically as possible any and all visual phenomena experienced during each epoch of flicker. A free report paradigm was employed in that observers were neither informed of, nor required to report any particular visual phenomena but were asked if they did experience any visual structure or other property to report and provide a description of it. These verbal reports were collected using a second IBM compatible PC connected to the experimental machine via the parallel port. This machine was set up to record the verbal reports in a series of wave files and achieved this while coordinating the experimental procedure in combination with the experimental machine using a mixture of custom designed and generic MATLAB© routines. The verbal reports were recorded into separate wave files for each observer and each trial and were analyzed offline.

2.3 Results

2.3.1 Reported categories of colour and form

The reported visual phenomena (hereafter referred to as subjective experiences) were usually highly complex in nature, and seemed, on the basis of observers' anecdotal reports, to be relatively uniformly distributed across the whole visual field. They were subject to constant structural variation such that existing forms and colours continually transformed into other forms or colours. Subjective experiences were thus and in general transitory phenomena, which could lead to the general experience of motion across the visual field. Form might also be defined by colour, either in terms of filling in or by virtue of their contour boundaries being of one or more colours. Analysis of all reports produced by all observers proceeded in the following way: classes of subjective experiences were formed, which for colours comprise the achromatic colours black (11% of all trials), white (26%), and grey (21%) and the chromatic colours red (10%), green (14%), blue (32%), yellow (28%), and purple (16%). Reports of brown (0.5% of all trials), orange (5%), and spectral (2%) were excluded from further analysis due to their rare occurrence. Classification of subjective forms was mainly based on subjective forms described by Eichmeier & Höfer [13] that resulted from periodic electrical stimulation, although not all of the classes of subjective experiences described by Eichmeier & Höfer were reported in this study (for example, poles and curves were never explicitly reported). Subjective forms could be classified in the following terms: lines (23% of all trials), circles (24%), waves (11%), radial patterns (including reports of sun ray like structures; 27%), gratings (including reports of honeycomb structures, fences or checkerboards; 17%), points (or dark marks; 33%), zigzags (9%), rectangles (including squares, rhombuses; 10%), and spirals (22%). The reported form classes triangles (7% of all trials) and nets (or spider web; 8%) were excluded from further analysis due to their rare occurrence. Reports of motion were mainly described as rotations (62% of all trials in which movements were reported), as motion from the center outwards (expansions, 32%), or as diffuse motion (26%), whereas motion forth and back in a 3-dimensional space (14%), motion up and down (9%), motion towards the center (7%), motion sidewards (6%), diagonal motion (4%), spiral motion (2%), and floating motion (2%) were less likely to be reported. The fact that the major share of reported motion was classified in terms of rotations or expansions while the remaining motions are rather diverse and rare, in addition to the fact that these motions were reported over almost the entire range of frequencies led to a decision to concentrate further analyses on variations in the distribution of forms and colours. Finally, it should be emphasized that a given epoch of stimulation might give rise to a reasonably diverse report structure which included the simultaneous and non-simultaneous appearance of one or more classes of forms, colours, and motion. Importantly, this entails the very strong possibility of patterns of interdependencies between subjective experiences.

2.3.2 Analysis of the distribution of subjective experiences over frequency

Experiment 1 was conducted in order to establish the distribution of subjective experiences over frequency. Given some qualitative variation in both the specific characteristics of the subjective experience (subjective colours could be red or blue, for example) and the class of the subjective experience (which could include colour and/or form) distributional analysis was carried out in a first step to determine the ranges of frequencies upon which specific subjective experiences were induced and in a second step to compare the overall distributions of both subjective forms and colours. For each class of subjective experience, histograms were calculated over stimulating frequency with bin widths of 1 Hz and probabilities equivalent to the number of reports (i.e. the number of participants reporting a given subjective experience) at a given frequency. Smoothed representations of the histograms were then derived by kernel density estimations of each histogram using a Gaussian kernel with a bandwidth h derived by means of the 'rule of thumb' algorithm by Silverman [137]. Using the Silverman algorithm ensures that the bandwidth h of the kernel, which determines the size of the smoothing window and therefore the degree of smoothing, is optimally adjusted to the data. Subsequent analysis employed a technique referred to as the SiZer (Significance of Zero Crossings of the Derivative) method [138]. The SiZer technique allows the analysis of data smoothes with the aim to derive the important underlying structure of the smooth, as opposed to noise artifacts and effects attributable to sampling variability. The role of SiZer is to attach statistical significance to peaks in the smoothed distributions by displaying where the curve significantly increases and decreases. When a peak is present, there is a zero-crossing in the derivative of the smooth. The peak is taken to be statistically significant when that zero-crossing is significant, i.e. a significant peak in a smoothed distribution is characterized by a significant increase of the curve on the left side, a possible region of no change of the curve, and a significant decrease of the curve on the right. The results of the SiZer analyses for each class of subjective experience are given in Figures C.1 (form) and C.2 (colour). These figures reveal either unimodal distributions or distributions with single prominent peaks for each class of subjective experience. Figures C.1 and C.2 show that report distribution for each class of subjective experiences is restricted to a particular range of stimulating frequencies (the lower coloured panels in Figures C.1 and C.2 show a range referred to as the SiZer midrange, i.e. the frequency range over which the number of participants reporting a particular class of subjective experience is significantly greater than the no report case) while the peak frequencies and SiZer midranges also vary over frequency according to the class of subjective experience. The SiZer ranges and peak frequencies of the report distributions are given in Table 2.1. Multiple comparisons of the report distributions over frequency using Kolmogorov-Smirnov tests revealed a number of significant differences between the frequency distributions of subjective experiences (see Table D.1). Taken as a whole, forms were reported across the 8 - 40 Hz range (range spanned by the SiZer ranges of all forms), while colours were reported across the range 5 - 56 Hz (SiZer ranges of all colours). Reports of form were given at a median frequency of 25 Hz while colours were reported at a median frequency of 30 Hz. Although on a first inspection subjective colours seem to follow a bimodal distribution over frequency (see Figure 2.1a), this cannot be confirmed by a SiZer analysis of the overall colour and form distributions showing unimodal density distributions with a Sizer midrange from 9 to 54 Hz for subjective colours (see Figure 2.2) and from 9 to 36 Hz for subjective forms.

Table 2.1: Subjective colours and forms reported in Experiment 1 with Sizer midranges, i.e. frequency ranges in which a significant number of participants reported seeing the colour or form, and the frequency of the report distribution peak in Hz.

Colour	SiZer range	F peak	Form	Sizer range	F peak
purple	12 - 21	18	line	8 - 25	20
blue	13 - 53	23	circle	10 - 36	22
green	12 - 22	18	radial	15 - 30	18
yellow	12 - 56	14	spiral	15 - 30	21
red	13 - 21	19	grating	8 - 39	24
white	7 - 52	30	point	9 - 40	35
black	9 - 20	11	rectangle	9 - 35	11
grey	5 - 55	47	zigzag	9 - 15	11
			wave	9 - 32	27

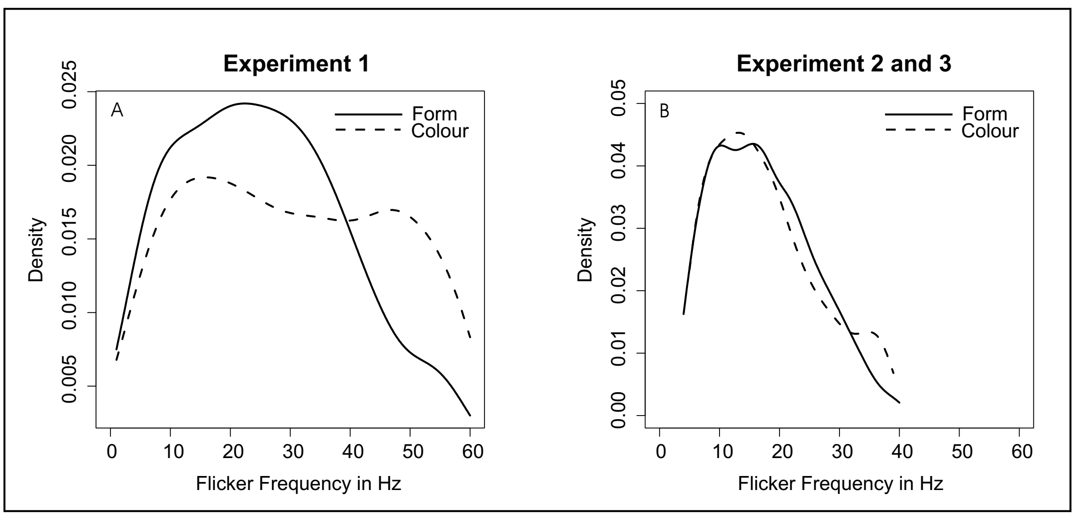


Figure 2.1: Density estimates for the overall distributions of subjective colour and form in Experiment 1 (a) and Experiments 2 and 3 (b). Given that the area under each curve equals 1, the height of the curve at a specific flicker frequency represents the probability for colour or form to be seen at this frequency relative to the probability of seeing colour or form at all other flicker frequencies.

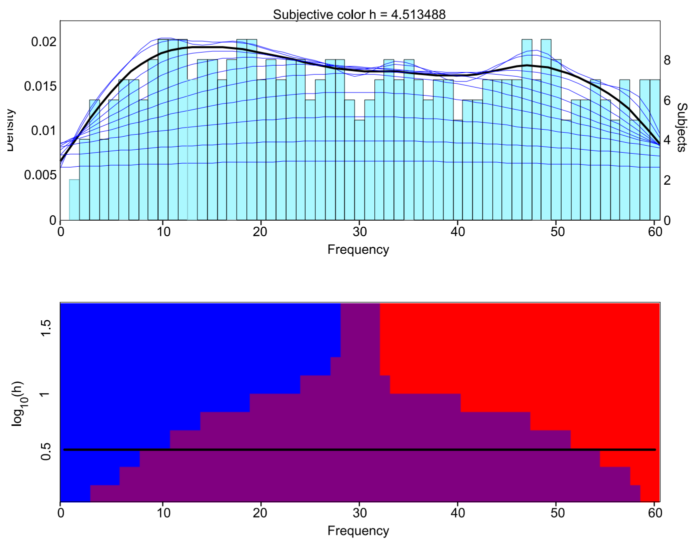


Figure 2.2: Graphical representation of the overall SiZer analysis for subjective colours reported in Experiment 1 showing unimodality of the response distribution. For further information see the caption of Figure C.1 and the text.

2.4 Discussion

Experiment 1 shows that it is possible to induce the experience of subjective colour and form on the strength of temporal information alone. In the case of subjective colour, this seems to contradict the descriptions of outcomes achieved in some previous research using Benham and Benham-like stimuli [71, 78, 132], in which the authors conclude that external spatial stimulation (and the following spatial interactions in the nervous system) is necessary in order to bring about the experience of subjective colour. Furthermore, no specific distribution of the stimulus magnitude in phase was necessary in our study for the experience of subjective colour. The necessity of magnitude variations over phase was claimed by Festinger et al. [77] who used a specific distribution of stimulation magnitude, which was said to mimic in shape the physiological response of neurons to flickering light. A critical difference between the studies mentioned above and the work presented here, which might explain the differences in results, is stimulus extension. Whereas observers in the experiments detailed here (and also in studies by Smythies [80]) were presented with a homogeneous ganzfeld of flicker, which filled the entire visual field, in all studies related to Benham-like stimuli, observers were presented with stimuli of rather small size. Stimulating the visual ganzfeld, on the other hand, distributes the presented information across the entire visual field which itself exhibits a non-uniform distribution of temporal sensitivities of the cells and conduction latencies from these cells to later stages of processing. The three different cone types of the retina have been shown to exhibit different temporal properties [131]: while the M-cones peak 51 ms after stimulation, this latency is 55 ms for L-cones and 61 ms for S-cones. Most interestingly, a relation between the peak stimulation frequencies of the subjective colours blue, green, and red, and the latency differences of the three cone types can be observed. The stimulation frequency at which most reports of blue are given is 23 Hz, corresponding to a period of about 43 ms. The frequency peaks are found at 18 Hz (56 ms) for green, and at 19 Hz (53 ms) for red. The differences in the delays are therefore 13 ms (blue-green), 10 ms (blue-red), and 3 ms (green-red). In the order of magnitude these values correspond well with the response latency differences of the cone types with 10 ms (S-M), 6 ms (S-L), and 4 ms (M-L). These differences in retinal coding of temporal information might result in later asynchronies which mimick the latency differences induced by an external coloured stimulation.

The differential synchronized activation of tuning columns in the visual cortex [134, 135] due to a differential sluggishness of the cells in the optic nerve might give rise to the appearance of subjective forms. In contrast to other reports [62, 63, 66, 67], the results of Experiment 1 suggest that there are different specific frequencies which are most effective in inducing the different subjective experiences. The categories of subjective forms and patterns reported by the observers in Experiment 1 can be compared not only to the subjective experiences induced by electrical stimulation [13], but also to the patterns described by Smythies [80]. Although the actual classifications may differ between the experimental paradigms, the main classes of subjective experiences (such as radial patterns, straight line patterns, curved line patterns, gratings or grids) can be found in all studies. These findings extend upon those of Smythies [80] by showing a direct frequency dependency of the probability of subjective form (and colour) experience.

Chapter 3

Interdependencies in the appearance of subjective visual experiences

3.1 A multidimensional model of co-occurrent subjective visual experiences

3.1.1 Rationale

In the above experiment subjective experiences were found to be particular to quite specific ranges of stimulation frequency. A second question concerns the pattern of relations between those experiences. Given that in each trial an observer could report any number of subjective experiences (including none), the question arises as to whether or not these different experiences may be considered related and whether there is a distinct pattern of interdependencies. In order to examine the reports for potential interdependencies the data of Experiment 1 were subjected to a multidimensional scaling (MDS).

3.1.2 Methods of analysis

The analysis was conducted in two steps: first, individual patterns of co-occurrences were assessed using Kruskal's non-metric multidimensional scaling (MDS). The MDS was calculated over all trials, but separately for each observer. Second, reliable interindividual consistencies between the patterns were derived by comparing the individual MDS configurations. The calculated multidimensional configurations aim to model both the distances between different subjective experiences, while at the same time minimizing the stress (i.e. the inverse of goodness of fit) of the resulting representation of the reports over a set of input distances [139] with the formula

$$\mathcal{S} = \sqrt{\frac{\sum_{i=1}^{n} (dist_{input} - dist_{model})^2}{(\sum_{i=1}^{n} dist_{model})^2}} \tag{3.1}$$

where $\mathcal{S}$ is the stress, $dist_{input}$ are the input distances, $dist_{model}$ are the distances of the model configuration, and n is the number of distances between the data points.

Input distances represented the degree to which two different subjective experiences (from the 8 colours and 9 forms described in Chapter 2) were experienced in the same stimulation epoch (i.e. trial). The input distances were calculated using a trial-by-trial summation/subtraction of differences and co-occurrences in the reports. That is, each pair (of 136 possible pairs) of subjective experiences (hereafter called pair) was assigned an initial distance value of 60 (average similarity or distance) from which the value of 1 was subtracted when the two subjective experiences co-appeared (i.e. decreasing the distance between the two) and to which the value of 1 was added when the two subjective experiences did not co-appear in a trial (i.e. increasing the distance between the two experiences). For trials in which none of the experiences was reported, the distance value did not change. A distance value of 0 marks two subjective experiences which co-appeared in every trial (initial value of 60 minus 60 trials of co-appearance), while a distance value of 120 (initial value of 60 plus 60 trials) marks two subjective experiences which were always differentially reported (e.g. either one or the other, but never both experiences were reported in a single trial). This trial-by-trial analysis was used to ensure the analysis of interdependencies of subjective experiences that co-occurred during a stimulation epoch (i.e. in time) and independent from the stimulation frequency of this stimulation epoch. In contrast, the results in Chapter 2 showed experiences to co-occur over frequency (as expressed by the different, but overlapping response distributions over frequency). Four participants did only report subjective experiences of some classes: the distance matrix of participant 1 extended only 15×15 data points as the participant did not report green and yellow; the distance matrix of participant 4 was 14×14 (green, grating, and rectangle not seen); participant 5 had a 15×15 distance matrix (zigzag and rectangle not seen); and the distance matrix of participant 6 was 14×14 (black, grey, and zigzag not seen). The matrices of the calculated distances are called input distances in the following, as they provide the input to the MDS modelling.

Applying MDS with different dimensionality, three-dimensional models were shown to be suitable for the representation of the input distances in all participants. The coordinates of the MDS models for each participant can be found in Appendix E.

The stress of the 3-dimensional representations derived from these distances has the following values on a scale of 0 to 0.5 (0 being the optimal fit with a minimal, i.e. no, difference between the input distances and the distances of the representation): .07, .09, .11, .05, .07, .13, .10, .08, .11 for participant 1 to participant 9, respectively.

Multiple t-tests were used to determine the distances between two given subjective experiences which were significantly smaller or larger than mean distance of all given distances in the model of one participant. Adjusted α was set to $(0.05/n)$, where n is the number of comparisons between distinct distances and the mean distance in the model being made and usually (for a 17×17 matrix) is 136. Pairs that are significantly close in the model (i.e. have a significantly small distance) were assumed to co-occur significantly during stimulation. In contrast, pairs with significantly large distances were assumed to exclude their mutual appearance. Tables of all pairs of significantly co-occurrent or inhibitory experiences for each participant can be found in Appendix E.

To assess the reliability of significantly co-occurring pairs over participants, all 136 possible pairs were tested for the frequency with which they were significant in the test sample. All subjective experiences which were significantly co-occurrent (i.e. having a significantly small distance) or excluding each other (i.e. significantly large distance) in at least 50% of the participants (i.e. at least 5 participants) are graphically represented in Figures 3.1, 3.2, and 3.3. For reasons of clarity, the colour-colour, form-form and colour-form pairs are depicted in different graphs.

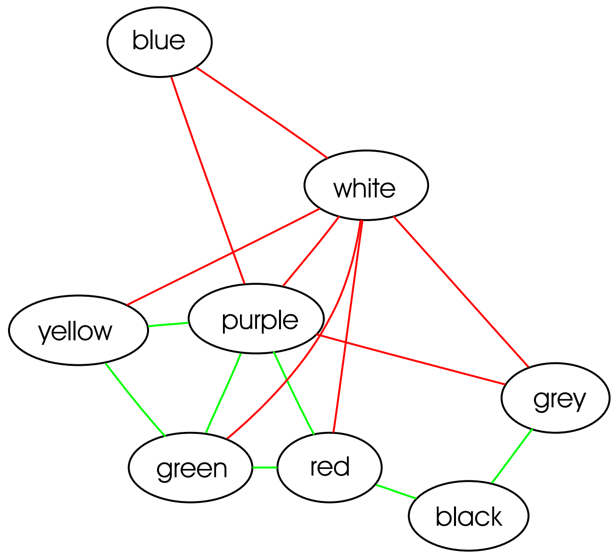


Figure 3.1: Graphical representation of the co-occurrence of subjective colours. Pairs of subjective colours which have significantly small or significantly large model distances in more than 50% of the participants are connected by green and red lines, respectively. Further information is given in the text.

3.1.3 Results

The interindividual analysis of the 3-dimensional representations allows not only a description of dependencies within the two domains of subjective experiences investigated, but also sheds some light on how they are related.

Some colours (i.e. white and blue) tend to be seen independently from the occurrence of other colours (see Figure 3.1). While the experience of purple excludes the experience of blue and grey, the experience of white shows inhibitory relations (i.e. significantly large model distances) to all chromatic colours, and grey. Despite this independence of white and blue (and partly grey), there are a number of reliable relations between colour reports in a given stimulation epoch (Figure 3.1). When black is reported, grey and red tend to occur in the same trial. The tight relation between the reports of yellow, purple, green, and red is even more interesting. The pairings of purple and yellow, and of red and green are

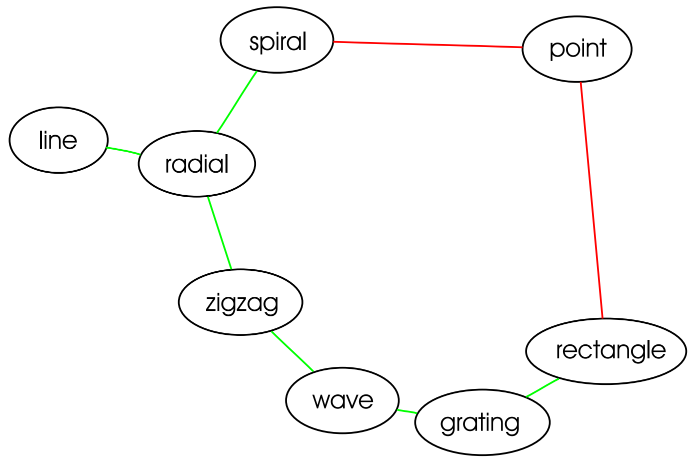


Figure 3.2: Graphical representation of the co-occurrence of subjective forms. Pairs of subjective forms which have significantly small or significantly large model distances in more than 50% of the participants are connected by green and red lines, respectively. Further information is given in the text.

suggestive in terms of colour-opponency, while red-purple and yellow-green might co-occur due to their high similarity. For the latter relations there are three possible scenarios: either the colours co-occur in time, or they develop out of each other, or the same phenomenological colours are named differentially (i.e. either green or yellow) due to a changing response criterion during a stimulation epoch.

Regarding form-form co-occurrences (Figure 3.2), one finds that the perception of points and circles is not reliably related to the experience of other subjective forms. In the multidimensional models, points reliably show a large distance to rectangles and spirals, suggesting that the experience of one excludes the experience of the other. Related to small model distances, some form-form pairs provide intuitive explanations for their co-occurrence, while the co-occurrence of others is less clear. Rectangles and gratings may co-occur, because gratings may be composed of a number of rectangles. Zigzags and waves are of the same topological class, but one is composed of straight lines and the other out of curved lines. Orthogonality might play a role in the perception of radial patterns and spirals.

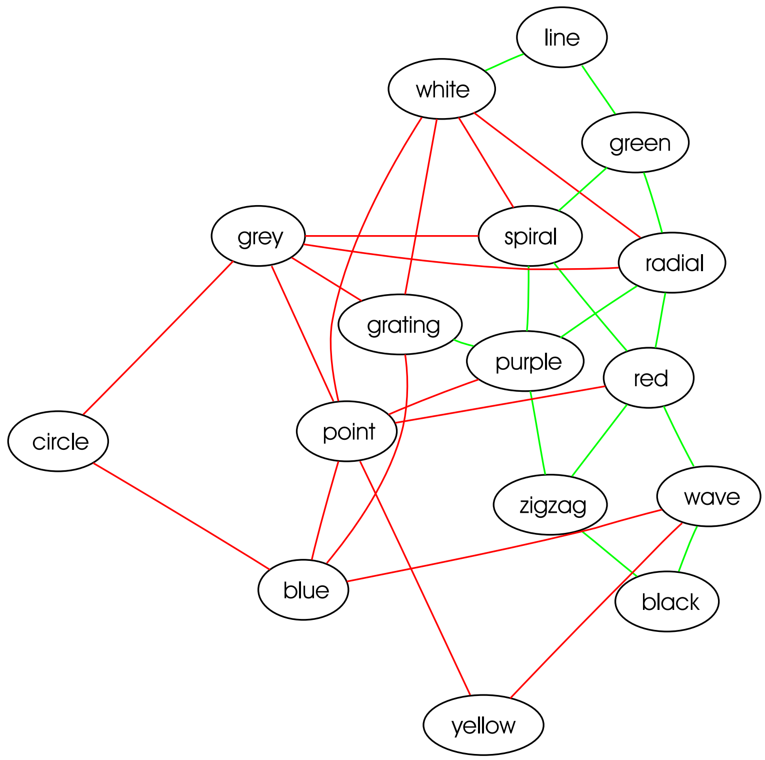


Figure 3.3: Graphical representation of the co-occurrence of subjective colours and forms. Pairs of subjective experiences which have significantly small or significantly large model distances in more than 50% of the participants are connected by green and red lines, respectively. Further information is given in the text.

Radial patterns are characterized by lines running along the radii from the center of the pattern to the periphery. In contrast, spirals usually have arrangements with lines perpendicular to the radii of the pattern, that is orthogonal to the lines of radial patterns. The co-occurrence of radials and lines, and radials and zigzags may give some hint that radial patterns are either composed of straight lines or of zigzag lines (note that lines and zigzags do not co-occur). Finally and unfortunately, the relation between waves and gratings is less clear. More insight into the understanding of the form-form co-occurrences might evolve from the phenomenological investigation of subjective form experiences described in Chapter 6.

Figure 3.3 represents quite clearly one hitherto undescribed aspect of the observer's verbal reports: in many instances experience of colour relates to experience of distinct forms (e.g. black, red, green, purple), while other colours seem to appear relatively independent of apparent form-based structure and either fill the visual field or are manifest as spatially ill-defined traces or blobs. This is especially true for reports of white, grey, yellow, and blue. Also, some forms (circle, point, rectangle) are not reliably experienced together with specific colours, but rather tend to be reported in relation to different colours by different participants. In addition, circles and points show specific patterns of inhibition with a number of colours. Large model distances can be found for the pairs circle-blue, and circle-grey, as well as for point-grey, point-white, point-purple, point-red, point-yellow, point-blue. That means, for example, that the report of a point or points is very unlikely to be accompanied by a report of grey, white, purple, red, yellow, or blue. At the same time it is not related to the experience of any other specific colour. The subjective experience of white is related to the experience of lines, but inhibitory with the experience of forms like radials, spirals, gratings, or points. Lines were also likely to co-occur with green. The perception of green was linked to spirals and radials, which in turn also could be related to red or purple. Waves and zigzags co-occurred with either red or black, and zigzags also showed some relation to the experience of purple. Waves, in contrast, had a large model distance to blue and to yellow, suggesting an inhibitory relation between these pairs. Finally, gratings were often reported with purple, but very rarely with white, grey, or blue. The co-occurrences between colours and forms match very well with the co-occurrences of either colour-colour or form-form pairs. For example, the relation between red and black, and between zigzags and waves is replicated by the fact that zigzags and waves tend to co-occur with the colours red and black. These complex patterns of co-occurrence and inhibition between different subjective experiences suggests that forms are often co-occurrent with some of the chromatic colours (red, green, purple) or black, while the experience of blue, yellow, white, and grey is either independent from any form experience or even negatively (i.e. in terms of mutual inhibitions) related to the experience of form.

3.1.4 Discussion

A complex pattern of mutual dependencies was found in the report probabilities for the different subjective experiences, be it colour or form. These results are mostly in agreement with the differences in report distributions described in Chapter 2 (see also Table D.1). On the basis of reports that the subjective experiences during one stimulation epoch are highly transient, it might be assumed that patterns of common appearance within a given epoch and between certain subjective experiences indicate principles of transformability from one experience to another. For instance, transformations within topological classes (such as the transformations of forms by means of changing of feature curvature, but not of feature configuration) appears to describe a number of relations in the multidimensional model: waves may be seen as the curved variation of zigzags; gratings might transform into a number of rectangles by spatially separating the grating elements. Support for the fact that the small distances between these subjective experiences are the result of transformations from one form into another over time also comes from findings in the original study of Smythies [80], who showed that straight and curved lines are only very rarely seen as parts of one pattern, i.e. rather than seeing zigzags and waves at the same time, it is more likely for them to evolve from each other. Similar transformations, although not strictly speaking topological, are conceivable for spirals and radials, where the latter might be the results of a fast spinning radial and for rectangles and gratings, which are both composed of angular line arrangements.

3.2 Progression of subjective visual experiences over time

3.2.1 Rationale

The finding of complex interdependencies in the experience of subjective form and colour as described in Section 3.1 raises the question of whether these interdependencies relate to specific progressions of subjective visual experiences over time. Two significantly co-occurring colours or forms might have a specific relation in time, such that one reliably appears before the other. Even more complex successions are conceivable, for example a chain of three subjective forms, which develop one after the other. Alternatively, even though two subjective experiences co-appear in a given stimulation epoch, the probability that one follows the other might be 50%, suggesting that each one can develop after the other with equal chance. The aim of the following analysis of the data of Experiment 1 was to investigate these temporal progression characteristics of the reported subjective experiences.

3.2.2 Methods of analysis

As in Section 3.1 the analysis was conducted separately for each participant with the aim to later assess the reliability of results between participants. For each participant the analysis only included colour-colour or form-form pairs which have been shown to be significantly co-occurrent (i.e. to exhibit significantly small model distances in the MDS, see tables in Appendix E).

Counts were derived from the original reports, representing the fact that a given subjective experience was directly preceded or followed by any other subjective experience of the same class (i.e. colour-colour or form-form). The difference between preceding and following experiences has to be made, as the two are statistically not related to each other. For example, red might be mainly preceded by blue, while blue, however, might be followed with equal probability by red and green. In relation to all colours included in the analysis, the significance of blue preceding red and red following blue may be different (although numerically identical).

For each subjective experience, and all its significantly co-occurring experiences, it was tested whether some (one or more) of the co-occurrent experiences preceded or followed the given subjective experience with a higher probability than expected by chance. For example, participant 1 (see Table E.2) reported gratings in co-occurrence with lines, circles, waves, and rectangles. Using χ^2-tests it was investigated whether gratings were equally likely to be preceded (or followed) by lines, circles, waves, or rectangles, or whether some of these relations were more likely than the others.

3.2.3 Results

Although the analyses did not reveal reliable interindividual patterns (which I define to necessitate the agreement of results between at least 50% of the participants), the individual patterns are interesting and will be described in the following. A summary of the results for all participants can be found in Figure 3.4.

In participant 1 the experience of gratings was significantly often preceded by the perception of lines ($\chi^2(3) = 9.0$, $p < .05$) compared to the experience of circles, waves, and rectangles with which gratings also co-occurred.

Spirals had a high likelihood of being preceded by waves or radials (compared to lines, gratings and zigzags) in participant 2 ($\chi^2(4) = 10.8$, $p < .05$).

A specific temporal progression of the experiences of purple, blue and yellow has been found in participant 3. Not only was yellow significantly preceded by blue (compared to green and purple, $\chi^2(2) = 8.0$, $p < .05$), but also blue was significantly followed by yellow (compared to green and purple, $\chi^2(2) = 6.4$,

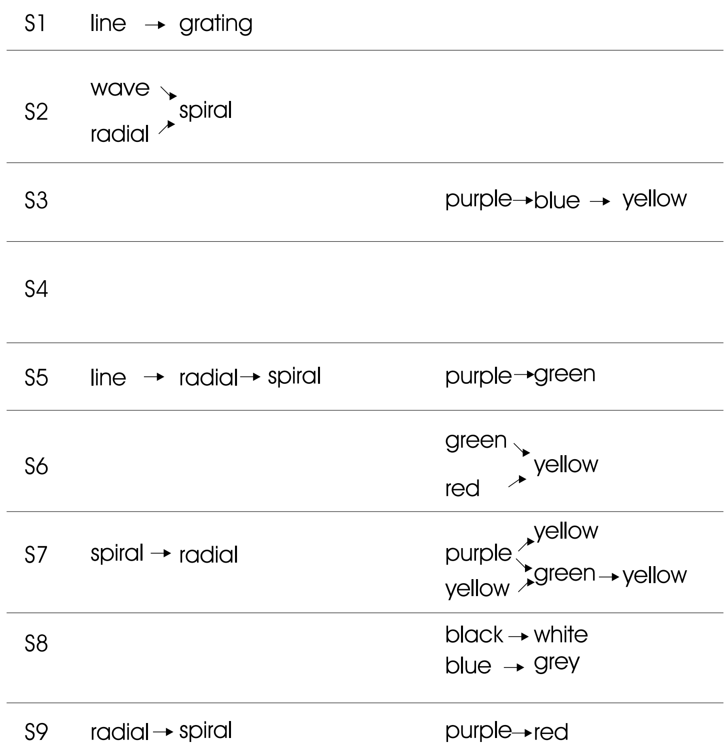


Figure 3.4: Summary of significant temporal relations between subjective colours and subjective forms. S1 to S9 are participant 1 to participant 9, respectively. Arrows mark the progression of subjective experiences over time (for example, for S1 line significantly often precedes grating). Further information is given in the text.

$p < .05$). This two-sided dependency strengthens the specificity of the progression from blue to yellow over time. Additionally, purple was significantly followed by blue (compared to green and yellow, $\chi^2(2) = 6.5$, $p < .05$), giving rise to the temporal chain of experiences from purple, to blue, to yellow.

Participant 4 showed no specific patterns of dependencies over time, suggesting an equal likelihood for all subjective experiences to precede or follow other subjective experiences.

In participant 5 a double confirmation of a progression from purple to green is found. Green is significantly preceded by purple (compared to yellow, $\chi^2(1) = 5.4$, $p < .05$) and purple is significantly followed by green (compared to yellow, $\chi^2(1) = 5.4$, $p < .05$). Similarly, spirals are preceded by radials (compared to lines, points and gratings, $\chi^2(3) = 9.5$, $p < .05$) and radials are followed by spirals (compared to lines and points, $\chi^2(2) = 10.4$, $p < .05$). This relation is also confirmed by the fact that radials followed by spirals are more likely than spirals followed by radials ($\chi^2(1) = 5.4$, $p < .05$). In addition, radials are significantly often preceded by lines (compared to points and spirals, $\chi^2(2) = 6.2$, $p < .05$) and lines followed by radials are more likely than radials followed by lines ($\chi^2(1) = 7.0$, $p < .05$). Together, these results suggest a temporal chain from lines, to radials, to spirals with an exclusion of radials to be preceded by spirals.

Temporal progression for colour has been revealed for participant 6 with yellow being significantly preceded by green and (less pronounced) red (compared to black, grey, blue, and purple, $\chi^2(5) = 14.0$, $p < .05$).

A complex pattern of colour progression was found for participant 7. While green was significantly preceded by purple and yellow (compared to black, grey, and red, $\chi^2(4) = 13.8$, $p < .05$), green was also significantly followed by yellow (compared to purple, black, grey, and red, $\chi^2(4) = 23.25$, $p < .05$). Purple was significantly followed by green and yellow (compared to black and red, $\chi^2(3) = 8.7$, $p < .05$). The relation between purple and yellow was further confirmed by the fact purple followed by yellow was more likely than yellow followed by purple ($\chi^2(1) = 6.0$, $p < .05$). The resulting pattern (see Figure 3.4) suggests that purple can be followed by yellow directly, but also with the intermediate experience of green. For forms, radials were shown to be significantly preceded by spirals (compared to lines, circles, and rectangles, $\chi^2(3) = 11.95$, $p < .05$) and spirals were significantly followed by radials (compared to lines, circles, and rectangles, $\chi^2(3) = 11.95$, $p < .05$), stressing the temporal progression from spirals to radials.

Two relations between colour experiences were derived for participant 8: black followed by white was more often reported than white followed by black ($\chi^2(1) = 6.3$, $p < .05$). Additionally, blue followed by grey appeared more often than grey followed by blue ($\chi^2(1) = 6.3$, $p < .05$).

Finally, participant 9 exhibited patterns of spirals being significantly preceded by radials (compared to points, $\chi^2(1) = 4.0$, $p < .05$) and purple being followed by red (compared to green, $\chi^2(1) = 4.0$, $p < .05$). The latter relation was supported by the fact that purple followed by red was more likely to be reported than red followed by purple ($\chi^2(1) = 4.0$, $p < .05$).

3.2.4 Discussion

There seem to be little consistency in the progression of subjective experiences over time between participants. Most suggestive seems the agreement between three of the participants concerning the progression from subjective radials to subjective spirals. However, one participant even shows the reverse pattern of spirals being followed by radials and the other five participants do not exhibit any specificities of the relation between these two forms. Whenever no significant relations were revealed (as is the case for most of the significantly co-occurring pairs of subjective experiences in all participants), this indicates that the apperception of these pairs of subjective experiences (either colour-colour or form-form) are not restricted in their appearance over time. There are different possibilities of how such independence of experiences from the experience history may be explained: a pair of subjective experiences may have an equal probability that one member of the pair precedes or follows the other member. Alternatively, the two subjective experiences might be separated by a third experience (or more experiences) of the same class (colour or form). These dependencies would not necessarily have been detected in the analysis, as the data only allows an analysis of reports directly following each other in time. However, some of these indirect relations have been found through the detection of directly related experiences, for example in participant 3 and 7. Another possibility is that the subjective experiences actually co-occur at the same moment in time and are differentially reported one after the other by the participants.

Chapter 4

Relation of subjective visual experiences to the temporal characteristics of the stimulation

4.1 Rationale

The tendency for subjective experiences of form and colour to be non-uniformly distributed over flicker frequency indicates the existence of a critical bandwidth of frequencies. Within this frequency range mechanisms responsible for the emergence of conscious visual states may be triggered by the periodic response of mechanisms sensitive to transient contrast changes at particular frequencies. This suggestion is also supported by the electroencephalographic (EEG) response to flicker, the amplitude of which indicates a strong, stimulus evoked steady state response under posterior electrodes, which exhibits maxima at the stimulating frequency and harmonics thereof [84]. On this basis it is reasonable to assume that the responses in occipital cortex are periodic and follow the frequency of stimulation. The role of phase-sensitive mechanisms has been emphasized in studies investigating the experience of subjective colours following electrical stimulation [68], the viewing of Benham disks [73] or Benham-like stimulations [71]. However, although stimulus features presented at specific phases during stimulus presentation were found to determine the perception of particular colours, these effects were either attributed to a decisive role of spatial information (i.e. the presentation of phase shifted flicker at adjacent regions of the stimulation field [71, 73]) or patterns of temporally modulated stimulus magnitude [68, 77]. In the studies presented here, neither spatial nor stimulus magnitude variations were necessary to induce subjective experiences of colour and form. However, if the phase of stimulation plays a critical role in establishing subjective colour and form, it might be observable in particular at the time of onset of the experiences. This avenue is explored in Experiments 2 and 3, which examine the time of onset of subjective experiences relative to the phase of intermittent stimulation.

4.2 Methods

The methods employed in Experiments 2 and 3 were as given in the general methods with the following exceptions or specifications.

Participants

Twelve practiced observers (4 male, mean age 24.4 years, vision normal or corrected to normal) participated in Experiment 2 while twelve practiced observers (5 male, mean age 23 years, vision normal or corrected to normal) participated in Experiment 3. Observers were paid for their participation at a rate of 8 Euro per hour.

Design and Procedure

Experiments 2 and 3 used a simple response-time paradigm in that observers were asked to press a response key as quickly as possible on first experiencing a particular subjective experience. Preceding the experiment, the participants were provided with a schematic representation of subjective forms (see Figure B.1). The target subjective experience was announced to observers in the form of a verbal instruction (red, blue, circle, line, etc.) given via headphones immediately prior to trial onset. In the event that the observer did not experience the target subjective experience, the trial was allowed to time out and a zero response time was recorded. Verbal instructions via headphones, stimulus generation, and response collection were all ensured by a PC running in MSDOS mode and programmed in C. Each trial consisted of a 30 second epoch of flickering stimulation followed by a 15 seconds dark or resting period. The ranges of frequencies concerned were narrower than those used in Experiment 1: in Experiment 2 and 3, subjective colours were examined between 5 and 39 Hz and subjective forms between 4 and 40 Hz. These ranges corresponded to the ranges over which around

75% of subjective experiences were reported in Experiment 1 and were considered sufficiently broad to allow important characteristics of the report distributions to be preserved. Consequently, Experiments 2 and 3 consisted of 175 (35 frequencies $\times$ 5 target colours) and 296 trials (37 frequencies $\times$ 8 target forms), divided into 3 and 4 sessions, respectively. As in Experiment 1, the frequency of flicker was maintained as trial-wise constant but was varied between trials. Both the presentation order of flickering frequencies and the requested target subjective experiences were varied pseudo-randomly over trials and subsequently divided across the experimental sessions in each experiment. This procedure was carried out separately for each observer. Observers were asked to respond to each type of subjective experience for each level of flicker frequency: Specifically, observers were required to respond to the emergence of purple, blue, green, yellow, or red in Experiment 2, and to lines, circles, radials, gratings, points, zigzags, rectangles, and spirals in Experiment 3. These subsets of target subjective experiences were those that had been reported most reliably in Experiment 1.

4.3 Results

Analyses of report frequency distributions in Experiment 2 and 3 were conducted in an identical fashion to the corresponding analysis of the Experiment 1 data. The SiZer midranges and distribution peaks for the report distributions over frequency for subjective colours and forms are given in Table 4.1.

4.3.1 Analysis of the distributions of subjective experiences over frequency

Forms were reported across the 8 - 26 Hz range (range spanned by the SiZer ranges of all forms; median of the response distribution over frequency: 16 Hz), while colours were reported across the range 9 - 26 Hz (SiZer range of all colours,

Table 4.1: Subjective colours and forms reported in Experiment 2 and 3 with Sizer midranges, i.e. frequency ranges in which a significant number of participants reported seeing the colour or form, and the frequency of the report distribution peak in Hz.

Colour	SiZer range	F peak	Form	Sizer range	F peak
purple	9 - 18	14	line	10 - 24	12
blue	9 - 18	10	circle	9 - 26	21
green	11 - 19	14	radial	9 - 22	12
yellow	10 - 26	13	spiral	11 - 24	17
red	10 - 16	11	grating	10 - 19	14
			point	10 - 26	13
			rectangle	8 - 21	9
			zigzag	10 - 19	14

median frequency: 16 Hz).

4.3.2 Response time analysis

Analysis of response times (in ms) to the apperception of an subjective experience revealed no significant differences between the response latencies to different subjective colours or to different subjective forms ($F(4{,}425) = 0.46$, ns, and $F(7{,}924) = 2.23$, ns, respectively). This implies that responses to different subjective experiences were given at approximately equivalent times during an epoch of flicker irrespective of the type of experience concerned. The mean response time to subjective colour was 7530 ms, the minimum and maximum response times were 742 ms and 29470 ms, respectively, whereas 50% (median) and 75% (3rd quartile) of all responses were given no later than 5218 ms and 10370 ms after flicker onset, respectively. For subjective form, the mean response time was 8842 ms, the minimum and maximum response times were 778 ms and 29550 ms, respectively. For subjective form 50% and 75% of all responses were given no later than 7028 ms and 12840 ms following flicker onset, respectively.

4.3.3 Analysis of response times over phase

The role of phase sensitive mechanisms for the experience of subjective colour and form was investigated through the analysis of the relation between the times of onset of the subjective experience (i.e. the response times) relative to the frequency cycle of intermittent stimulation. The phase of the response distributions was computed relative to stimulating frequency. For each trial, the phase angle of the flicker frequency cycle at which the manual response was given, was calculated by

$$\Phi = \frac{(RT mod \frac{1000}{F}) * 360°}{\frac{1000}{F}} \tag{4.1}$$

where Φ is the phase angle, RT reaction time and F the flicker frequency in the respective trial. Although the measure of the phase angle of the response depends on the flicker frequency, it constitutes an expression of the response time in relation to the flicker frequency, but independent from its actual value for a given trial. A problem which arises from this computation is the fact that an assumed (mainly constant) motor component in the response time has a differential effect on the phase angle depending on the actual flicker frequency in the trial (for example, a 150 ms execution component of the response time would correspond to 1.5 or 2.4 cycles of flicker for 10 and 16 Hz flicker frequency, respectively). Therefore, summarizing over all participants and trials (i.e. all different frequencies) should result in an uniform distribution of response times over all phase angles due to a an equally distributed summation of noise (i.e. the motor component) to the actual time of appearance of an subjective experience. However, this is not what is found in the analysis of response time distributions relative to the flicker frequency phase angle. The analysis of the response relative to stimulation phase revealed all responses to be distributed normally (with $p > 0.01$, Watson's goodness of fit test, see Table 4.2) following a von Mises distribution (i.e. the circular analogue of the normal distribution on a line [140, 141], see Figure 4.1b). This indicates that, irrespective of the absolute time at which a subjective experience starts to be ex-

Table 4.2: Statistics of the Watson goodness-of-fit test of the phase data against the von Mises distribution for Experiment 2 and 3. D is the test statistic; p is the level of significance. Note that values of $p > .01$ signal a non-significant deviation of the data from the test distribution, i.e. a significantly good fit of the data on a 1% significance level.

Colour	D	p	Form	D	p
purple	0.0715	$> .01$	lines	0.017	$> .1$
blue	0.0377	$> .1$	circle	0.0508	$> .1$
green	0.0503	$> .1$	radial	0.0558	$> .05$
yellow	0.0246	$> .1$	spiral	0.0186	$> .1$
red	0.0351	$> .1$	grating	0.0258	$> .1$
			point	0.0333	$> .1$
			rectangle	0.0298	$> .1$
			zigzag	0.0232	$> .1$

perienced, the onset time of the subjective experience relates quite specifically to a particular phase of the evoking flicker. Figure 4.1a illustrates circular distributions related to the onset times of subjective rectangles and subjective blue (the circular distributions for all subjective colours and forms can be found in Figures F.1 and F.2). Interestingly, the onset of different subjective experiences may be distributed around different phases: Figure 4.1c displays the mean directions of the response distributions for subjective forms (point 38°, zigzag 104°, circle 125°, radial 171°, rectangle 175°, line 180°, grating 320°, and spiral 353°) and subjective colours (yellow 103°, green 133°, red 258°, purple 275°, and blue 312°). It can be seen that certain subjective experiences appear at close phases in the flicker cycle (i.e. lines and rectangles; blue and purple), while others are clearly separated in phase (i.e. radial vs. spiral; blue vs. yellow).

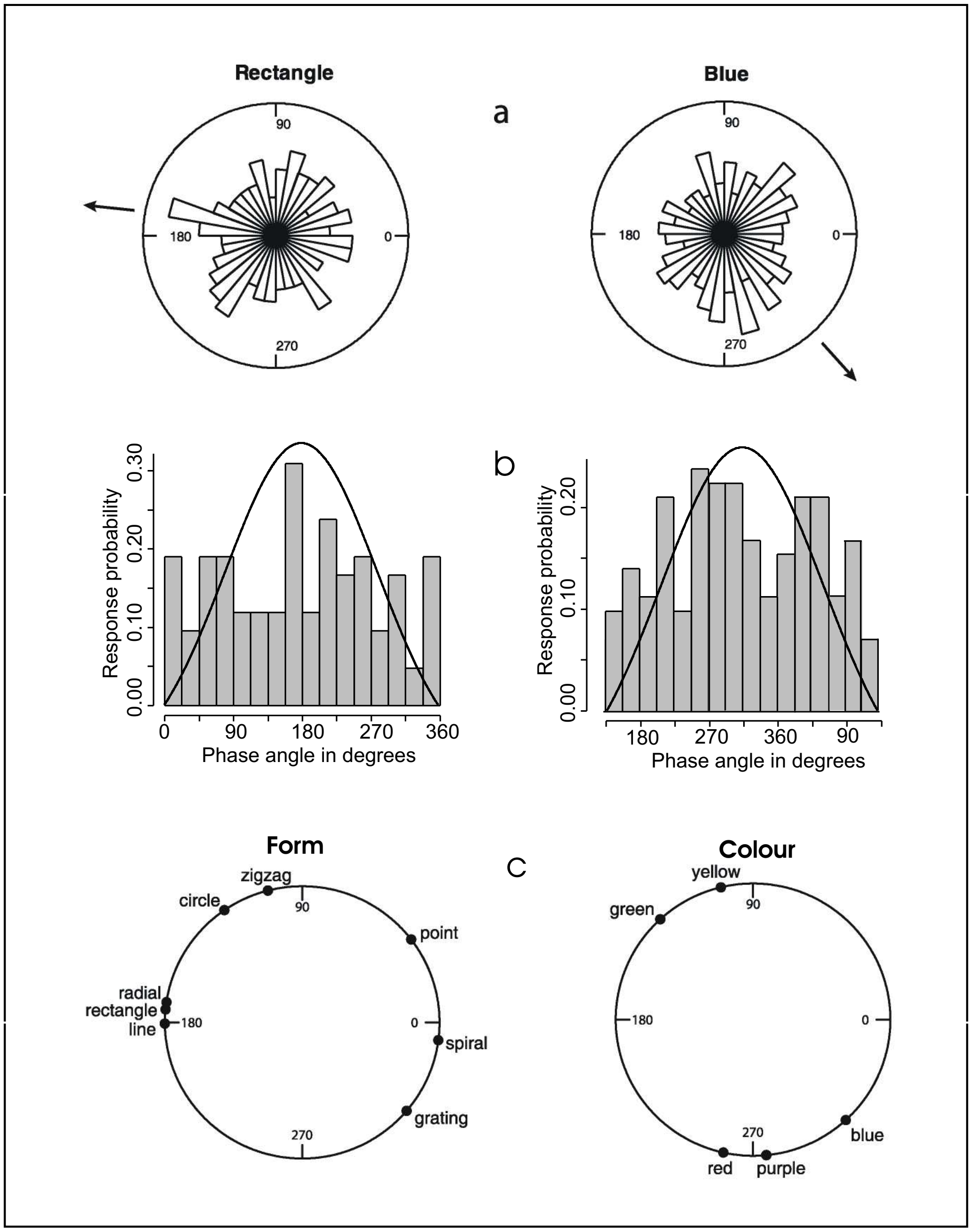


Figure 4.1: (a) Circular diagrams indicating the distribution of response times expressed in terms of phase in the flicker frequency cycle. The specific cases shown here are subjective rectangles and subjective blue. 360 degrees on the circle (in counter-clockwise direction) correspond to a single flicker frequency cycle. Arrows indicate the mean direction (i.e. a measure of central tendency) in phase. (b) Diagrams of the same data as in (a), this time plotted on a line, centered around the mean direction and overlaid with a normal distribution. (c) Mean direction in phase of subjective forms and colours.

4.4 Discussion

The present study indicates the relevance of stimulus phase for the experience of subjective colour. This result corroborates previous studies (i.e. [73]) emphasizing the role of phase information. In our study, a relation of the phase specificity to the opponent colour system can be noted: the opponent colour pairs red-green and blue-yellow are clearly separated in their time of appearance relative to the flicker cycle. The question arises whether colour opponency might not only be coded spatially (as by colour opponent ganglion cells), but also temporally. Colours might be coded in the temporal frequency domain, expressed by neural oscillations in specific frequency ranges. As shown by Cottaris & De Valois [117], the two colour-opponent systems exhibit different processing delays from the retina to V1 (the red-green cells in V1 responding faster than the blue-yellow cells). It might be that these latency differences rather than being a fixed time, are an expression of oscillatory processes modulating colour coding, where red-green opponency is coded with a different latency than yellow-blue opponency, while the intra-opponent colours (i.e. red and green) might be coded in similar frequency ranges. Should the opponent colours be coded in a similar frequency range, the problem arises as how to temporally separate the two different colours. One possibility would be the coding in phase. Whereas a single (or at least similar) frequency is responsibly for coding the opponent colours, the phase at which this coding oscillation is assessed by other mechanisms (for example, slower oscillations 'reading' the information of the coding oscillation) defines which colour is seen. The dependency of the experience of subjective forms on the phase of the flicker cycle is less clear, although some relations (e.g. radials and spirals, one being the orthogonal line arrangement of the other) might similarly be explained by a phase-sensitive opponency coding.

Chapter 5

Spontaneous visual experiences during constant ganzfeld stimulation

5.1 Rationale

Experiments 4 and 5 described in this chapter served as control experiments for Experiments 1 to 3 and aimed to assess whether subjective experiences can be induced by factors other than the flicker characteristic of the light presented. In particular, viewing a stimulation in the experimental apparatus described above might give the spontaneous impression of certain colours or forms independent of the temporal aspects of the presented light (i.e. flicker or non-flicker), for example due to effects related to sensory deprivation [50, 51]. These effects will be estimated by collecting reports of subjective experiences during the stimulation with a constant ganzfeld of illumination with instructions equivalent to the ones used in Experiment 1 to 3 (see Appendix B). Free reports of subjective experiences will be collected, followed by forced-choice experiments investigating spontaneous subjective experiences during constant illumination. Specifically, the probability of spontaneous reports, co-occurring pairs of experiences, the onset time of spontaneous experiences, and a hypothetical phase relation of report times will be measured. Subsequently, the reports collected under constant stimulation will be related to the results of the Experiments 1 to 3 and the correction due to effects from constant illumination will be discussed.

5.2 Methods

The methods employed in Experiments 4 and 5 were as given in the general methods with the following exceptions or specifications.

Participants

Twelve paid observers (4 male, mean age 24 years, vision normal or corrected to normal) participated in Experiment 4, and twelve paid observers (5 male, mean age 24 years, vision normal or corrected to normal) participated in Experiment 5.

Observers were paid for their participation at a rate of 8 Euro per hour.

Design and Procedure

Experiment 4 and 5 consisted of two parts: a trial of freely reported subjective experiences and a forced-choice experiment. The order of the two parts was counterbalanced between participants, such that 50% of the participants experienced the free-report trial before the first session, and 50% after the last session of the forced-choice experiment. Preceding the experiment, the participants were provided with a schematic representation of subjective forms (see Figure B.1).

During the free-report trial, participants viewed constant illumination for 60 seconds (equivalent to the presentation duration in Experiment 1) and where asked to freely report all subjective experiences of colour (Experiment 4) or form (Experiment 5) which occurred to them. The verbal reports were noted down by the experimenter.

The second part of Experiments 4 and 5 used a simple response-time paradigm in that observers were asked to press a response key as quickly as possible on first experiencing a particular subjective experience. The target subjective experience was announced to observers in the form of a verbal instruction (red, blue, circle, line, etc.) given via headphones immediately prior to trial onset. In the event that the observer did not experience the target subjective experience, the trial was allowed to time out and a zero response time was recorded. Verbal instructions via headphones, stimulus generation, and response collection were all ensured by a PC running in MSDOS mode and programmed in C. Each trial consisted of a 30 second epoch of constant illumination followed by a 15 seconds dark or resting period. Consequently, Experiments 4 and 5 consisted of 150 (5 target colours $\times$ 30 repetitions) and 240 trials (8 target forms $\times$ 30 repetitions), divided into 2 and 4 sessions, respectively. The requested target subjective experiences were varied pseudo-randomly over trials and subsequently divided across the experimental sessions in each experiment. This procedure was carried out separately for each observer. Observers were asked to respond to each type of subjective experience: specifically, observers were required to respond to the emergence of purple, blue, green, yellow, or red in Experiment 4, and to lines, circles, radials, gratings, points, zigzags, rectangles, and spirals in Experiment 5. These subsets of target subjective experiences were those that had been tested in Experiments 2 and 3.

5.3 Results

5.3.1 Descriptive analysis of spontaneous visual experiences in free report

In the free-report trial with constant illumination some subjective experiences of colour and form were reported. 41.7% of the participants (5 participants of 12) in Experiment 4 did not report any subjective colour, while 4 participants (33.3%) reported one colour, and 3 participants (25%) two to four colours. White, blue, and yellow were reported by 3 participants (25%), purple by 2 (16.7%), and red and green by one participant each (8.3%). Two participants (16.7%) in Experiment 5 did not experience any subjective form, four participants (33.3%) reported one form, and 6 participants (50%) reported two to three different forms. Lines and points were reported by 6 participants (50%) each, while circles and gratings were reported by 3 (25%) and 2 (16.7%) participants, respectively. Spirals, zigzags and rectangles were reported by one participant (8.3%) each.

For the participants reporting two or more experiences, co-occurring pairs of experiences can be specified. These were white-blue (reported by 2 participants of 12), white-yellow, white-red, blue-yellow, blue-red, green-yellow, green-purple, and yellow-purple (each reported by 1 participant) for colours. The following form-form pairs were found: line-point (3 participants), line-grating (2 participants), line-circle (2 participants), line-spiral, line-rectangle, grating-rectangle (each reported by 1 participant).

5.3.2 Impact of the results of Experiment 4 and 5 on the findings of Experiment 1

The colours and forms freely reported during constant illumination in Experiment 4 and 5 can serve as a baseline condition for the reported subjective experiences in Experiment 1. These spontaneously reported colours and forms during constant stimulation might represent experiences that are related to the stimulation with a constant ganzfeld of illumination. Therefore, the number of reports at each frequency of Experiment 1 were corrected by the percentages of reportage described above. For example, when blue was reported by five of the nine participants at one stimulation frequency in Experiment 1, it can be estimated from the data presented above that two of these participants (i.e. 25% of nine participants) actually gave a response that would have been expected during constant illumination. Therefore, the number of reporting participants was corrected from five to three for this presentation frequency. This procedure was repeated for all subjective experiences and all presentation frequencies. In cases where the correction resulted in a negative frequency of reportage, this was set to zero.

The corrected histograms and SiZer plots can be found in Figures G.1 and G.2. Due to a reduced number of reports the estimates of SiZer ranges are more difficult to determine. However, the SiZer range of all colours and forms may be estimated on the basis of the 'no change' areas in the SiZer plots. These SiZer ranges were then compared to the SiZer ranges of subjective experiences in the original data of Experiment 1 (see Table 5.1). It was revealed that the lower and upper borders of the ranges for black, grey, red, green, purple, as well as for radials, waves, spirals, gratings, zigzags, and rectangles did not differ from the lower and upper borders of the respective experiences in the original data of Experiment 1 by more than 3 Hz. In contrast, the ranges for white, blue, yellow,

Table 5.1: Sizer midranges of the subjective colours and forms reported in Experiment 1 and Sizer midranges corrected by the probability of subjective experiences during constant stimulation. Subjective experiences whose SiZer ranges underwent substantial changes are given in italic.

	Sizer range			Sizer range	
Colour	original	corrected	Form	original	corrected
purple	12 - 21	13 - 20	*line*	8 - 25	17 - 25
blue	13 - 53	19 - 25	*circle*	10 - 36	18 - 33
green	12 - 22	11 - 24	radial	15 - 30	15 - 30
yellow	12 - 56	12 - 35	spiral	15 - 30	13 - 31
red	13 - 21	15 - 20	grating	8 - 39	6 - 37
white	7 - 52	24 - 55	*point*	9 - 40	18 - 38
black	9 - 20	9 - 20	rectangle	9 - 35	8 - 32
grey	5 - 55	5 - 55	zigzag	9 - 15	8 - 12
			wave	9 - 32	9 - 32

lines, points, and circles were narrower than in the original data of Experiment 1. The reports at low stimulation frequencies of white (7 - 23 Hz) and blue (13 - 19 Hz) reported in Experiment 1 cannot be found in the corrected data. This suggests that reports of white and blue at these lower frequencies are artifacts. Reports of blue and yellow given at high stimulation frequencies (26 - 53 Hz and 36 - 56 Hz, respectively) cannot be confirmed by the analysis of the corrected data, again suggesting the reports of blue and yellow at these frequencies are not due to flickering stimulation. Additionally, the reports of lines, points, and circles given at low stimulation frequencies (8 - 16 Hz for lines, 9 - 17 Hz for points, and 10 - 17 Hz for circles) in Experiment 1 are not reliable when considering the corrected data. This again suggests that these low frequency reports may be due to spontaneous visual imagery arising in an illuminated ganzfeld. This narrowing of the stimulation frequency ranges at which subjective experiences are reported gives a more precise estimate of the bandwidth of frequencies reliably inducing subjective experiences, and supports the notion of frequency-specific mechanisms underlying the emergence of subjective experiences.

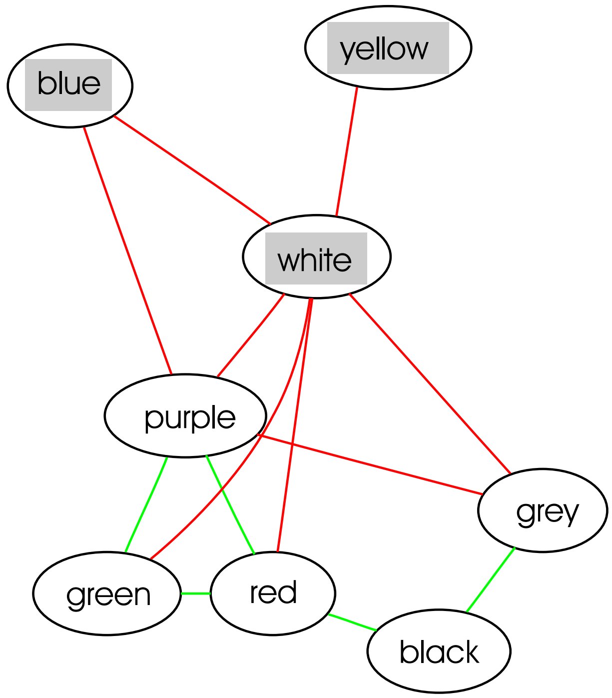


Figure 5.1: Graphical representation of the co-occurrence of subjective colours in Experiment 1 corrected for co-occurring pairs during constant stimulation. The correction was only applied to significantly small distant pairs. Pairs of subjective colours which had significantly small or significantly large model distances in more than 50% of the participants after correction are connected by green and red lines, respectively. Colours which were reported most often (each by 25% of the participants) during constant stimulation are underlaid by a grey rectangle. For comparison with the original model see Figure 3.1. Further information is given in the text.

In addition to the frequency ranges, one can take the reports during constant stimulation, and especially the co-occurring pairs as a correction parameter for the models of interdependencies derived by multidimensional scaling in Experiment 1. For the correction, co-occurrent experiences during constant stimulation are assumed to have a low distance in a space of subjective experiences. Therefore the number of participants showing a significantly low distance in a given pair was corrected by the percentage of reportage in Experiment 4 and 5. For example,

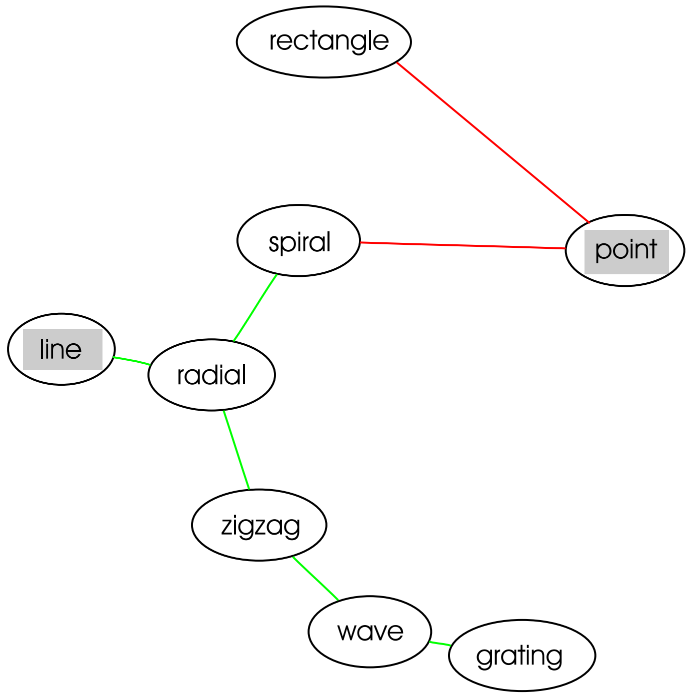


Figure 5.2: Graphical representation of the co-occurrence of subjective forms in Experiment 1 corrected for co-occurring pairs during constant stimulation. Grey rectangles mark forms reported by 50% of the participants during constant stimulation. For comparison with the original model see Figure 3.2. For further information see Figure 5.1 and the text.

purple and yellow were significantly close in 5 participants (out of 9) in the original MDS of Experiment 1 and therefore displayed as a reliable co-occurrence in Figure 3.1. However, the pair purple-yellow was reported by 1 participant in Experiment 4, corresponding to 8.3% of the participants. Therefore, co-occurrence in 0.75 participants in Experiment 1 can also be attributed to co-occurrences while viewing a constant ganzfeld of illumination. When the number of participants was corrected by this value, only about 4 participants of 9 (that is less than 50%) show a close purple-yellow relation. Equivalent corrections were performed for all pairs of subjective experiences reported in Section 5.3.1. As a result, the co-occurrences of purple and yellow, green and yellow, and gratings and rectangles, diminished to less than 50% of the participants. The corrected representations of pairings of subjective experiences can be found in Figures 5.1 and 5.2. In addition, colours and forms reported relatively frequently during constant stimulation (i.e. line, point, blue, yellow, and white) are marked in these Figures. It is evident that the experience of blue, yellow, and white is not related to the experience of any other colour. The same holds for the experience of points and other forms. In addition, blue and yellow are not co-occurring with any form, and points are not positively related to any colour (see Figure 3.3). This suggests that the specific patterns of co-occurrences are directly related to the stimulation with flickering light, while constant stimulation mostly stimulates the independent experiences of colour. However, it has to be noted that lines which were reported relatively frequently during constant stimulation show a co-occurrence relation to radials, and lines co-occur with white and green. The interpretation of these specific patterns therefore should be considered with care.

5.3.3 Descriptive analysis of spontaneous visual experiences in a forced-choice paradigm

The presentation of 30 trials of constant light in the second part of Experiments 4 and 5 aimed at investigating whether the probability of reporting subjective experiences changes over a series of trials during the experiment. No such effect was found for subjective colour (Experiment 4) or subjective form (Experiment 5). The number of participants reporting a given target colour or form did not differ between the 30 experimental trials (separate χ^2-tests for each subjective experience testing the number of reports over all 30 trials; all non-significant). Therefore the mean number of participants reporting the experiences under constant illumination was taken as the baseline condition for the comparisons with Experiment 2 and 3. The mean probabilities of spontaneous report during constant illumination over all trials for the different experiences were: yellow 53.3% (6.4 participants of 12), blue 41.7% (5 participants), purple 45.8% (5.5), red 28.1% (3.4), and green

24.4% (2.9), line 56.4% (6.8), point 54.2% (6.5), circle 36.9% (4.4), radial 33.9% (4.1), spiral 27.5%(3.3), zigzag 27.5% (3.3), grating 26.1% (3.1), and rectangle 13.1% (1.6).

The response times to different target colours differed significantly ($F(4, 691) = 7.172, p < .05$) among each other with yellow being reported significantly faster than green, purple and red (separate post-hoc Bonferroni tests with $p < .05$). The mean response times for the different colours were 8962 ms (yellow), 11163 ms (blue), 12023 ms (red), 12819 ms (purple), and 13476 ms (green). Differences in response times were also found for subjective form ($F(7, 984) = 11.143, p < .05$). Separate post-hoc pairwise comparisons (Bonferroni tests with $p < .05$) revealed lines (10882 ms) to be reported faster than zigzags (15343 ms) or spirals (13898 ms), circles (11717 ms) to be reported faster than zigzags, and points (8751 ms) to have shorter response times than circles, radials (12735 ms), gratings (13174 ms), zigzags, rectangles (14345 ms), or spirals.

Besides the absolute response times, Experiments 2 and 3 examined the relation of responses to the phase of the cyclic flicker stimulation. As the stimulation in Experiments 4 and 5 was constant over time, no phase information was present in these stimuli. However, to test against the idea that the phase effects in Experiments 2 and 3 arose at chance or were generated by artifacts in the analysis procedure, a similar analysis was conducted for Experiments 4 and 5. Each of the 30 trials with a given subjective experience and for a given participant was randomly assigned a model stimulation frequency of between 7 and 36 Hz (approximately corresponding to the frequency ranges tested in Experiments 2 and 3), such that each of these frequencies is assigned to exactly one trial per experience $\times$ participant combination. Using these model frequencies, the phase information for each trial was calculated as described in Formula 4.1. Separate Watson-tests on this circular data (see Chapter 4 for further information on circular statistics) revealed all responses to be distributed uniformly over phase (see Table 5.2). This indicates that responses to subjective experiences during constant illumination are

Table 5.2: Statistics of the Watson goodness-of-fit test of the hypothetical phase data of Experiment 4 and 5 against the uniform distribution. D is the test statistic; p is the level of significance. Note that values of $p > .01$ signal a non-significant deviation of the data from the test distribution, i.e. a significantly good fit of the data on a 1% significance level.

Colour	D	p	Form	D	p
purple	0.1047	$> .1$	line	0.052	$> .1$
blue	0.0861	$> .1$	circle	0.0994	$> .1$
green	0.067	$> .1$	radial	0.1243	$> .1$
yellow	0.1443	$> .1$	spiral	0.1332	$> .1$
red	0.0797	$> .1$	grating	0.0615	$> .1$
			point	0.0344	$> .1$
			rectangle	0.047	$> .1$
			zigzag	0.0644	$> .1$

given independently of model stimulation frequencies and phases. Evidently, this is a strong support for the fact that the phase specificity revealed in Chapter 4 is not an artifact of the statistical analyses, but rather and importantly is a characteristic of the responses given to experiences of subjective colour and form.

5.3.4 Impact of the results of Experiment 4 and 5 on the findings of Experiment 2 and 3

Again, as described in Section 5.3.2, the number of reports at each frequency and for each type of experience in Experiment 2 and 3 were corrected by the percentages of reportage given in Section 5.3.3. The original and corrected SiZer ranges of all subjective experiences in the forced-choice Experiments 2 and 3 are given in Table 5.3.

The lower and upper limits of the SiZer ranges do not differ by more than 3 Hz between the original and the corrected data for blue and purple, and circles, radials, gratings, zigzags, rectangles, and spirals. The corrected ranges for green

Table 5.3: Sizer midranges of the subjective colours and forms reported in Experiment 2 and 3 and Sizer midranges corrected by the probability of subjective experiences during constant stimulation. Subjective experiences whose SiZer ranges underwent substantial changes are given in italic.

	Sizer range			Sizer range	
Colour	original	corrected	Form	original	corrected
purple	9 - 18	6 - 18	*line*	10 - 24	9 - 16
blue	9 - 18	7 - 19	circle	9 - 26	9 - 25
green	11 - 19	7 - 19	radial	9 - 22	8 - 21
yellow	10 - 26	10 - 21	spiral	11 - 24	10 - 25
red	10 - 16	8 - 23	grating	10 - 19	9 - 20
			point	10 - 26	11 - 20
			rectangle	8 - 21	6 - 21
			zigzag	10 - 19	9 - 21

and red were expanded compared to the original ranges, green reports being reliable also between 7 and 10 Hz (a range not covered by the original data), and red reports being significant also between 17 and 23 Hz. In contrast, yellow reports between 22 and 26 Hz found in the original data were not included in the corrected SiZer ranges. Similar effects hold for lines and points, where reports between 17 and 24 Hz, and 21 and 26 Hz, respectively, were not shown to be significant in the corrected SiZer ranges. This suggests that a correction of responses by the probability of spontaneous reports of subjective experiences reduces the SiZer ranges of certain experiences (yellow, lines, and points), while the ranges of other experiences (green and red) are extended due to clearer signal-to-noise ratio in the data.

5.4 Discussion

The comparison of flicker-induced free report and constant-light-induced free report of subjective experiences (Section 5.3.1 and 5.3.2) suggests that the reports of white, blue, yellow, lines, points, and circles are partly arising spontaneously in an illuminated ganzfeld, especially in the lower and upper frequency ranges.

In addition, the co-occurrences of green with purple or yellow, and of gratings with rectangles found in the multidimensional scaling models of Experiment 1 are attributable to the effects of constant ganzfeld illumination.

When comparing subjective experiences reported with a forced-choice response during flicker to experiences reported during constant illumination (Section 5.3.3 and 5.3.4), the experiences of yellow, lines, and points in the higher frequency ranges are found to arise as a consequence of constant ganzfeld stimulation.

The probability of reports and the report times for the different subjective experiences in the forced-choice experiment with constant illumination correspond very well: experiences with a high probability of report (such as yellow, points, or lines) are reported significantly earlier during a stimulation epoch than other experiences. This suggests that these experiences may be the result of some other factors (such as a response bias) than the flickering stimulation, while other subjective experiences (such as red, green, zigzags, spirals) only develop after some period of continuous stimulation with the constant light and are more likely to represent spontaneous neuronal activities in response to sensory deprivation [50, 51].

In relation to the phase characteristics of subjective experiences outlined in Chapter 4, it seems interesting that the manual responses are tightly related to the stimulation phase even for experiences shown to be partly induced by other factors than the rhythmic stimulation. These experiences reported in Experiment 4 and 5 were shown not to generate phase specificity in circular analysis. However, the phase specificity in Experiment 2 and 3 may be based on the fact that the majority of reported experiences (even of yellow, lines, or points) still can be assumed to be generated by the flickering stimulation, and therefore provides some substantial input into the phase data of Experiments 2 and 3. Experiences generated by other factors than the flickering stimulation might be too sparse to have a substantial influence on the variability of the phase specificity.

As mentioned above, the experiences reported during constant ganzfeld illumination in Experiments 4 and 5 might represent spontaneous internal subjective experiences generated by the visual system of the observers due to visual deprivation. This possibility is emphasized by the fact that most kinds of subjective experiences that have been described during flicker stimulation were also reported during constant illumination. In addition, the reported experiences seem to show a high resemblance to experiences reported during complete or partial sensory deprivation described in the literature [52, 53]. It is especially interesting that Vernon [53] reported the number of subjective experiences to be higher in cases of weak homogeneous and constant illumination than during complete sensory deprivation in darkness. The moderate constant illumination provided in Experiments 4 and 5 might especially trigger the mechanisms responsible for the effects described in [53]. One possible explanatory approach of the emergence of such spontaneous subjective experiences relates to an idea described by Smythies [81] which aims to explain subjective visual experiences during flicker stimulation. Smythies suggested that the flicker stimulation generates unfamiliar brain activations and forces the system to generate hypotheses on what these activities actually represent. A similar account is conceivable for the emergence of subjective experiences during sensory deprivation. During prolonged stimulation with constant light effects of receptor fatigue, lateral inhibitions on the neuronal level, and feedback-connections between sub-cortical and cortical areas may generate a distinct pattern of neural activity in the brain. This pattern may be equivalent to activation representing ‘real stimulus’ characteristics and therefore may lead to the apperception of subjective experiences.

Chapter 6

Phenomenology of subjective visual experiences

6.1 Description of subjective colours

6.1.1 Rationale

The previous experimental investigations of subjective colour discussed in the preceding chapters relied on the verbal reports given by the participants. In Experiment 1, the free report study, observers freely described their subjective experiences without being primed with specific categories of colour or form. In Experiment 2 and 4 target colours were announced to the observers preceding each experimental trial. However, these verbal reports do not conclusively confirm the similarity of experiences between observers, as colours of quite different characteristics might be classified into the same categories in this verbal naming procedure. In addition, the rather broad classification of colours into 8 categories (blue, yellow, red, green, purple, white, black, grey) does not allow to investigate the relation of the exact colour to the stimulation parameters such as stimulation frequency.

The aim of Experiment 6 presented here was to describe the reported subjective colours using an objective measure of colour. The method of adjusting the red-green-blue-values (RGB-values) on a computer screen was used to derive the dominant wavelength of subjective colours experienced in each stimulation epoch. These dominant wavelengths representing the reported colours were then subject to detailed intra- and interindividual analysis. The ranges of wavelengths reported for each colour category were assessed, as well as interindividual differences in these ranges. Finally, the dominant wavelength of the reported colours was set into relation to the stimulation frequency.

6.1.2 Methods

The methods employed in Experiment 6 were as given in the general methods with the following exceptions or specifications.

Participants

Five practiced observers (all female, mean age 26.2 years, vision normal or corrected to normal) participated in Experiment 6. Observers were paid for their participation at a rate of 8 Euro per hour.

Design and Procedure

Experiment 6 consisted of two parts: (i) the ability of participants to reliably match colours using RGB-values on a computer screen was assessed. (ii) Participants matched the subjective colours they experienced during flicker stimulation on a computer screen using RGB-values. In part (ii) the flicker presentation (and experience of colour) and the matching of colour were presented in two different apparatuses. The participant had to switch from one apparatus to the other to reproduce the experienced colours. Therefore, it is necessary for the participants to hold the colour impression they have during flicker presentation in memory and to reproduce this colour on a different apparatus from memory. Part (i) of the experiment aimed to model these memory requirements and to show the reliability of colour reports under such conditions of reproduction.

Part (i) consisted of 220 trials of colour matching performed during one experimental session of 60 to 90 minutes. The stimuli were presented on a PC running in Windows98 with the experiment being programmed in Java. The first 20 trials were designed to familiarize the participant with the task of matching colour using RGB-values on a computer screen. The experimental layout is shown in Figure 6.1. The target colour was always displayed on the right part of the screen, while the match was shown to the left. Following the onset of a randomly generated target colour to the right (upper part of Figure 6.1), the participant was asked to use sliding buttons below the colour frames to match a colour as accurately as possible to the target colour on the left part of the screen (lower part of Figure 6.1). In the following 200 trials, which were aimed at measuring the ability of participants to reproduce a given target colour held in memory, the target colour was presented for 1 second and then disappeared. Colour matching was only possible after disappearance of the target colour, so that the target colour had to be kept in memory. The task was performed without any time restrictions. When the participants wished to validate the matched colour, they clicked on the left lower button 'Choose colour' and the next trial started. The button 'No colour' on the right was not functional in this experimental session, but was displayed for reasons of compatibility with the experimental sessions that followed. During the experiment, both the RGB-values of the target colour and the RGB-values of the generated colour were stored in ASCII-format files.

The second part of Experiment 6 used a simple response-time paradigm in which observers were asked to press a response key as quickly as possible on first experiencing a particular subjective experience and subsequently to match the experienced colour on a second PC. The target subjective experience was announced to observers in the form of a verbal instruction (red, blue, green, yellow, purple) given via headphones immediately prior to trial onset. In the event that the observer did not experience the target subjective colour, the trial was allowed to time out and a zero response time was recorded. Verbal instructions via headphones, stimulus generation, and response collection were all ensured by a PC running in MSDOS mode and programmed in C. Each trial consisted of a 20 second epoch of flickering stimulation followed by a dark, or resting, period during which the matching was performed. The matching was not time restricted, the next trial was started by the observer by pressing a button on the computer keyboard. The range of frequencies tested was 11 to 18 Hz and every frequency $\times$ colour combination was repeated 5 times over the entire experiment to ensure a suitable number of colour reports. Consequently, Experiment 6 consisted of 200 trials (8 frequencies $\times$ 5 target colours $\times$ 5 repetitions), divided into 4 sessions of about 60 minutes each. As in previous experiments, the frequency of flicker was maintained as trial-wise constant but was varied between trials. Both the

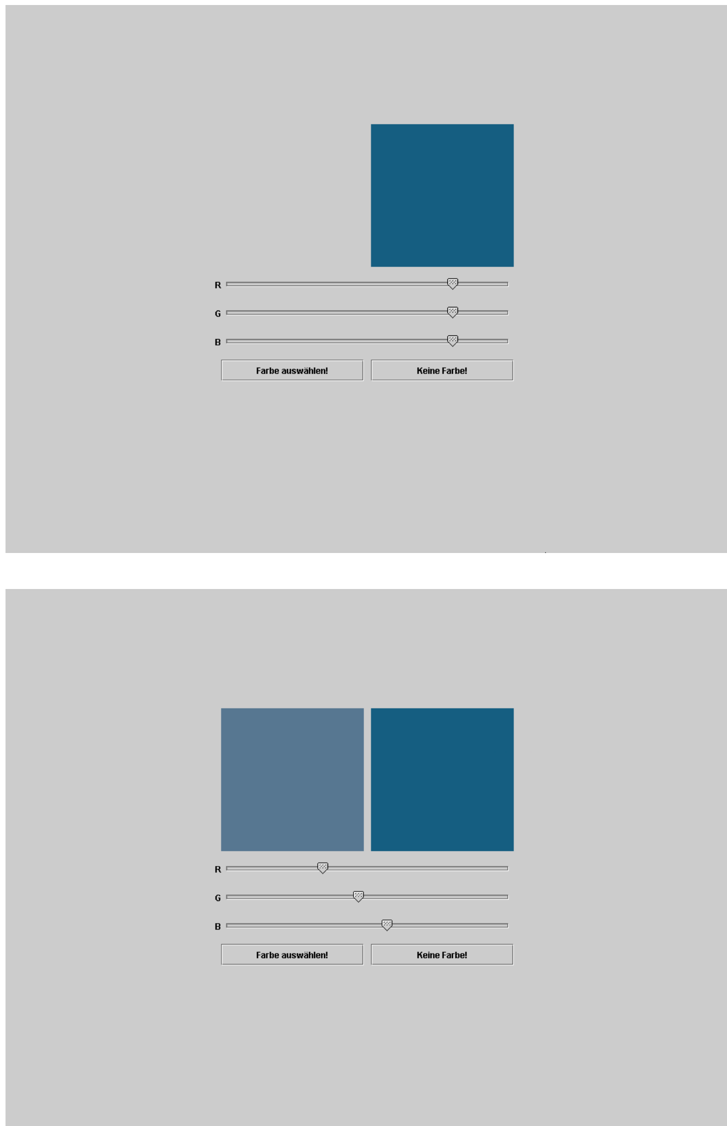


Figure 6.1: Screen shots of the task for the first 20 trials in session 1 of Experiment 6. The upper figure shows the initial configuration in a randomly chosen trial with the target colour on the right, while the lower figure depicts the situation after the participant has attempted to match the colour given on the right.

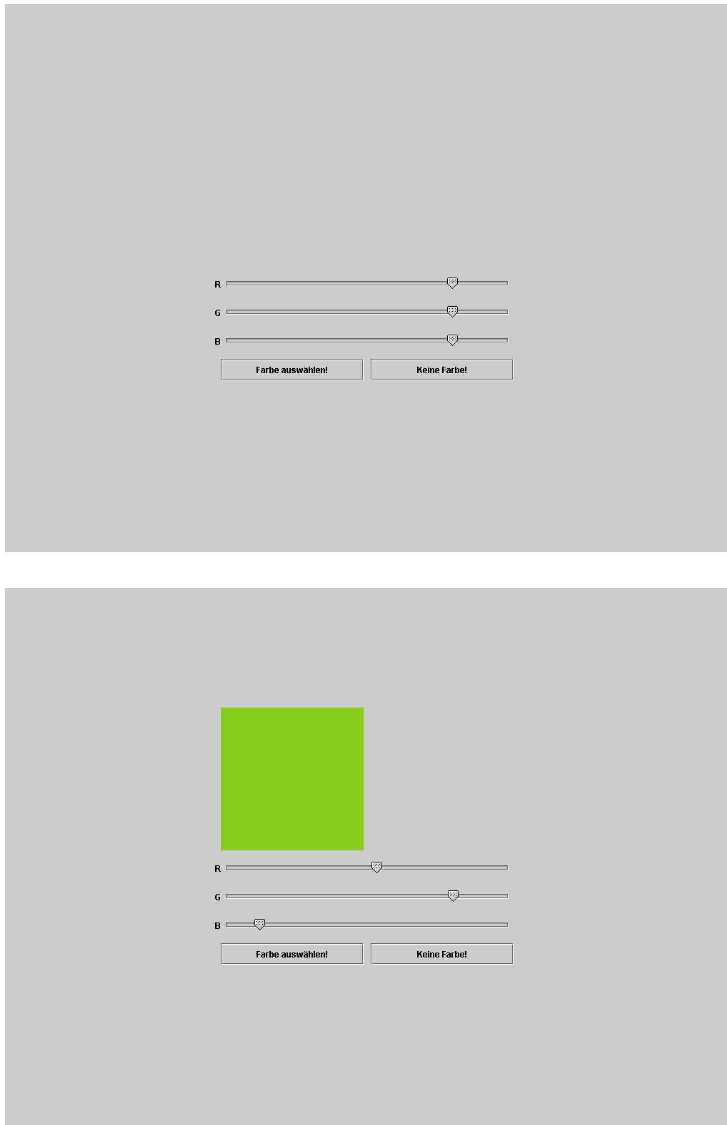


Figure 6.2: Screen shots of the colour adjustment task following flicker stimulation in Experiment 6. The upper figure shows the initial configuration, while the lower figure depicts the situation after the participant has attempted to match the colour he had experienced during flicker stimulation.

presentation order of flickering frequencies and the requested target subjective experiences were varied pseudo-randomly over trials and subsequently divided across the experimental sessions in each experiment. This procedure was carried out separately for each observer.

For the colour matching, the observers turned to the Windows98 PC with the colour matching software described above. The observers were presented with a light grey screen (see upper part of Figure 6.2) and were asked to generate the colour they perceived during flicker stimulation using the RGB-value slides. The generated colour appeared on the left of the screen (lower part of Figure 6.2). When the matching was finished, the participants clicked on the button 'Choose colour' and the generated colour was written in RGB-values into ASCII-format files. Should no colour have been seen during the flicker stimulation, the participants were asked to click the button 'No colour'.

Methods of analysis

A colour can be represented by its dominant wavelength. A monochromatic light with a wavelength equivalent to this dominant wavelength would have the same hue as the colour for which the dominant wavelength was determined, even though the saturation of the two colours may differ. The dominant wavelength is a one-dimensional representation of the hue information of a colour and provides a suitable measure for statistical analysis.

In the CIE-diagram (see Figure 6.3) colours of equal dominant wavelength fall onto a line from the white point of the CIE-diagram to the outer border representing all spectral hues with full saturation. This characteristic was used to determine the dominant wavelength of the colours matched by the observers. First, the measured RGB-values were transformed into xy-coordinates of the CIE-diagram. By drawing a line from the white point of the CIE-diagram through the matched colour the dominant wavelength was determined at the border of the CIE-diagram (Figure 6.3). Practically, this was achieved using a JAVA applet

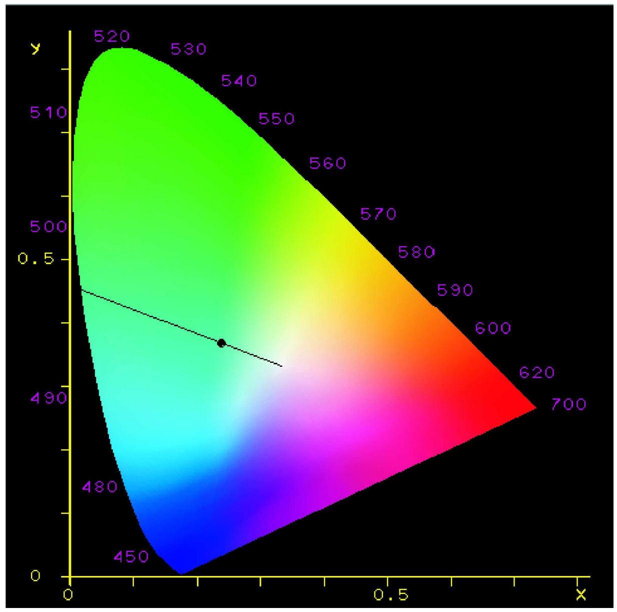


Figure 6.3: CIE colour diagram with a demonstration of how the dominant wavelength of a colour is determined. Spectral colours are represented at the U-shaped border, while purplish non-spectral colours are found at the lower flat line of the diagram. The white point is the origin of a linear function going through a colour to determine the dominant wavelength of that colour.

that automatically transformed RGB-values into dominant wavelength. It has to be noted that not all visible colours can be represented by dominant wavelength directly. All colours lying in the triangle between the white point and the lower left and right corners of the diagram (corresponding to percepts purple, and purplish red, and purplish blue) cannot be matched by a dominant wavelength, but always need a mixture of two monochromatic sources to be represented. However, these colours may be represented in one-dimensional wavelength information by using the inverse dominant wavelength. The inverse dominant wavelength is defined as the wavelength at the spectral border met by the line through the colour and the white point extended over and above the white point.

6.1.3 Results

Matching of computer generated colours

Participants were generally able to match very well the dominant wavelength of a real colour which had been presented to them shortly and had to be reproduced from memory. The target colours in session 1 were both of either positive or inverse dominant wavelength. In about 9% of all trials participants matched an inverse wavelength to a positive wavelength or vice versa. These trials were not further analyzed as the two calculated wavelengths cannot be compared in a sensible way. Most of these errors related to colours whose dominant wavelength can be found in the lower left and right corners of the CIE-diagram and were especially frequent for purplish target colours (i.e. target colours with inverse dominant wavelength; 16.1% errors for inverse target wavelength vs. 5.5% errors for positive target wavelengths). These errors may be due to a switch between positive and inverse wavelength which accompanies an only small phenomenological difference of the colour hue.

However, for all other trials in which positive and inverse wavelengths were matched with positive and inverse wavelengths, respectively, the observers showed a good ability to reproduce the target colour. In more than 75% of all trials, the matched colour did not differ more than 15 nm from the target colour (see Table 6.1). For individual participants the 75% thresholds were comparable: threshold deviations ranged from 12nm (76.2%), 14 nm (75.3%), 15 nm (75.4%), 16 nm (76.6%), to 19 nm (75.1%).

Matching of subjective colours

On the basis of the findings of session 1 that colour matching of a shortly presented colour kept in memory is reliable, the colour matching data of subjective colours experienced during flickering stimulation was analyzed.

Colour was reported in 60.3% of all trials with no differences for the differ-

Table 6.1: Accuracy of colour matching in part 1 of Experiment 6. The deviation on the left is a classification of the deviation of the matched colour from the target colour in nanometers (nm). Counts are the number of trials (out of 910) in which a deviation equal or smaller to the deviation given on the left was measured. The cumulative probability of a given deviation is depicted on the right. Details are given in the text.

Deviation	*Count*	*Cumulative*
0	51	5.60%
5	365	45.71%
10	169	64.29%
15	105	75.82%
20	67	83.19%
25	38	87.36%
30	28	90.44%
35	27	93.41%
40	15	95.05%
45	11	96.26%
50	11	97.47%
> 50	23	100.00%

ent colours ($\chi(4) = 9.4, p > .05$; blue being reported in 59% of all trials where blue was the target colour, green in 60%, yellow in 69%, purple in 72%, and red in 41.5%). All green and yellow reports could be transformed into positive dominant wavelength, whereas all purple reports were characterized by inverse dominant wavelength. Blue and red were partly matched with colours having inverse dominant wavelengths (25.4% and 9.6% of all trials where those colours were experienced, respectively). In the following statistical analysis, reports of blue and red with positive or inverse wavelengths were treated separately.

Two separate repeated-measures analyses of variance with the main factor colour (comprising 4 and 3 categories in the two analyses, respectively: blue positive, green positive, yellow positive, red positive; and blue inverse, purple inverse, red inverse) and wavelength as the dependent variable confirmed that all reported subjective colours can be clearly separated on the basis of the dominant wavelength of their RGB-matches. The analysis of colours with positive dominant wavelength revealed a main effect of colour ($F(3, 12) = 64.016, p < .05$, mean wavelengths: blue 474 nm, green 534 nm, yellow 570 nm, red 606 nm) and significant differences with $p < .05$ for all possible colour pairs. Similarly, the analysis for inverse wavelength colours revealed a main effect of colour ($F(2, 6) = 651.637, p < .05$, mean wavelengths: blue -566 nm, purple -550 nm, red -499 nm) and significant ($p < .05$) pairwise differences between the colours. These findings are illustrated in the lower part of Figure 6.4. The mean dominant wavelength and standard deviations of the matched colours are also given for each individual participant in Figure 6.4. In general, colours with inverse dominant wavelength (that is, 'purplish' colours) show very little variation within subjects, and also less variation between participants than positive wavelength colours. The same pattern is true for reports of yellow. The experiences of blue, green, and red, however, show some intra- and interindividual variation suggesting that these colours can be seen in different qualities: blue might also be a greenish blue, yellow may be seen as more greenish, or more reddish, and red may partly appear yellowish. Interestingly, while red, green, and blue are possibly coded directly in earliest stages of the visual system (i.e. the cones), yellow and purple are very likely to be colours whose experience only results from interactions of colour coding mechanisms (i.e. in retinal ganglion cells and later stages of processing).

Based on the result that the experience of subjective colour and form relates to specific frequency ranges (see Chapter 2), it can be assumed that the dominant wavelength of reported colours also relates to the frequency of the flicker stimulation. The following analysis was only conducted for colours having a positive dominant wavelength, i.e. blue, green, yellow, and red, and only for trials where such a positive wavelength was reported. Relating the mean dominant wavelength of all trials with a dominant wavelength to the stimulation frequency using linear

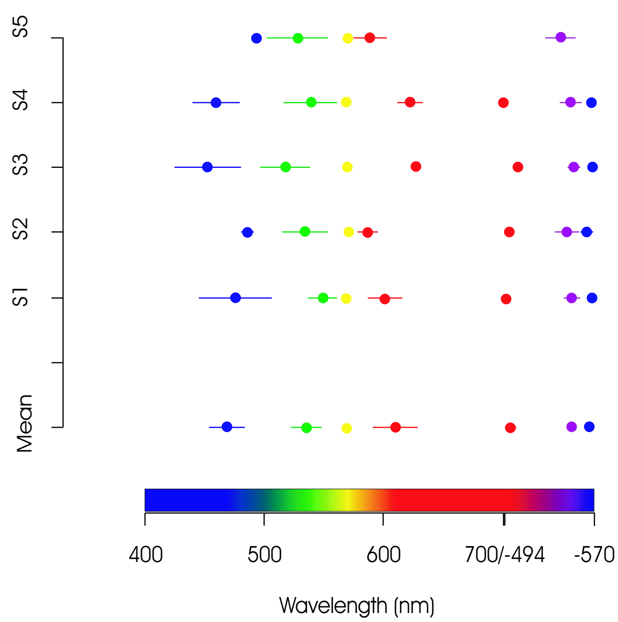


Figure 6.4: Experiment 6: dominant wavelengths of matched colours. S1 to S5 represent results of participant 1 to 5, respectively, while the lower line represents the mean data for all participants. The mean wavelengths of colour matches for the five colours surrounded by lines of one standard deviation are given. Matches with positive dominant wavelength are plotted on the left, and matches with inverse dominant wavelength can be found on the right. A continuous representation of colour as reported in the experiment is plotted at the bottom of the figure; the colour loci on the continuum are defined by the mean wavelengths of the colours over all participants.

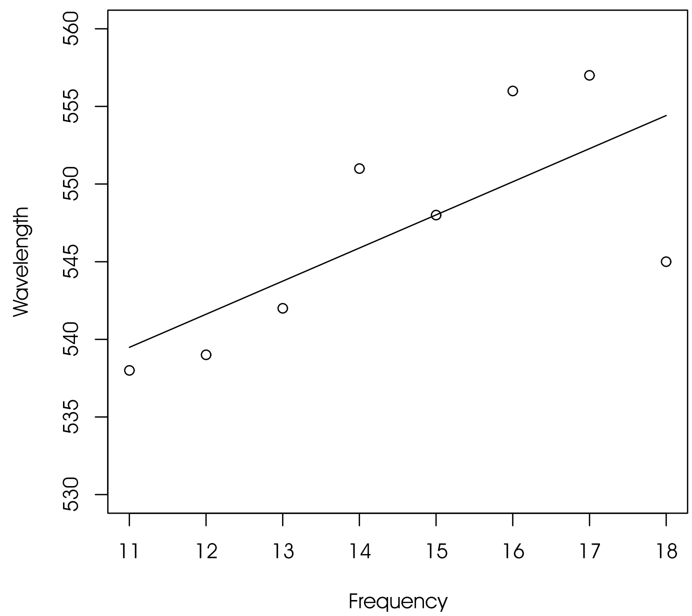


Figure 6.5: Experiment 6: Regression of the stimulation frequency and the dominant wavelength of reported colours. The points mark mean dominant wavelength for all trials with a positive dominant wavelength at a given stimulation frequency. The line represents the regression fit to the data with a correlation of $r = .71$.

regression revealed wavelength and stimulation frequency to be significantly correlated ($r = .712, p < .05$). In addition, the wavelength (W) increased significantly with increasing frequency (F) (see Figure 6.5, regression: $W = 2.119 * F + 516.274$, significance of the slope: $F(1, 6) = 6.17, p < .05$). The slope of the regression suggests that in the tested range of frequencies from 11 to 18 Hz the wavelength of the experienced colour increases by about 2 nm per 1 Hz increase in the stimulation frequency.

Interestingly, when considering the different colours (blue, green, yellow, and red) separately, no significant regressions can be found between the stimulation frequency and the reported wavelength. This means that within each colour category, the dominant wavelength remains more or less constant for different stimulation frequencies. However, a shift in the report probability of different colours appears over frequency (Figure 6.6). The relative frequency of report of each

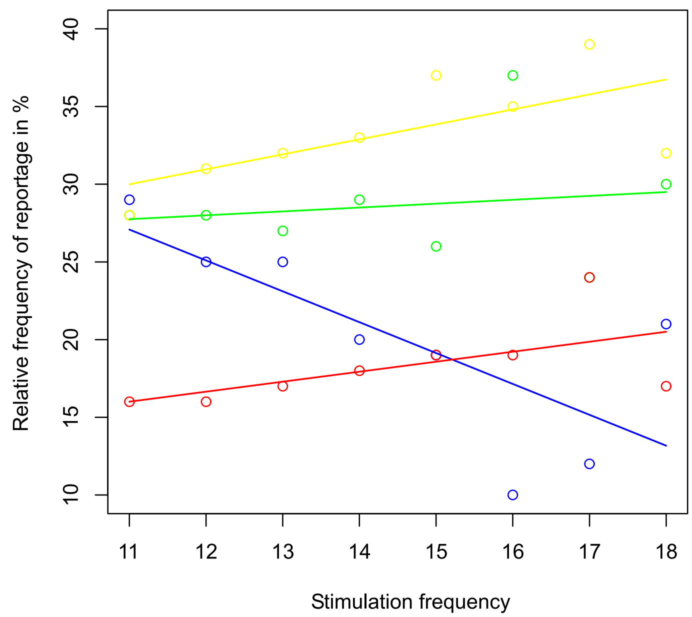


Figure 6.6: Experiment 6: Regression of the relative number of reports of a colour over stimulation frequency. 100% correspond to all reports of colour with a positive dominant wavelength given at a specific stimulation frequency.

colour was calculated in relation to the number of trials where any colour with a positive dominant wavelength was reported at a given stimulation frequency. Separate regression analyses for each colour revealed that the relative number of reports remains constant for green and red (insignificant slope of the regression, see Figure 6.6). However, the relative number of blue reports decreases significantly with increasing stimulation frequency (correlation: $r = -.748, p < .05$, regression: $N = -1.988 * F + 48.952$, where N is the relative number of reports, significance of the slope: $F(1, 6) = 7.611, p < .05$). While the relative number of yellow reports is significantly correlated with the stimulation frequency ($r = .674, p < .05$), the slope of the regression is only borderline significant (regression: $N = .964 * F + 19.393$, significance of the slope: $F(1, 6) = 5.005, p = .067$). However, there is a trend that the number of yellow reports increases with increasing frequency.

6.1.4 Discussion

Experiment 6 showed that (i) participants are able to reliably match colours which have been kept in memory for a short period of time. (ii) Colour categories are clearly separable on the basis of their dominant wavelengths for all participants. (iii) Intra- and interindividual variability for the 'primary' colours blue, green, and red is larger than for yellow and all purplish colours. And (iv) the wavelength of experienced colours depends on the stimulation frequency.

The fact that certain colours show more variability than others may be attributable to interindividual differences in the architecture of the retina. It has been shown that the relative numbers of different cone types vary widely between individuals [96, 142], even though surprisingly this seems to have little effects on the function of the visual system. Other individual differences at the physiological level having little influence on the perception of 'real' objects and colours are conceivable [143, 144]. The data of Experiment 6 suggests that individuals may differ concerning the spectral sensitivity of their different cone types. As an example, participant 3 might have S-cones sensitive to relatively low wavelengths and L-cones sensitive to relatively high wavelengths. The pattern might be different for participant 5 having S-cones that respond to relatively high wavelengths and L-cones responding to relatively low wavelengths (see Figure 6.4). Interestingly, these interindividual variations are minimized when perceiving colours such as yellow and purple. While yellow is the result of a computation of activity from L-, M- and S-cones (see Section 1.3.1) in the retinal ganglion cells, the percept of purple is possibly generated at a later processing stage where the activity of S- and L-cones is combined. However, the perception of both colours necessitates computational processing to be carried out before they can be represented in the visual system. It is possible that the small variations exhibited in the reported wavelengths of these colours are due to some balancing between different inputs, which occurs at this computational stage. The reason why individual physiological differences do not manifest themselves in ‘everyday life’ might be that these sluggish individual responses are balanced out in later processing stages of the visual stream.

The dependency of the wavelength of subjective colour on the stimulation frequency corroborates the results of Experiment 1 stressing the frequency specificity of subjective experiences. On the basis of the findings (ii) and (iv), it can be assumed that this dependency of colour on stimulation frequency is not continuous, but relates to different categories of colour. That is, an increasing stimulation frequency does not continuously increase the dominant wavelength of the experienced colour. Rather, at certain stimulation frequencies transitions from one colour category (e.g. blue) to another colour category (e.g. green) take place. This suggests that the subjective colours experienced during flickering stimulation do not cover the whole (i.e. continuous) range of natural colours that can be perceived by a human observer. Rather, the experiences seem restricted to a number of ‘primary’ or basic colour categories, in this case blue, green, yellow, red, and purple. This finding suggests a critical role of early colour coding stages for the experience of subjective colours. As has been outlined in Section 1.3.1, most cells in the LGN are tuned to stimuli along the cardinal red-green and yellow-blue axes [112]. Cortical colour cells, on the other hand, have been shown to respond to many other hues [105, 113], representing the full continuous gamut of natural colours. Thus, it may be assumed that the experience of subjective colours induced by flickering light are based on processing stages from the retina up to the LGN. The information thus generated is necessarily further transferred in the visual processing stream to reach consciousness. However, it seems likely that no further active processing, such as by top-down influences, occurs to the information stemming from these early visual areas.

6.2 Description of subjective forms

6.2.1 Rationale

Similar to the experience of colour, subjective forms were only described verbally in previous experiments. The aim of Experiment 7 was to collect graphical representations of subjective forms and to provide a better estimate of the similarity of reported forms within and between observers.

6.2.2 Methods

The methods employed in Experiment 7 were as given in the general methods with the following exceptions or specifications.

Participants

Six observers (1 male, mean age 30 years, vision normal or corrected to normal), participated in Experiment 7. Three of the participants (A, B, and C) were naive with respects to flicker induced subjective experiences and had never seen the examples given in the instructions of Experiments 3 and 5 (see Figure B.1). Observers were paid for their participation at a rate of 8 Euro per hour.

Design and Procedure

Experiment 7 used a simple response-time paradigm in which observers were asked to press a response key as quickly as possible on first experiencing a particular subjective form and subsequently to draw the experienced form on a sheet of paper. The target experience was announced to observers in the form of a verbal instruction (line, point, rectangle, wave, zigzag, circle, radial, spiral, grating) given via headphones immediately prior to trial onset. In the event that the observer did not experience the target form, the trial was allowed to time out and a zero response time was recorded. Verbal instructions via headphones, stimulus generation, and response collection were all ensured by a PC running in MSDOS mode and programmed in C. Each trial consisted of a 20 second epoch of flickering stimulation followed by a dark or resting period during which the drawing was performed. The drawing was not time restricted, the next trial was started by the observer by pressing a button on the computer keyboard. The frequencies tested ranged from 11 to 19 Hz and every frequency $\times$ form combination was repeated twice over the entire experiment to ensure a suitable number of form reports. As a result, Experiment 7 consisted of 162 trials (9 frequencies $\times$ 9 target forms $\times$ 2 repetitions), divided into 3 sessions of about 60 minutes each. As in previous experiments, the frequency of flicker was maintained as trial-wise constant but was varied between trials. Both the presentation order of flickering frequencies and the requested target experiences were varied pseudo-randomly over trials and subsequently divided across the experimental sessions in each experiment. This procedure was carried out separately for each observer.

For drawing the experienced forms the participants turned to a table where paper sheets with six square boxes were prepared. The participants either crossed a mark indicating 'No form was seen' or drew the experienced forms into the boxes using a ballpoint pen. Participants were explicitly asked only to draw the target forms of each trial. The drawings were later scanned into a PC using a resolution of 300 dpi and a grey-scale colour scheme.

6.2.3 Results

Form was reported on 47% of all trials with no differences in report frequency for different forms ($\chi(8) = 13.7, p > .05$; circle being reported in 58% of all trials where circle was the target form, grating in 48%, line in 50%, point in 52%, radial in 50%, rectangle in 33%, spiral in 48%, wave in 37%, and zigzag in 40%). Four of the participants (A, B, D, and F) reported all target forms, participant E never reported rectangles, and participant C never reported circles, points, rectangles, or zigzags.

The drawings of the subjective forms by the participants are given in Appendix H. Some characteristics of the drawings will be explored in the following for each form category separately.

The response 'circle' rarely corresponded to the experience of a single circle (about 13% of all trials where circles were reported). More often the experience was composed of a number of circles, which were either nested (i.e. one within the other, about 35%), displayed one next to another (about 56%), or both (about 14%). In about 19% of circle-present trials other experiences, such as lines, radials, and triangles were drawn as well. In addition, in about 22% of the trials a number of small circles formed other complex figures, which might be classified as circles, radials, or lines. The experienced circles are rather similar between individual participants.

A grating is per definition composed of more than one element, so the forms drawn for gratings were all rather complex in nature. In general, the drawings may be classified into four different categories: (i) a grating composed of a number of small points. This type of grating was only reported by participant B. (ii) A grating composed of straight lines which were overlaid to form a grating (29%). (iii) A grating composed of overlaid curved lines (about 12%). And (iv) honeycomb-like patterns, which were usually composed of a number of polygon shapes (46%). The different types of gratings were also found to co-occur in a minority (6%) of the trials. In 8% of the trials circles were drawn in addition to the target gratings. Some interindividual differences seem to exist for the perception of subjective gratings. While type (i) was only reported by participant B, straight line patterns (ii) were drawn by participants A, C, E, and F, and curved line patterns (iii) by A and C. Polygon-composed gratings (iv) were reported by the participants A, C, D, and E.

A single line was only reported in one trial. Usually, the report of the form category 'line' corresponded to a number of lines in various configurations. Lines were either straight (77%) or curved (33%), while both types appeared together in some trials. Partly, other forms, such as radials, waves, zigzags, circles, or gratings, either co-occurred with lines or were composed of lines (31%). Besides a tendency of participant D to report only straight lines, no interindividual differences in the reportage of lines were observed.

A single point was drawn in 5% of all trials, while normally a larger number of points appeared. Points generally tended to form other shapes (46%), or co-occurred with other forms (25%). Interestingly, there was a difference in points concerning their spatial extension. They were either very small (with virtually no spatial extension, 54%) or larger (but usually smaller than circles, 48%). Again, these two types of points could both be drawn in a single trial. Interindividually, the forming of shapes out of points was especially pronounced in some participants (A and B, and partly D), while participant E tended to report only small points without any spatial configuration.

A radial pattern is defined here as a pattern where lines run from the centre to the periphery along the radii of a virtual circle. 76% of all drawings in response to the target 'radial' can be classified according to this definition. Again, the radial patterns were composed of straight lines (50%) or curved lines (43%). The drawings of curved-line radials have some similarity with spirals and might represent a point in the transition process from radials to spirals, or vice versa. In about 19% of all trials, more than one radial was drawn by the participants. All participants drew radials which correspond to the above definition. While participants B and C showed some preference for curved-line radials, D and E exhibited a preference for straight line patterns.

Four different kinds of rectangles were observed: single rectangles (6%), multiple nested rectangles (8%), multiple overlapping rectangles (30.5%), and multiple rectangles which were drawn next to each other (55.5%). Interestingly, none of these classes appeared together in a trial. A strong interindividual effect was observed in the drawing of rectangles: single rectangles were only reported by participant B, while nested and overlapping configurations were only reported by participant A.

The majority of reported spirals were a configuration of lines running from the centre to the periphery more or less perpendicular to the radius of a virtual circle (35% of all trials with a reported spiral). This configuration was reported by all participants, while participant A and B also reported coil-like configurations (37%) and the two were partly combined in participant B (i.e. spirals were formed out of coils, 8%). In most of the trials, a single spiral was reported. Multiple spirals were drawn by all participants, but D, in 21% of the trials.

Waves were always reported in multiples, and in 20% of the trials waves were accompanied by other forms (radials, spirals, lines, circles, points). The reported waves differed in their amount of curvedness, expressed by the number of peaks in a drawn wave. Simple waves with one or two peaks were reported more often (about 45% of the trials) than complex waves with 3 - 6 peaks (about 30%) or very complex waves with more than 6 peaks (about 25%). Individually, participants A and F tended to report more simple waves, while participant C mostly reported waves of a complex type.

Zigzag patterns that were reported can be classified into zigzags with sharp edges (65% of all trials where zigzags were reported) or more round edges (30%). There is some individual preference for one or the other type: participant E always drew round-shaped zigzags, participant B reported both types, and all other participants drew sharp-edged zigzags. Interestingly, while single zigzag lines were rarely reported, multiple zigzags could be organized in a specific fashion. The different zigzag lines could be drawn one above or besides one another either with in-phase peaks (about 53% of the trials) or with peaks which are spatially out of phase by some intermediate degree (12%) or by 180 degrees (19%).

6.2.4 Discussion

Despite some individual specificities in the reported and drawn forms, a high interindividual accordance between the experiences can be inferred. For each form category, there exists at least one type of pattern which is drawn by at least 50% of the participants. These patterns can be described as following: multiple circles drawn next to each other, gratings composed of straight lines or polygons, straight and curved lines, small and large points, distinct radials formed out of straight or curved lines, multiple rectangles drawn next to each other, distinct spirals, simple and complex waves, sharp zigzag patterns.

These reported forms clearly resemble the drawings of subjective forms obtained in studies of stroboscopic ganzfeld stimulation [80] and electrical or magnetical stimulation [13].

Most interestingly, the forms also resemble patterns which can be generated in experimental physics by bringing surfaces into resonant oscillation. An example are ordered wave states on the surface of a liquid that was stimulated by some vertically applied vibration [133]. The thus reported spatial configurations included radial patterns, as well as gratings in the form of honeycomb patterns.

Furthermore, by computational modelling of epileptic brain activity, Tass [136, 145] induced the spontaneous formation of patterns of activity that correspond to the form categories radials, circles, spirals, points, rectangles, and gratings of the experiment presented here. These findings are well in accordance with the suggestion of Stwertka [134] that subjective forms observed during stroboscopic visual stimulation are self-organizing macrostates of spatio-temporal coherence in the cortex.

In combination with the result that the experience of subjective form is restricted to specific frequency ranges, the following scenario might emerge from these findings: the repeated stimulation applied to the visual system by viewing flickering light generates some resonant oscillations very early in the neuronal tissue. Lateral interactions which are necessary for generating such resonances are found in the visual processing stream as early as in the retina. These resonant oscillations may be characterized by specific patterns of activation in the neuronal substrate (comparable to the ones described in [136]). It might be assumed that these activations in very early stages of the visual processing are similar to the ones that would be induced by perceiving ‘real’ stimuli of the same form. In being transferred further through the visual system, these form-like neuronal activations might activate the corresponding spatially distributed orientation columns in the cortex, thereby generating the experience of the forms described by the observers of flickering light.

Chapter 7

Electrophysiological correlates of subjective colour

7.1 Rationale

The aim of Experiment 8 described in this chapter was to investigate electrophysiological correlates of subjective colour. While a few electroencephalographic (EEG) studies concerning subjective form are reported in the literature [86, 87], subjective colour has not yet been studied electrophysiologically. In most models the experience of subjective colour has been attributed to early processing stages in the visual system (e.g. [130, 132]). However, for the conscious apperception of these experiences extended processing in the higher cortical areas is necessary. Experiment 8 aimed to investigate EEG-correlates of the cortical processes which are related to the reportage of subjective colour.

The measured EEG response on the scalp is the result of a synchronized activation of large neuronal assemblies in the brain at certain oscillation frequencies. Therefore, synchronization of neurons is represented by an increase of EEG power, while desynchronization is marked by a decrease of EEG power values (see for example [45]). The oscillatory components of the EEG are generally divided into the following frequency bands: delta covering oscillations between approximately 0 and 3.5 Hz, theta between around 4 - 7.5 Hz, alpha 8 - 13 Hz, beta 13 - 30 Hz, and gamma 30 - 60 Hz [146, 147]. In addition, it has been shown that the alpha band can be divided into a lower and upper alpha band, which are largely independent of each other [148] and functionally non-equivalent [149].

Different functionalities have been attributed to the different frequency bands (see [150] for a review). The two frequency bands described most extensively in the literature about visual perception, and also of most relevance for the present study, are the alpha and gamma EEG bands.

Alpha activity can be found in humans in the relaxed awake state with closed eyes [146]. A stimulation or activation of a person usually results in a decrease of alpha power, representing a state of cognitive activation [45, 146]. Klimesch states [149] that the desynchronization of alpha rhythms (i.e. the decrease of alpha power) reflects the activity of cortical areas involved in assessing, searching, and retrieving semantic long-term memory information. Specifically, a desynchronization of the lower alpha band is thought to reflect attentional processes and task demands, and is topographically widespread over the entire scalp [45, 149]. In contrast, a desynchronization of the upper alpha band reflects stimulus related cognitive processes, such as sensory-semantic information processing, and is topographically restricted [45, 149].

Interestingly, EEG alpha rhythms have also been associated with visual detection and discrimination performance and the perception of multistable figures. Ergenoglu et al. [151] have shown that the relative power of the EEG alpha band was low in trials in which an at-threshold stimulus was detected, as compared to trials, in which the stimulus could not be detected by the observers. The finding that good perceptual performance is related to small alpha power in a reference interval preceding task performance was confirmed in a study by Hanslmayr et al. [152] in a perceptual discrimination task.

Consistent with these findings, EEG studies of perceptual reversals revealed decreasing alpha activity preceding multistable transitions [153, 154, 155]. Multistable figures such as the Necker cube are characterized by spontaneous transitions between two perceptual interpretations of a single input reaching awareness. Using magnetoencephalographic (MEG) measurements, a continuous decrease of endogenous alpha activity was shown to precede the reversal between two stimulus interpretations [156]. In addition to changes in alpha activity, a role for gamma band activation during the perception of multistable figures has been claimed [157]. Although the reported enhancement of gamma power was highest at fronto-central locations, it could also be observed in parietal and occipital areas. However, variations in gamma activity power could not be replicated in MEG investigations of multistable percepts [156].

Gamma band activity is functionally associated with linking perceptual information (the so-called 'binding' of stimulus features) and memory processes [158].

However, gamma activity has also been related to attentional demands, where attentional engagement enhanced the 40 Hz EEG response [159]. In relation to perception, gamma activity is assumed to correlate with the perception of coherent visual patterns. Tallon et al. [160] found a specific 30 Hz power increase in the case of the presentation of a coherent object, which could be real (i.e. a real triangle) or illusory (i.e. a Kanizsa triangle). Tallon-Baudry and Bertrand [161] especially emphasize the role of oscillatory induced gamma activity for the representation of objects. Both Basar-Eroglu et al. [158] and Tallon-Baudry and Bertrand [161] agreed that gamma activity may be rather widespread over the brain. Therefore, gamma activity may be assumed as a generalized brain mechanism with different functional correlates depending on its location and generators.

A relation of EEG frequency bands to the different scales of cortical integration was suggested by von Stein and Sarnthein [162, 163]. While local synchronization during visual processing evolved in the gamma frequency range, synchronization between neighboring temporal and parietal areas during multimodal semantic processing evolved in the beta frequency range, and long fronto-parietal interactions during working memory retention and mental imagery were present in the theta and alpha frequency range.

Klimesch [45, 149] stressed the fact that the EEG frequency bands should be determined separately and individually for each experimental participant. As the ranges of EEG bands differ between human subjects, using standardized bands for the EEG analysis results in a loss of information due to an incorrect association between EEG bands and actual brain frequencies. Individually derived EEG frequency bands allow to detect band-specific activations even with individually differing EEG frequency distributions.

In Experiment 8 EEG responses during and related to the experience of subjective colour will be investigated with a special focus on the involvement of different frequency bands of the EEG in the conscious experience of subjective colour.

7.2 Methods

The methods employed in Experiment 8 were as given in the general methods with the following exceptions or specifications.

Participants

Four healthy practiced volunteers (all female, mean age 27 years) participated in the experiment. All had normal or corrected to normal vision. Participant CB and KM were left-handed, participant GR and KO were right-handed. Participants were paid for their participation at a rate of 8 Euro per hour.

Design and Procedure

Experiment 8 used a simple response-time paradigm in which observers were asked to press a response key with the left index finger as quickly as possible on first experiencing a particular subjective colour. The target colour was announced to observers in the form of a verbal instruction (red, blue, green, yellow, purple, white, black, grey) given via headphones immediately prior to trial onset. In the case of a button press response the flicker presentation terminated with the button press. In the event that the observer did not experience the target subjective colour, the trial was allowed to time out and a zero response time was recorded. After completion of a trial (with or without response) the observers were asked to name all other subjective colours which appeared to them during the flicker epoch. These responses were written down by the experimenter. Verbal instructions via headphones, stimulus generation, and response collection were all ensured by a PC running in MSDOS mode and programmed in C. Each trial consisted of a 20 second epoch of no stimulation serving as a baseline condition for the EEG recording, followed by a 20 second epoch of flickering stimulation. The verbal instruction was always given before the baseline condition, ensuring that the memory load of remembering the target colour was similar in the baseline and in the experimental flicker condition. The beginning of the next trial was always initiated by the experimenter. Frequencies between 13 and 20 Hz, which have been shown to be most effective in inducing subjective colour, were tested, while the frequency of flicker was maintained as trial-wise constant but was varied between trials. Both the presentation order of flickering frequencies and the requested target subjective colour were varied pseudo-randomly over trials. This procedure was carried out separately for each observer and each of the two sessions per observer. Consequently, every frequency $\times$ colour combination was tested twice in the course of the entire experiment. Including EEG preparation an experimental session lasted about 2 hours (including 45 minutes of proper experimental testing).

EEG

The EEG was recorded from 64 Ag-AgCl electrodes according to the extended 10-20 system with a sampling rate of 500 Hz. The electrodes were mounted in an elastic cap and referenced to Cz while ground was fixed to the left arm. Electrode impedance was kept below 5 kOhm. The EOG was registered with standard electrodes F9 and F10 at the outer canthi of each eye serving as horizontal EOG. Electrodes Fp1 and one additional electrode below the left eye served as vertical EOG. EEG activity was amplified using BrainAmpMR amplifiers (BrainProducts) with a sampling rate of 500 Hz filtered with a low cutoff at 1 Hz high cutoff frequency of 100 Hz. The following 18 electrodes were included in the later analyses: F5, Fz, F6, T7, C5, C6, T8, P5, Pz, P6, PO7, PO3, Poz, PO4, PO8, O1, Oz, and O2.

Experimental triggers were sent to the EEG at the beginning of the baseline epoch of each trial, at the beginning of the flicker epoch, and at the time of the manual response (or at the end of a no-response trial).

Methods of analysis

To account for the individual differences in electrophysiological brain responses as described by Klimesch [45], the following analyses were conducted separately for each participant. Subsequently, the patterns of activity revealed for individual participants were compared with the aim to establish general patterns of electrophysiological activities during the experience of subjective colour.

No-response trials were only very rarely trials where no subjective colour at all was perceived (less than 1% of all trials, and 2.5% of all no-response trials). In all other trials without a manual response, other colours than the target colour were perceived and reported verbally following the trial. Therefore, and because the specific temporal pattern of colour emergences is unknown in these trials, no-response trials are not suitable as control conditions and are excluded from the further analysis.

With the aim to increase the power of the statistical analyses no differentiation between the different colours was applied, that is responses to the different colours were all treated as responses to the category 'colour'.

Three specific stimulation epochs were defined within each trial: (i) a baseline epoch, consisting of 2000 ms during the baseline condition (i.e. no stimulation) starting 10 s after trial onset (in the middle of the black screen interval). (ii) A flicker baseline epoch, representing an epoch of flicker stimulation during which no response was given and the likelihood of subjective colour was low. To avoid artifacts induced by the flicker onset, this epoch started 500 ms after flicker onset and was of duration 2000 ms. As manual responses given earlier than 2500 ms following flicker onset were only found in 7% of the trials of Experiment 8, the above procedure ensures a very low probability of subjective colour to be experienced within this flicker baseline epoch.(iii) The flicker epoch immediately preceding the response to a subjective colour was of duration 2000 ms.

A fast Fourier transformation (FFT) using a hanning window (10%) was cal-

Table 7.1: Lower and upper limits of the individual alpha frequency ranges in Hz. Further information is given in the text.

Participant	Lower	Upper
CB	7,0	12,5
GR	6,5	13,5
KM	8,0	13,5
KO	7,0	14,0

culated on the three different epochs described above for each trial separately. The frequency resolution of the FFT was set to 0.5 Hz, including normalized data for the frequency range from 1 Hz to 100 Hz. The FFT was calculated on a time window of 512 ms that was shifted along the 2000 ms epochs in 100 ms steps, such that for each 2000 ms epoch fast fourier transformations for 20 short time periods were derived. Following the FFT the mean power values for all trials were calculated separately for each subject, each EEG frequency bin (of 0.5 Hz) and each of the 20 periods of the three stimulation epochs.

The individual alpha frequency (IAF) ranges were determined by the method developed and described by Klimesch [149]. For the baseline epoch, the power spectra were calculated for each participant and each of the 18 electrodes. By visual inspection, the beginning of the ascent and the end of the descent of the alpha peak were derived for each participant and electrode. The individual alpha bandwidths were calculated as the mean of the thus determined IAF ranges over all electrodes and are given in Table 7.1.

The IAF range was divided into two mostly equal parts to form the lower alpha frequency range and the upper alpha frequency range. Based on the literature (e.g. [45, 158]), the other EEG-frequency ranges were defined on the basis of the the IAF ranges as following: the theta frequency range was defined to cover 2 Hz below the lower alpha frequency range, and delta was defined as the range from

1 Hz up to the theta frequency range. The beta frequency ranges covered 10 Hz above the higher alpha frequency range, and the gamma frequency range consisted of a 20 Hz range above the beta frequency range. The different frequency ranges for each participant can be found in the figures in Appendix I.

As Experiment 8 aimed to investigate electrophysiological correlates of subjective colour experiences, it was necessary to eliminate electrophysiological activity due to the the individual brain activity, the experimental situation (for example, memory load), and the effect of flicker on the visual system. Electrophysiological activity during the baseline epoch (i.e. no stimulation) may account for individual activation differences and activations due to memory processes during holding of the target colour in a memory store. The flicker baseline epoch is assumed to generate additional activity which is specific for a stimulation with flickering light that is not (yet) accompanied by subjective experiences. In contrast, activation during the flicker epoch shortly before a response is given is thought to contain activity of all these different kinds in addition to activity specific for the experience of subjective colour. The power values for each subject, each frequency bin and each of the 20 periods were thus corrected using the subtractive method as follows:

$$P_{diff} = (P_{Flicker} - P_{Baseline}) - (P_{BaselineFlicker} - P_{Baseline}) \qquad (7.1)$$

where P_{diff} is the corrected power of the EEG, $P_{Baseline}$ is the power during the baseline condition without stimulation, $P_{BaselineFlicker}$ is the power of the flicker baseline condition, and $P_{Flicker}$ is the EEG power in the epoch 2000 ms before a response was given. The right term of the equation represents activity due to flickering stimulation, but without individual or memory components, while the left term represents the activation due to flicker and subjective experiences, but minus the individual or memory components. The subtraction of the two terms therefore results in the EEG power in response to a subjective experience, without the activation induced by flicker, individual variability, or memory requirements.

The corrected power values were then subject to regression analyses of the power against time. The analyses were done separately for each participant, each of the 18 electrodes, and each of the 6 frequency bands. The aim of these analyses was to determine changes in the power of different EEG frequency bands over time. The time window considered was beginning 2000 ms before a response that signalled the experience of a target colour and ending at the response time. The EEG power values were assumed to increase or decrease significantly when the slope of the regression had a positive or negative sign (for increases or decreases, respectively) and was significant with $\alpha < .05$.

7.3 Results

Participant CB

The target colours were reported by participant CB in 75% of all trials. 22.9% of those target present responses were given in trials where no other subjective colour was perceived and reported.

The regression analysis of EEG power over time revealed the following patterns of activity for the different frequency bands of the EEG. In the *delta* frequency range between 1 and 4 Hz (Figure I.1), EEG power increased significantly during the 2000 ms before response at right temporal, central, parietal, and parieto-occipital locations. In addition, a power increase was observed at left parietal and parieto-occipital electrodes. *Theta* activity (4.5 - 6.5 Hz, Figure I.2) decreased significantly at right frontal, left frontal, and left temporal locations. A general decrease (excluding the fronto-central electrode) was observed for *low alpha* rhythms (7 - 9.5 Hz, Figure I.3), whereas the *high alpha* activity (10 - 12.5 Hz, Figure I.4) increased fronto-centrally and decreased on the right hemisphere (but not frontally), the central line, and PO3. *Beta* power (13 - 23 Hz, Figure I.5) increased in a generalized manner over the entire scalp. In addition, a widespread increase in *gamma* power (23.5 - 53.5 Hz, Figure I.6, not present at Oz and PO4) was found, accompanied by a fronto-central activity decrease.

Participant GR

Participant GR gave target present responses in 36.7% of all trials, while no other colours were reported in 27.7% of those target present trials.

The regression analysis revealed a left parietal activity increase in the *delta* band (1 - 3.5 Hz, Figure I.7) for participant GR, whereas no activity change was observed in the *theta* frequency band (4 - 6 Hz, Figure I.8). *Low alpha* activity (6.5 - 10 Hz, Figure I.9) increased over the entire left hemisphere, the right frontal, central, temporal, parietal, and occipital areas, and at POz and Oz. In contrast, the *high alpha* activity (10.5 - 13.5 Hz, Figure I.10) decreased at the following electrodes: Fz, F6, C6, P6, PO4, O2 on the right hemisphere, PO7, PO3, O1 on the left hemisphere, and Oz. While *beta* power (14 - 24 Hz, Figure I.11) decreased at Pz and PO7, it increased at Fz and on the right scalp at F6, P6, C6, PO4, PO8, O2. The *gamma* activity (24.5 - 54.5 Hz, Figure I.12) in participant GR was characterized by a general decrease of power (that excluded only T8, Pz, PO7, and O1).

Participant KM

The target colours were reported by participant KM in 76.6% of all trials. 4.1% of these target present responses were not accompanied by other colour reports.

Participant KM showed a generalized increase of *delta* power (1 - 5 Hz, Figure I.13) over the entire scalp. *Theta* activity (5.5 - 7.5 Hz, Figure I.14) was increasing with time at the parieto-occipital electrodes PO3, POz, PO4, but decreasing at the right temporal location. A decrease that spared the central line and the parieto-occipital electrodes PO3 and PO4 was observed for *low alpha* power (8 - 10.5 Hz, Figure I.15). *High alpha* activity (11 - 13.5 Hz, Figure I.16) showed a decrease at all parietal, parieto-occipital, and occipital areas, as well as an increase at the right temporal electrode. A pattern of activity decrease was also found for the *beta* frequency range (14 - 24 Hz, Figure I.17) at Pz, POz, PO3, and O1. Finally, *gamma* activity (24.5 - 54.5 Hz, Figure I.18) decreased frontally, but increased at central, right temporal, parieto-central, parieto-occipital (excluding PO3), and occipital scalp locations.

Participant KO

Participant KO reported the target colour in 53.9% of all trials with 2.9% of these trials being restricted to the report of the target colour.

Whereas an increase in activation in the *delta* band (1 - 4 Hz, Figure I.19) was restricted to Pz, the activity increase for *theta* frequencies (4.5 - 6.5 Hz, Figure I.20) was more widespread and excluded only P5, PO7, PO8, and O1. *Low alpha* power (7 - 10.5 Hz, Figure I.21) decreased at all electrodes, but the left parietal and parieto-occipital ones. In contrast, *high alpha* activity (11 - 14 Hz, Figure I.22) increased at the left temporal and occipital locations, as well as at the outer parieto-occipital locations on both hemispheres. *Beta* power (14.5 - 24.5 Hz, Figure I.23) decreased significantly at P5 and PO3, and showed an increase at Fz and T7. The increase in *gamma* activity (25 - 55 Hz, Figure I.24) was rather widespread over the scalp and was only not found at F5, F6, C6, P5, Pz, PO3.

Comparative analyses between participants

The aim of the following analysis is to derive interindividually reliable patterns of changes in EEG power in the different frequency bands. Separately for each electrode and each frequency band, the number of participants was calculated showing a significant increase or decrease of power over time. An activity change was assumed to be reliable interindividually if it was present and had the same sign in at least 3 out of 4 participants. It has to be noted that the exact frequencies of the different EEG bands differed slightly between participants. For this reason the following analysis is related to the EEG frequency bands rather than distinct EEG frequencies. The results of the analysis are displayed in Figures I.25 to I.30 and will be described in the following.

The neural activation during a 2000 ms period preceding responses to subjective colour was characterized by a significant increase in *delta* band power at the left parietal electrode (P5). No reliable changes in power were found for EEG responses in the *theta* band. The *lower alpha* band was characterized by a bilateral decrease of activation at frontal (F5, F6), central (C5, C6), temporal (T7, T8) and occipital (O1, O2) locations, and a right-hemispheric decrease at parietal (P6), and parieto-occipital (PO8) locations. In contrast, the power decrease in the *high alpha* band was less widespread and covered right parietal (P6), parieto-occipital (PO4), and occipital (O2) locations, as well as left and central parieto-occipital electrodes (POz, PO3). The *beta* band was characterized by a significant and reliable increase of power over the fronto-central electrode (Fz). Interestingly, the change of power at Fz in the *beta* band is directly inverse to the change in the *gamma* band with a significant and reliable decrease of power at this location. In addition, increasing *gamma* power was observed to be widespread over the entire scalp at central (C5), temporal (T8), parieto-occipital (PO7, POz, PO8), and occipital (O1, O2) locations. Differences in activation for the two hemispheres are therefore especially pronounced for delta activation with a left-sided increase, and for the low and high alpha bands with a more widespread decrease of power on the right hemisphere. In contrast, changes of activation in the gamma band were not specific to a hemisphere, but appeared widely over the brain.

7.4 Discussion

The changes of EEG power show a consistent picture across the participants, which agrees very well with the functional role ascribed to the different frequency bands in previous studies. The observed desynchronization of activity in the alpha frequency bands suggests an increase of task demands in a period preceding the experience and response to a subjective colour. The decreasing alpha activity in interaction with the increasing gamma power may correspond to an increasing differential activity of cortical areas and pathways related to cognitive function and attention. Specifically, the widespread decrease of low frequency alpha power may reflect the involvement of attentional processing [149], while the right parietal and occipital desynchronization of high alpha activity may point to more stimulus related cognitive processes [149] or processing of sensory-semantic information [45], such as the retrieval of colour categories and names from long term memory.

In Experiment 8, participants usually reported seeing a number of other colours preceding or co-occurring with the experience of the target colour. A switch between different colours may necessitate the inactivation of a subjective colour to allow the generation of a conscious experience of another colour. In this respect, the experience of subjective colour may be similar to the perception of multistable figures, where one interpretation of the figure is deactivated and replaced by another interpretation. The decrease of alpha power preceding the report of subjective colour may reflect such a transition. Specific changes of activations in the alpha frequency bands have been reported during the perception of multistable figures (see for example, [153, 156]). Strüber and Herrmann [156] hypothesize that the alpha activity during the perception of one interpretation of a multistable figure constantly decreases until it reaches a critical threshold and a perceptual switch occurs. One may add that the constantly decreasing synchronization of alpha rhythms may allow the cortical networks to synchronize in other processing rhythms (such as gamma), which might code the representation of a new percept.

The idea that low alpha activation might provide an endogenous and necessary condition for the successful conscious experience of a stimulus is also emphasized in the studies of Ergenoglu et al. [151] and Hanslmayr et al. [152]. In these studies, it was shown that a stimulus presented at perceptual threshold is more likely to be detected when the power of alpha rhythms is relatively low directly preceding the stimulus presentation. The effect of such alpha desynchronization preceding stimulus detection was especially pronounced in the parietal and occipital areas [151].

The complementary result of a gamma activity increase preceding the experience of subjective colour similarly corresponds to patterns of EEG activity observed during the perception of multistable figures. Basar-Eroglu et al. [157] reported enhanced gamma band activation at frontal, parietal, and occipital areas preceding the switch of a multistable perception. The increase of gamma power all over the scalp observed in Experiment 8 corresponds well with this pattern of a widespread increase of gamma activation. Puzzling, and difficult to explain on the basis of the existing literature, is the fronto-central decrease in gamma activity, while an increase of beta power is observed at the same location. One possible explanation of this effect may be a shift of the specific frequencies enhanced during the experience of subjective colour from higher (gamma) to lower (beta) frequencies at the fronto-central brain locations. Representation of subjective colour may be reflected by frequencies in the gamma range all over the brain, but in frontal areas, where the respective frequencies are lower and to be found in the beta range.

The parietal increase of power in the delta frequency range is well in accordance with findings by Basar et al. [150] claiming delta frequencies to be related to signal detection and occurring at parietal locations during visual stimulation. In addition, Harmony et al. [164] reported increasing delta activity to occur in tasks where attention to internal processing was necessary. Activation of the delta band in these tasks was particularly prominent in the left hemisphere. The increasing delta power observed reliably over participants in Experiment 8 might therefore represent the brain activity in relation to internally directed attention and the detection of the internal visual stimulus, i.e. the subjective colour.

The decrease of alpha and increase of gamma activity observed in Experiment

8 may reflect the necessary prerequisite for the experience of a subjective colour. During the stimulation with flickering light, spontaneous alpha activity may arise, partly triggered by the flickering stimulation, partly reflecting mental states of relaxation without any specific perception [45]. This high synchronization of cortical networks in the alpha frequency band may block the cortical expression of colour-specific activations generated early in the visual stream (e.g. in the retina), which are constantly transferred to the cortex. Alpha activity may then decrease due to endogenous factors [156] until it reaches an internal threshold. At this point, colour-specific activations from earlier processing stages are given the opportunity to enter the cortical processing stages. This then may give rise to the activation of cortical networks in other frequency domains, such as in the gamma band, able to represent a colour. This activation may then be equivalent to the conscious experience of a colour.

Chapter 8

General Discussion

The aim of this final chapter is (i) to summarize the results of the eight experimental studies presented in this thesis, (ii) to develop a theoretical model of the neural and cortical processes underlying the experience of subjective colour, and (iii) to suggest possible mechanisms of the experience of subjective form, and the relation between subjective form and colour. Finally, (iv) some future prospects for the research and investigation of subjective experiences will be explored.

8.1 Summary of the experimental evidence

In the experimental studies described in this thesis, participants were usually stimulated with a spatially homogenous ganzfeld of temporally modulated (i.e. flickering) light. It was observed that the participants reliably reported subjective colour (white, black, grey, blue, yellow, red, green, purple) and form (line, circle, radial, spiral, rectangle, grating, wave, zigzag, point) during the stimulation. Forms were most reliably reported between 8 and 40 Hz, while colour reports were most reliable between 5 and 56 Hz. In addition, the differences of the report distributions over frequency were found for the different subjective experiences. For subjective colour the differences in stimulation frequency efficacy may relate to the temporal characteristics of the retinal cone types (see Chapter 2).

In a given stimulation epoch, usually more than one subjective experience was reported. The investigation of the relation between these reports within trials (Chapter 3) revealed a complex pattern of interdependencies in the occurrence of subjective experiences. While some experiences tend to co-occur, others clearly inhibit their mutual appearance. Largely, these interdependencies are in agreement with the overlapping frequency distributions described in Chapter 2. However, the temporal sequence in which different experiences were reported within trials did not exhibit a specific pattern of succession.

The report of subjective experiences was shown to be directly related to the phase of the flickering stimulation (Chapter 4). In the case of subjective colour, the results suggest a relation of the coding of colour-opponency to different phases of the stimulation frequency, or even the neuronal processing frequency.

As subjective experiences have also been described in the absence of temporally modulated stimulation (e.g. [50, 52]), responses to stimulation with a constantly illuminated ganzfeld were collected (Chapter 5). Subsequently, the reported experiences were used as correction parameters for the results reported above. These corrections emphasized the frequency specificity of subjective experiences by generally reducing the report frequency ranges, and helped to tighten the pattern of interdependencies between experiences. Additionally, the findings supplied further evidence for the statistical validity of the phase sensitivity of subjective experiences.

Investigation of the phenomenology of subjective experiences (Chapter 6) revealed that subjective colour categories are well separable on the basis of the dominant wavelength of colour matches accomplished by the observers. It was shown that intra- and interindividual variabilities in the reported colours may be based on the physiological properties of the colour coding system. Furthermore, the dominant wavelength is related to the stimulation frequency in a specific way, such that changes in colour categories (rather than changes on a colour continuum) seem to be related to changes in the stimulation frequency. Drawings of the subjective forms experienced by the participants exhibited an astonishing similarity to forms reported to evolve in computational models of epileptic brain activation [136] or in resonant systems [133].

Information on the cortical processes underlying the experience of subjective colour was obtained using EEG recordings (Chapter 7). Reports of subjective colour were reliably preceded by a desynchronization of the alpha band and a global increase in gamma-band synchronization. While the changes in the alpha band may relate to perceptual switching and the detection of an internal stimulus, the gamma-band increase may reflect the formation of a unified percept reaching consciousness.

8.2 A theoretical model of subjective colour

In the following, a theoretical model of subjective colour will be developed on the basis of the evidence presented in this thesis and results and models reported in the literature. The model is grounded in physiological mechanisms schematically represented in Figure 8.1.

When flickering light impinges on the retina, retinal receptors are stimulated repeatedly with periods depending on the actual frequency of stimulation. For example, with a frequency of 20 Hz, a new light impulse meets the retina every 50 ms and stays on for 25 ms, followed by 25 ms of darkness. Considering the stimulation frequencies used in our experiments (1 - 60 Hz, that is periods of between 100 ms and 17 ms) these intervals between two light impulses critically interfere with the response latencies and integration times of the retinal cone types. Schnapf et al. [131] showed response latencies of cones to be about 51 ms for M-cones (with an integration time of 19 ms), 55 ms (28 ms integration time) for L-cones, and 61 ms (34 ms integration time) for S-cones. In Experiment 1 it was shown that the period differences of the peak stimulation frequencies for the subjective colours blue, green, and red approximately correspond to the cone latencies reported in [131] (see Section 2.4). This finding, and the models developed by Courtney and Buchsbaum [130] as well as by Grunfeld and Spitzer ([132], see Section 1.3.3 for a detailed description), strongly suggest that the processing stages following the retinal level are differentially activated depending on the interaction between cone latencies and the stimulation frequency. It is still not yet entirely clear where in the visual processing stream this next stage of a joint signal resulting from the cone activations takes place. In Figure 8.1 it is displayed to be situated somewhere between the retinal, lateral-geniculate, and cortical level. In the literature, colour opponent cells have been reported as early as in the bipolar and ganglion cells of the retina [2], but also in the LGN [98] and the cortex (e.g. [105]).

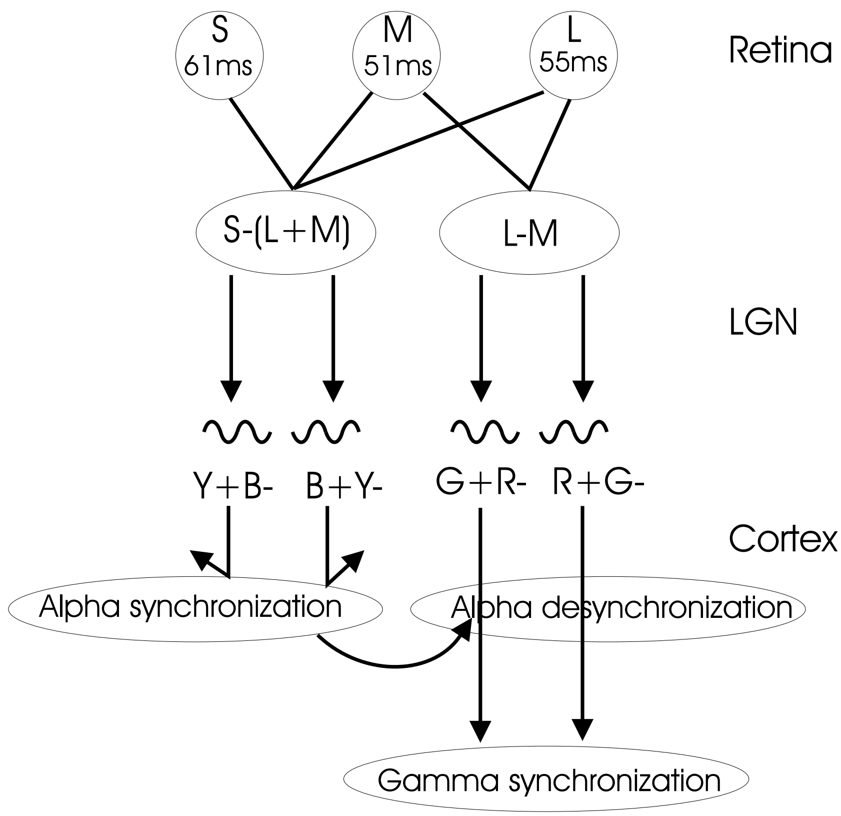


Figure 8.1: A theoretical model of subjective colour. S, M, and L denote the different cones types in the retina. The peak latencies of the different cone types are given. LGN is the lateral geniculate nucleus. S-(L+M) and L-M represent the joint signals resulting from the activations of the different cone types and found between the retinal and the cortical level. The information of this joint signal is fed into opponent cells, here shown as Y+B-, B+Y-, G+R-, R+G-. Y+B-, for example, gives an excitatory response to a yellow stimulus and an inhibitory response to a blue stimulus. The curves above the opponent cells represent the hypothetical phase relation with which these cells may respond. When information is further transferred to the cortex, a high alpha synchronization may block the information flow from lower to higher areas (shown on the left). However, an intrinsic desynchronization of alpha activity may appear, letting the information pass and leading to a gamma synchronization as a sign of colour representation (shown on the right). Further information is given in the text.

A critical result of the studies presented in this thesis is finding a phase specificity of subjective experiences (see Chapter 4). It was shown that while responses to the emergence of yellow and green were given at 103° and 133° of the flicker cycle, respectively, responses to red, purple, and blue were found at 258°, 275° and 312°, respectively. This shows in particular that the opponent colour pairs red-green and blue-yellow are clearly separated in phase. By assuming that the responses reflect the relation of the actual time of experience onset to stimulation phase, it was concluded that phase may be an efficient method to code colour opponency. During perception, the eye is known to carry out minimal movements to prevent continuous stimulation of the receptors, which would result in a fading of the perceptual image due to receptor fatigue. So, when the retina is stimulated for an prolonged period of time (at least some hundred milliseconds) the result is a repeated firing of cells at different levels of the visual processing stream. This repeated firing may be periodic in the sense that it can be assigned a specific frequency. The findings presented in Chapter 4 and reported by Young [68] suggest that the oscillatory activities of opponent colour cells may exhibit different phases in relation to each other. This idea is illustrated in Figure 8.1 by the function curves above the opponent cells. The activity of opponent colours (e.g. blue and yellow) might have more or less opponent phases, whereas the activity of yellow and green, or blue and red may be characterized by a similar phase. It might be the case that colour-opponent cells coding a given pair of colours (e.g. Y+B- and B+Y- cells) are physiologically similar, so that the phase-specific coding may provide an additional method of differentiating between the activations resulting from the stimulation with different colours.

These phase characteristics may be observable in the appearance and report of subjective colour due to the existence of a physiological gating mechanism which generally blocks the activation from early processing areas to access the cortex. However, when the gate is opened, the experience of the subjective colour may depend on which of the oscillatory opponent activations is at its maximum at the moment. When the gate opens at early phases in the relation to the stimulation frequency, yellow or green may be observed, when it opens at late phases, red or blue may be experienced.

Indeed, in Chapter 7, a possible gating mechanism is described. Synchronization of large parts of the brain with an alpha rhythm is usually accompanied by a state of relaxation of the person in absence of any perceptual or cognitive content. Thus, a high alpha activity makes it difficult, if not impossible, for any perceptual content to be represented in the cortex and to reach consciousness. This idea is supported by findings of better perceptual detection performance when alpha activation is low compared to when it is high [151]. On the basis of their findings on perceptual switches with bistable figures, Strüber and Herrmann [156] suggested that in a perceptual situation without external changes of the visual input, alpha activation may spontaneously and endogenously decrease. When the decreasing alpha activation reaches a threshold, synchronization in other frequency bands becomes possible, and a new percept (e.g. the alternative interpretation of the bistable figure) may become manifest. During the stimulation with flickering light, a decrease of alpha band activation preceded the report of subjective colour. Reaching the internal threshold of alpha activation may represent the gate mentioned above, which, when opened, allows information from lower processing areas to enter the cortex and form perceptual representations in other frequency bands. Most likely, the increase in gamma activation described in Chapter 7 may be a possible mechanism for the representation of subjective colour in cortical processing stages.

The presented model of the experience of subjective colour did not consider the perception of achromatic colours, and purple. However, purple is reliably reported during the stimulation with flickering light. The experience of purple may possibly be generated by a concurrent activation of red- and blue-coding cells. Evidence for this assumption is provided by the fact that the phase at which purple is reported, is directly intermediate between the phases of red and blue reports, even though it is less strictly related to a specific phase than the other colours. It may be hypothesized that purple may be perceived when the maxima of concurrent activations of red-excitatory and blue-excitatory cells coincide with the opening of the gate mechanisms described above. As red and blue are assumed to have similar phases of activity, there is a strong likelihood that both activations enter the cortical processing stages concurrently. If they do so, purple is experienced, otherwise, either red or blue is seen. A similar mechanisms would be expected for yellow-excitatory and green-excitatory cells. However, as no distinct colour category seems to be related to the colour mixture of green and yellow, the resulting greenish-yellow or yellowish-green colours may be reported as green or yellow, but not as an intermediate colour category.

8.3 Mechanisms of subjective form and the relation between subjective colour and form

In the following, a possible scenario underlying the experience of subjective form will be outlined. The most astonishing property of the subjective forms investigated here is their similarity to resonant systems, such as vibrating surfaces of water or sand (e.g. [133]). The cellular organization in the retina is characterized not only by feed-forward projections, but also by a large number of lateral inhibitory connections. These lateral connections are provided by horizontal and bipolar cells [88], and may be assumed to have specific temporal properties in terms of transfer latencies. When the retina is stimulated with flickering light, the period of stimulation may interfere (similarly as outlined above for the experience of subjective colour) with the latencies of the lateral connections in the neuronal tissue. It may be assumed that the repeated stimulation in interaction with the ongoing lateral information transfer drives the population of cells in the neuronal tissue at retinal level into a state of resonance. This state of resonance may generate patterns of differential cell activation that resemble resonance patterns in physical systems [133]. Interestingly, these patterns of activation at the retinal level might also resemble patterns of activation that would result from the stimulation with real figures. For example, a real honeycomb-pattern presented to an observer may result in a similar pattern of retinal cell activation as a pattern induced by light flickering at 24 Hz. Subsequently, the activity generated by resonance phenomena might be transmitted further in the visual processing stream, finally activating orientation columns in the cortex and thus representing certain well-defined forms [135]. The activation might have to pass the same gating mechanism for reaching cortical processing stages as described above for subjective colour. On the basis of the findings presented in this thesis, it is not possible to identify with certainty the level of form generation (retinal or higher areas), nor the exact mechanisms of further processing leading to the experience of form. However, the fact that subjective experiences are strictly related to rather narrow frequency ranges strongly implies that both, subjective colour and form, are the result of an interaction of temporal characteristics of the visual system with the temporal characteristics of the flickering stimulation.

A further question to be answered relates to the co-occurrence of subjective colour and form. A possible explanation of this phenomenon relies on the fact that in the visual system, the cells coding colour are as well responsible for the representation of spatial properties of the stimulus. The interdependencies in the reports described in Chapter 3 suggest that it is especially the cells coding the colours red and green, that are most likely to be involved in the resonant pattern formation described above, forming the percepts of red or green radials, spirals, zigzags, and waves. This might be the case due to the specific temporal properties of the red/green coding cells and therefore the specific temporal resolution with which information is transferred into the lateral connections.

8.4 Future prospects

The studies presented in this thesis showed that the investigation of flicker induced subjective experiences helps us to understand the processing in the visual system. It may be assumed that the postulated processes, for example the phase specificity of colour perception, also hold for the perception of 'real' stimuli. Therefore, it seems promising to apply the knowledge about visual processes revealed by studying subjective experiences in future investigations of 'real' colour and form perception.

But even when remaining with the phenomenon of subjective experiences, there are a variety of open questions, which can be answered in future research projects. Even though many participants reported subjective motion during the stimulation with flickering light, motion was not considered in detail in this thesis. It seems interesting to investigate whether a distinct relation between subjective colour, form, and motion perception and the underlying physiological processes exists.

Besides, physiological investigations of the phase sensitivity on the single cell level might provide interesting insides into the temporal characteristics of visual processing.

A further question relates to the exact type of stimulation necessary for the apperception of subjective experiences. The present study used square-wave flickering light, but other investigations using stroboscopic stimulation [79] were equally successful in inducing subjective experiences. One might wish to investigate to which extent the subjective experiences survive deterioration of the flickering stimulation (for example, in terms of regularity of the stimulation).

Furthermore, the application of monocular, compared to binocular, stimulation may shed some light on the exact locus of generation of subjective experiences. The evidence collected in this thesis and summarized in the models above would suggest an early locus of generation, which nonetheless necessitates the involvement of higher processing areas to ensure the conscious apperception of the subjective experiences.

Finally, further investigations of subjective experiences using electroencephalographic or brain-imaging techniques might help to better understand the processes and their loci underlying the apperception of both subjective and real colour and form.

Appendix A

Form of consentment

Einverständniserklärung zur Teilnahme an der Untersuchung ”Flicker und Farb- und Formwahrnehmungen” (Untersuchungsleiter: Dipl.Psych. Cordula Becker)

Liebe Teilnehmerin, lieber Teilnehmer,

Sie haben sich entschlossen, an unserer Untersuchung teilzunehmen, welche sich damit beschäftigt, wie durch flackerndes Licht Farb- und Formwahrnehmungen hervorgerufen werden können. Dafür werden Sie in eine Box hineinschauen, in welcher mehr oder weniger schnell rhythmisch flackerndes Licht erzeugt wird. Es ist bekannt, dass bei dafür besonders empfindlichen Personen solch flackerndes Licht epileptische Anfälle auslösen kann. Um das Risiko eines solchen Anfalls zu minimieren, möchten wir Sie bitten, die folgenden Fragen wahrheitsgemäß zu beantworten.

Außerdem können Sie sich natürlich jetzt oder auch später noch dafür entscheiden, nicht an der Untersuchung teilzunehmen, bzw. die Untersuchung abzubrechen. Auf jeden Fall möchten wir Sie bitten, uns zu informieren, wenn Sie während der Untersuchung ein Unwohlsein verspüren, Kopfschmerzen bekommen oder Sie bezüglich der Wirkung des Lichtes verunsichert sind. Es besteht dann jederzeit für Sie die Möglichkeit, die Untersuchung abzubrechen und sich zu erholen.

Ich habe bereits einen epileptischen Anfall erlitten. Ja / Nein

In meiner Familie (Eltern, Geschwister, Kinder) sind Fälle von Epilepsie bekannt. Ja / Nein

Ich bin wegen neurologischer Beschwerden in Behandlung. Ja / Nein

Ich nehme täglich größere Mengen Alkohol zu mir. Ja / Nein

Ich nehme regelmäßig Drogen (wie Ecstasy, Kokain, Heroin) zu mir. Ja / Nein

Ich leide unter starker Migräne. Ja / Nein

Ich bestätige, die Fragen wahrheitsgemäß beantwortet zu haben. Ich erkläre meine Bereitschaft zur Teilnahme an der Untersuchung und kenne die Möglichkeit, jederzeit die Untersuchung abbrechen und von der Teilnahme zurücktreten zu können.

Unterschrift Teilnehmer/in

Appendix B

Instructions

Instruction Experiment 1

Liebe Teilnehmerin, lieber Teilnehmer,

Vielen Dank für Ihre Teilnahme an unseren Untersuchungen!

Die Untersuchung teilt sich auf drei Termine auf, die jeweils eine Dauer von etwa 45 Minuten haben. Für die Dauer der Untersuchung werden Sie Kopfhörer tragen und Ihr Kinn auf einer Kinnstütze so ablegen, dass Sie bequem in die Unersuchungsvorrichtung blicken können. Bitte stellen Sie den Sitz der Geräte mit Hilfe des Versuchsleiters so ein, dass Sie diese bequem über einen längeren Zeitraum tragen können. Bitte verändern Sie den Sitz der Geräte danach nicht mehr. Als Brillenträger können Sie Ihre Brille aufbehalten. Die Untersuchung wird in einem abgedunkelten Raum durchgeführt.

Jede Sitzung besteht aus 20 Durchgängen. In jedem Durchgang wird Ihnen für 60 Sekunden flackerndes Licht gezeigt. Bitte halten Sie die Augen während der Präsentation des Lichtes auf jeden Fall geöffnet. Nach jedem Durchgang gibt es eine Pause von 30 Sekunden, während derer das Licht ausgeschaltet ist und Sie sich erholen können. Dabei können Sie auch kurz die Augen schließen. Der Beginn des nächsten Durchgangs wird Ihnen durch die Kopfhörer angesagt. Bitte öffnen Sie bei dieser Ansage die Augen wieder. Es ist am günstigsten, wenn Sie die Augen nicht direkt auf das Licht fokussieren, sondern durch die Box "hindurchsehen".

Ihre Aufgabe besteht darin, so genau wie möglich zu beschreiben, was Sie sehen. Ihre Aussagen werden dabei mit dem Mikrofon aufgenommen. Bitte sprechen Sie laut und deutlich. Das flackernde Licht kann Illusionen von Farbe, Formen und Bewegungen hervorrufen. Sie sollen angeben, ob bei Ihnen Illusionen auftreten und diese dann genau beschreiben. Achten Sie dabei bitte besonders auf Farben, Formen und Bewegungen. Nennen Sie den Zeitpunkt des Auftretens, beschreiben Sie Veränderungen, die räumliche Aufteilung der Illusionen (links, rechts, mittig, beide Augen). Beschreiben Sie bitte so viel wie möglich, damit wir möglichst viele Ergebnisse sammeln können.

Das Ende der Untersuchung wird Ihnen über Kopfhörer angesagt. Dann können Sie vorsichtig den Kopf aus der Kinnstütze nehmen und die Kopfhörer abnehmen, auf den Tisch vor Ihnen legen und den Raum verlassen.

Sollten Sie während der Untersuchung ein Unwohlsein verspüren oder falls Sie aus anderen Gründen die Untersuchung abbrechen möchten, nehmen Sie bitte ebenfalls die Kopfhörer ab und verlassen Sie den Raum.

Instruction Experiment 2

Liebe Teilnehmerin, lieber Teilnehmer,

Vielen Dank für Ihre Teilnahme an unseren Untersuchungen!

Die Untersuchung teilt sich auf drei Termine auf, die jeweils eine Dauer von etwa 45 Minuten haben. Für die Dauer der Untersuchung werden Sie Kopfhörer tragen und Ihr Kinn auf einer Kinnstütze so ablegen, dass Sie bequem in die Unersuchungsvorrichtung blicken können. Bitte stellen Sie den Sitz der Geräte mit Hilfe des Versuchsleiters so ein, dass Sie diese bequem über einen längeren Zeitraum tragen können. Bitte verändern Sie den Sitz der Geräte danach nicht mehr. Als Brillenträger können Sie Ihre Brille aufbehalten. Die Untersuchung wird in einem abgedunkelten Raum durchgeführt.

Jede Sitzung besteht aus 60 Durchgängen (die letzte nur aus 55 Durchgängen). Nach etwa der Hälfte der Durchgänge wird eine Pause angekündigt. Sie können dann entweder kurz den Raum verlassen, oder sich im Raum kurz ausruhen. Das Experiment wird durch einen Tastendruck fortgesetzt. Außerdem wird Ihnen von Zeit zu Zeit angesagt, wieviel Durchgänge noch verbleiben.

In jedem Durchgang wird Ihnen für 30 Sekunden flackerndes Licht gezeigt. Bitte halten Sie die Augen während der Präsentation des Lichtes auf jeden Fall geöffnet. Nach jedem Durchgang gibt es eine Pause von 15 Sekunden, während derer das Licht ausgeschaltet ist und Sie sich erholen können. Dabei können Sie auch kurz die Augen schließen. Der Beginn des nächsten Durchgangs wird Ihnen durch die Kopfhörer angesagt. Bitte öffnen Sie bei dieser Ansage die Augen wieder. Es ist am günstigsten, wenn Sie die Augen nicht direkt auf das Licht fokussieren, sondern durch die Box "hindurchsehen".

Das flackernde Licht kann Illusionen von Farbe, Formen und Bewegungen hervorrufen. In diesem Versuch achten Sie bitte nur auf Farbwahrnehmungen (rot, blau, gelb, grün, lila). Vor jedem Durchgang hören Sie per Kopfhörer, auf welche Farbe sie in diesem Durchgang achten sollen. Ihre Aufgabe besteht darin, eine Taste der Maus zu drücken, wenn Sie diese Farbe wahrnehmen. Drücken Sie die Maustaste in jedem Durchgang dabei nur einmal (es kommt uns nur auf das erste Auftreten der Illusion an). Sollten Sie die Taste mehrmals drücken, ist das aber auch kein Problem. Wenn Sie die entsprechende Farbe nicht sehen, drücken Sie bitte keine Taste (es ist normal, dass man nicht in allen Durchgängen jede Farbe sieht). Bitte denken Sie daran, dass es sich um Illusionen handelt, d.h. das die Farben unter Umständen nicht so deutlich und kräftig sind, wie z.B. in einem Malkasten. Antworten Sie aber bitte auch nicht auf Farben, die Sie schon bei konstantem Licht in der Box (wird vorher demonstriert) wahrnehmen (z.B. kann Ihnen das Licht insgesamt etwas bläulich erscheinen; antworten Sie hier nicht auf blau, sondern warten Sie ob sich ein anderer Eindruck von blau ergibt).

Das Ende der Untersuchung wird Ihnen über Kopfhörer angesagt. Dann können Sie vorsichtig den Kopf aus der Kinnstütze nehmen und die Kopfhörer abnehmen, auf den Tisch vor Ihnen legen und den Raum verlassen.

Sollten Sie während der Untersuchung ein Unwohlsein verspüren oder falls Sie aus anderen Gründen die Untersuchung abbrechen möchten, nehmen Sie bitte ebenfalls die Kopfhörer ab und verlassen Sie den Raum.

Instruction Experiment 3

Liebe Teilnehmerin, lieber Teilnehmer,

Vielen Dank für Ihre Teilnahme an unseren Untersuchungen!

Die Untersuchung teilt sich auf vier Termine auf, die jeweils eine Dauer von etwa 60 Minuten haben. Für die Dauer der Untersuchung werden Sie Kopfhörer tragen und Ihr Kinn auf einer Kinnstütze so ablegen, dass Sie bequem in die Unersuchungsvorrichtung blicken können. Bitte stellen Sie den Sitz der Geräte mit Hilfe des Versuchsleiters so ein, dass Sie diese bequem über einen längeren Zeitraum tragen können. Bitte verändern Sie den Sitz der Geräte danach nicht mehr. Als Brillenträger können Sie Ihre Brille aufbehalten. Die Untersuchung wird in einem abgedunkelten Raum durchgeführt.

Jede Sitzung besteht aus 74 Durchgängen. Nach etwa der Hälfte der Durchgänge wird eine Pause angekündigt. Sie können dann entweder kurz den Raum verlassen, oder sich im Raum kurz ausruhen. Das Experiment wird durch einen Tastendruck fortgesetzt. Außerdem wird Ihnen von Zeit zu Zeit angesagt, wieviel Durchgänge noch verbleiben.

In jedem Durchgang wird Ihnen für 30 Sekunden flackerndes Licht gezeigt. Bitte halten Sie die Augen während der Präsentation des Lichtes auf jeden Fall geöffnet. Nach jedem Durchgang gibt es eine Pause von 15 Sekunden, während derer das Licht ausgeschaltet ist und Sie sich erholen können. Dabei können Sie auch kurz die Augen schließen. Der Beginn des nächsten Durchgangs wird Ihnen durch die Kopfhörer angesagt. Bitte öffnen Sie bei dieser Ansage die Augen wieder. Es ist am günstigsten, wenn Sie die Augen nicht direkt auf das Licht fokussieren, sondern durch die Box "hindurchsehen".

Das flackernde Licht kann Illusionen von Farbe, Formen und Bewegungen hervorrufen. In diesem Versuch achten Sie bitte nur auf Formwahrnehmungen. Vor der Untersuchung zeigt Ihnen der Versuchsleitung eine Abbildung mit Beispielen für die vorkommenden Formen. Diese Abbildung entspricht nicht genau dem, was Sie eventuell sehen werden, sondern vermittelt nur einen annähernden Eindruck und soll als Orientierungshilfe dienen. Vor jedem Durchgang hören Sie per Kopfhörer, auf welche Form Sie in diesem

Durchgang achten sollen. Ihre Aufgabe besteht darin, eine Taste der Maus zu drücken, wenn Sie diese Form wahrnehmen. Drücken Sie die Maustaste in jedem Durchgang dabei nur einmal (es kommt uns nur auf das erste Auftreten der Illusion an). Sollten Sie die Taste mehrmals drücken, ist das aber auch kein Problem. Wenn Sie die entsprechende Form nicht sehen, drücken Sie bitte keine Taste (es ist normal, dass man nicht in allen Durchgängen jede Form sieht). Bitte denken Sie daran, dass es sich um Illusionen handelt, d.h. das die Formen unter Umständen nicht so deutlich und klar sind, wie z.B. auf einem Bild. Antworten Sie aber bitte auch nicht auf Formen, die Sie schon bei konstantem Licht in der Box (wird vorher demonstriert) wahrnehmen (z.B. kann Ihnen das Licht insgesamt etwas kreisförmig angeordnet erscheinen; antworten Sie hier nicht auf kreisförmig, sondern warten Sie ob sich ein anderer Eindruck von kreisförmig ergibt).

Das Ende der Untersuchung wird Ihnen über Kopfhörer angesagt. Dann können Sie vorsichtig den Kopf aus der Kinnstütze nehmen und die Kopfhörer abnehmen, auf den Tisch vor Ihnen legen und den Raum verlassen.

Sollten Sie während der Untersuchung ein Unwohlsein verspüren oder falls Sie aus anderen Gründen die Untersuchung abbrechen möchten, nehmen Sie bitte ebenfalls die Kopfhörer ab und verlassen Sie den Raum.

Instruction Experiment 4

Liebe Teilnehmerin, lieber Teilnehmer,

Vielen Dank für Ihre Teilnahme an unseren Untersuchungen!

Die Untersuchung teilt sich auf zwei Termine auf, die jeweils eine Dauer von etwa 60 Minuten haben. Für die Dauer der Untersuchung werden Sie Kopfhörer tragen und Ihr Kinn auf einer Kinnstütze so ablegen, dass Sie bequem in die Unersuchungsvorrichtung blicken können. Bitte stellen Sie den Sitz der Geräte mit Hilfe des Versuchsleiters so ein, dass Sie diese bequem über einen längeren Zeitraum tragen können. Bitte verändern Sie den Sitz der Geräte danach nicht mehr. Als Brillenträger können Sie Ihre Brille aufbehalten. Die Untersuchung wird in einem abgedunkelten Raum durchgeführt.

Jede Sitzung besteht aus 75 Durchgängen. Nach etwa der Hälfte der Durchgänge wird eine Pause angekündigt. Sie können dann entweder kurz den Raum verlassen, oder sich im Raum kurz ausruhen. Das Experiment wird durch einen Tastendruck fortgesetzt. Außerdem wird Ihnen von Zeit zu Zeit angesagt, wieviel Durchgänge noch verbleiben.

In jedem Durchgang wird Ihnen für 30 Sekunden Licht gezeigt. Bitte halten Sie die Augen während der Präsentation des Lichtes auf jeden Fall geöffnet. Nach jedem Durchgang gibt es eine Pause von 15 Sekunden, während derer das Licht ausgeschaltet ist und Sie sich erholen können. Dabei können Sie auch kurz die Augen schließen. Der Beginn des nächsten Durchgangs wird Ihnen durch die Kopfhörer angesagt. Bitte öffnen Sie bei dieser Ansage die Augen wieder. Es ist am günstigsten, wenn Sie die Augen nicht direkt auf das Licht fokussieren, sondern durch die Box "hindurchsehen".

Das Licht kann Illusionen von Farbe, Formen und Bewegungen hervorrufen. In diesem Versuch achten Sie bitte nur auf Farbwahrnehmungen (rot, blau, gelb, grün, lila). Vor jedem Durchgang hören Sie per Kopfhörer, auf welche Farbe sie in diesem Durchgang achten sollen. Ihre Aufgabe besteht darin, eine Taste der Maus zu drücken, wenn Sie diese Farbe wahrnehmen. Drücken Sie die Maustaste in jedem Durchgang dabei nur einmal (es kommt uns nur auf das erste Auftreten der Illusion an). Sollten Sie die

Taste mehrmals drücken, ist das aber auch kein Problem. Wenn Sie die entsprechende Farbe nicht sehen, drücken Sie bitte keine Taste (es ist normal, dass man nicht in allen Durchgängen jede Farbe sieht). Bitte denken Sie daran, dass es sich um Illusionen handelt, d.h. das die Farben unter Umständen nicht so deutlich und kräftig sind, wie z.B. in einem Malkasten. Antworten Sie aber bitte auch nicht auf Farben, die Sie gleich zu Beginn in der Box wahrnehmen (z.B. kann Ihnen das Licht insgesamt etwas bläulich erscheinen; antworten Sie hier nicht auf blau, sondern warten Sie ob sich ein anderer Eindruck von blau ergibt).

Vor Beginn der ersten Sitzung oder nach der letzten Sitzung wird Ihnen für 60 Sekunden Licht gezeigt. Sie müssen keine Taste drücken, sondern Sie werden gebeten zu berichten, ob und was für Illusionen (bitte berichten Sie alles) Sie wahrnehmen. Der Versuchsleiter wird diese Berichte notieren.

Das Ende der Untersuchung wird Ihnen über Kopfhörer angesagt. Dann können Sie vorsichtig den Kopf aus der Kinnstütze nehmen und die Kopfhörer abnehmen, auf den Tisch vor Ihnen legen und den Raum verlassen.

Sollten Sie während der Untersuchung ein Unwohlsein verspüren oder falls Sie aus anderen Gründen die Untersuchung abbrechen möchten, nehmen Sie bitte ebenfalls die Kopfhörer ab und verlassen Sie den Raum.

Instruction Experiment 5

Liebe Teilnehmerin, lieber Teilnehmer,

Vielen Dank für Ihre Teilnahme an unseren Untersuchungen!

Die Untersuchung teilt sich auf vier Termine auf, die jeweils eine Dauer von etwa 50 Minuten haben. Für die Dauer der Untersuchung werden Sie Kopfhörer tragen und Ihr Kinn auf einer Kinnstütze so ablegen, dass Sie bequem in die Unersuchungsvorrichtung blicken können. Bitte stellen Sie den Sitz der Geräte mit Hilfe des Versuchsleiters so ein, dass Sie diese bequem über einen längeren Zeitraum tragen können. Bitte verändern Sie den Sitz der Geräte danach nicht mehr. Als Brillenträger können Sie Ihre Brille aufbehalten. Die Untersuchung wird in einem abgedunkelten Raum durchgeführt.

Jede Sitzung besteht aus 60 Durchgängen. Nach etwa der Hälfte der Durchgänge wird eine Pause angekündigt. Sie können dann entweder kurz den Raum verlassen, oder sich im Raum kurz ausruhen. Das Experiment wird durch einen Tastendruck fortgesetzt. Außerdem wird Ihnen von Zeit zu Zeit angesagt, wieviel Durchgänge noch verbleiben.

In jedem Durchgang wird Ihnen für 30 Sekunden Licht gezeigt. Bitte halten Sie die Augen während der Präsentation des Lichtes auf jeden Fall geöffnet. Nach jedem Durchgang gibt es eine Pause von 15 Sekunden, während derer das Licht ausgeschaltet ist und Sie sich erholen können. Dabei können Sie auch kurz die Augen schließen. Der Beginn des nächsten Durchgangs wird Ihnen durch die Kopfhörer angesagt. Bitte öffnen Sie bei dieser Ansage die Augen wieder. Es ist am günstigsten, wenn Sie die Augen nicht direkt auf das Licht fokussieren, sondern durch die Box "hindurchsehen".

Das Licht kann Illusionen von Farbe, Formen und Bewegungen hervorrufen. In diesem Versuch achten Sie bitte nur auf Formwahrnehmungen. Vor der Untersuchung zeigt Ihnen der Versuchsleitung eine Abbildung mit Beispielen für die vorkommenden Formen. Diese Abbildung entspricht nicht genau dem, was Sie eventuell sehen werden, sondern vermittelt nur einen annähernden Eindruck und soll als Orientierungshilfe dienen. Vor jedem Durchgang hören Sie per Kopfhörer, auf welche Form Sie in diesem Durchgang achten sollen. Ihre Aufgabe besteht darin, eine Taste der Maus zu drücken, wenn Sie diese Form wahrnehmen. Drücken Sie die Maustaste in jedem Durchgang dabei nur einmal (es kommt uns nur auf das erste Auftreten der Illusion an). Sollten Sie die Taste mehrmals drücken, ist das aber auch kein Problem. Wenn Sie die entsprechende Form nicht sehen, drücken Sie bitte keine Taste (es ist normal, dass man nicht in allen Durchgängen jede Form sieht). Bitte denken Sie daran, dass es sich um Illusionen handelt, d.h. das die Formen unter Umständen nicht so deutlich und klar sind, wie z.B. auf einem Bild. Antworten Sie aber bitte auch nicht auf Formen, die Sie gleich bei Beginn in der Box wahrnehmen (z.B. kann Ihnen das Licht insgesamt etwas kreisförmig angeordnet erscheinen; antworten Sie hier nicht auf kreisförmig, sondern warten Sie ob sich ein anderer Eindruck von kreisförmig ergibt).

Vor Beginn der ersten Sitzung oder nach der letzten Sitzung wird Ihnen für 60 Sekunden Licht gezeigt. Sie müssen keine Taste drücken, sondern Sie werden gebeten zu berichten, ob und was für Illusionen (bitte berichten Sie alles) Sie wahrnehmen. Der Versuchsleiter wird diese Berichte notieren.

Das Ende der Untersuchung wird Ihnen über Kopfhörer angesagt. Dann können Sie vorsichtig den Kopf aus der Kinnstütze nehmen und die Kopfhörer abnehmen, auf den Tisch vor Ihnen legen und den Raum verlassen.

Sollten Sie während der Untersuchung ein Unwohlsein verspüren oder falls Sie aus anderen Gründen die Untersuchung abbrechen möchten, nehmen Sie bitte ebenfalls die Kopfhörer ab und verlassen Sie den Raum.

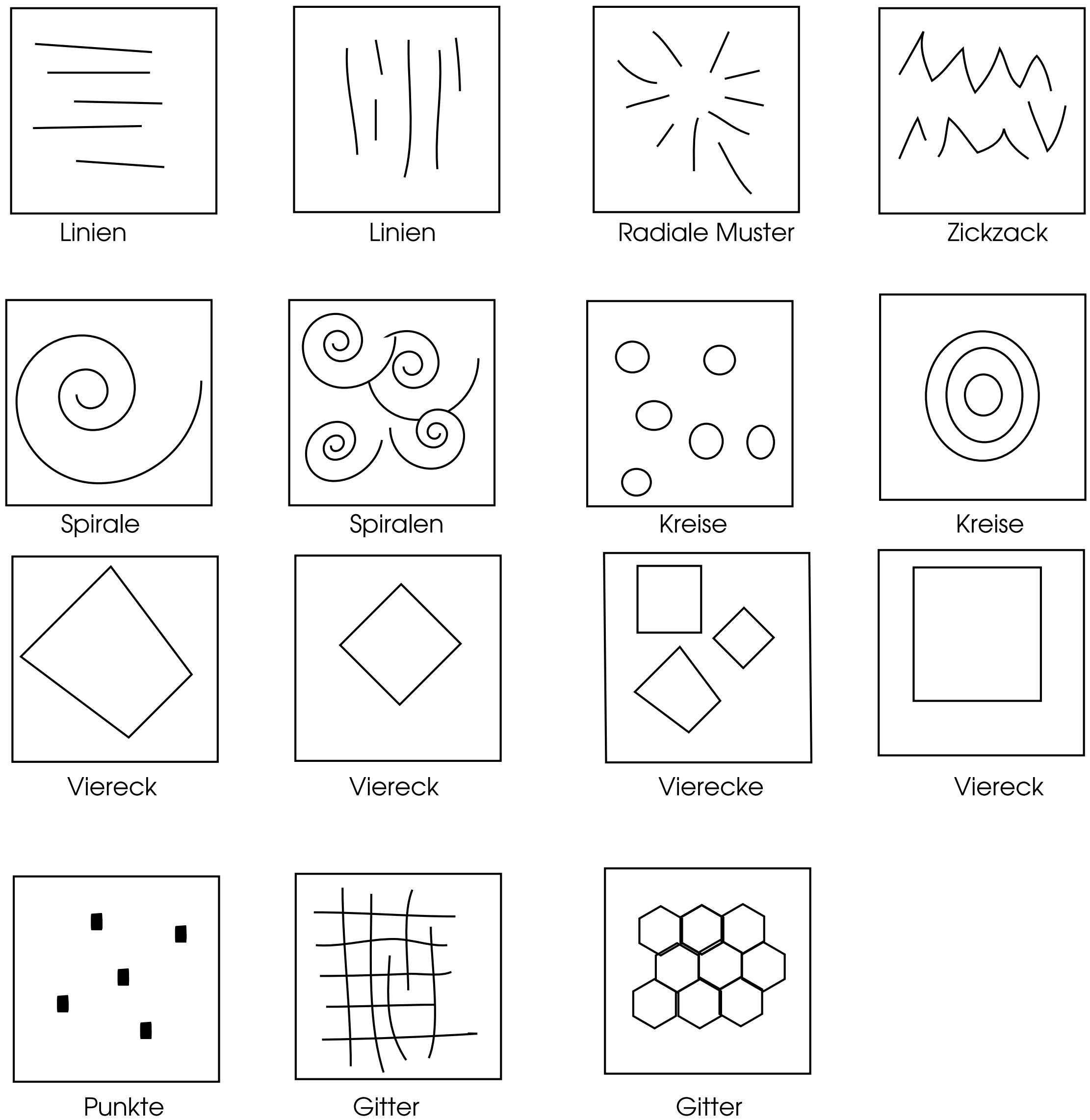


Figure B.1: Example drawings of subjective forms used for complementing the instructions of Experiment 3 and 5. The drawings were derived on the basis of verbal reports in Experiment 1 and drawings of subjective forms in the literature (e.g. in [13]).

Instruction Experiment 6

Liebe Teilnehmerin, lieber Teilnehmer,

Vielen Dank für Ihre Teilnahme an unseren Untersuchungen!

Die Untersuchung teilt sich auf fünf Termine auf, die jeweils eine maximale Dauer von etwa 60 Minuten haben. Für die Dauer der Untersuchung werden Sie Kopfhörer tragen und Ihr Kinn auf einer Kinnstütze so ablegen, dass Sie bequem in die Untersuchungsvorrichtung blicken können. Bitte stellen Sie den Sitz der Geräte mit Hilfe des Versuchsleiters so ein, dass Sie diese bequem über einen längeren Zeitraum tragen können. Bitte verändern Sie den Sitz der Geräte danach nicht mehr. Als Brillenträger sollen Sie Ihre Brille aufbehalten. Die Untersuchung wird in einem abgedunkelten Raum durchgeführt.

Die erste Sitzung beinhaltet 220 Durchgänge. In den ersten 20 Durchgängen wird Ihnen auf der rechten Seite eine Farbe dargeboten. Diese Farbe bleibt bis zu Ihrer Antwort sichtbar. Ihre Aufgabe ist es mit Hilfe der Maus und den Schiebereglern auf dem Bildschirm (diese repräsentieren den Rot-, Grün-, und Blauanteil der Farbe) die dargestellte Farbe so gut wie möglich auf der linken Seite zu replizieren. Sie können sich bei dieser Aufgabe soviel Zeit lassen, wie sie benötigen. Wenn Sie die Farbe eingestellt haben, klicken Sie bitte auf den entsprechenden Knopf, um den nächsten Durchgang zu starten. In den verbleibenden 200 Durchgängen wird Ihnen die Ausgangsfarbe dann nur für eine Sekunde (60 Sekunden) dargeboten, Sie müssen sich diese Farbe so genau wie möglich merken, und ebenfalls mit den Schiebereglern auf der linken Seite einstellen. Lassen Sie sich dabei Zeit! Wenn Sie fertig sind, drücken Sie wiederum die Taste. Diese Sitzung wird automatisch beendet. Am oberen Bildschirmrand wird eine Anzeige der bereits absolvierten Durchgänge eingeblendet.

Die weiteren vier Sitzungen sind alle gleich. Jede Sitzung besteht aus 50 Durchgängen. Ihnen wird von Zeit zu Zeit angesagt, wieviel Durchgänge etwa noch verbleiben.

In jedem Durchgang wird Ihnen für 20 Sekunden flackerndes Licht gezeigt. Bitte halten

Sie die Augen während der Präsentation des Lichtes auf jeden Fall geöffnet. Es ist am günstigsten, wenn Sie die Augen nicht direkt auf das Licht fokussieren, sondern durch die Box "hindurchsehen". Nach jedem Durchgang gibt es eine Pause von mindestens 10 Sekunden, während derer das Licht ausgeschaltet ist und Sie sich erholen können. Dabei können Sie auch kurz die Augen schliessen.

Das flackernde Licht kann Illusionen von Farbe, Formen und Bewegungen hervorrufen. In diesem Versuch achten Sie bitte nur auf Farbwahrnehmungen (rot, blau, gelb, grün und violett). Vor jedem Durchgang hören Sie per Kopfhörer, auf welche Farbe sie in diesem Durchgang achten sollen. Ihre Aufgabe besteht darin, eine Taste der Maus zu drücken, wenn Sie diese Farbe wahrnehmen. Drücken Sie die Maustaste in jedem Durchgang dabei nur einmal (es kommt uns nur auf das erste Auftreten der Illusion an). Sollten Sie die Taste mehrmals drücken, ist das aber auch kein Problem. Wenn Sie die entsprechende Farbe nicht sehen, drücken Sie bitte keine Taste (es ist normal, dass man nicht in allen Durchgängen jede Farbe sieht). Bitte denken Sie daran, dass es sich um Illusionen handelt, d.h. das die Farben unter Umständen nicht so deutlich und kräftig sind, wie z.B. in einem Malkasten. Antworten Sie aber bitte auch nicht auf Farben, die Sie schon bei konstantem Licht in der Box (wird vorher demonstriert) wahrnehmen (z.B. kann Ihnen das Licht insgesamt etwas bläulich erscheinen; antworten Sie hier nicht auf blau, sondern warten Sie ob sich ein anderer Eindruck von blau ergibt).

Wenn das Flackern beendet ist, wenden Sie sich bitte zu dem Computer (Laptop), an welchem Sie die Farbe einstellen. Sollten Sie keine Farbe gesehen haben (also auch die Maustaste nicht gedrückt haben), klicken Sie bitten "Keine Farbe!" an. Klicken Sie auf jeden Fall nur einmal, und beobachten Sie die obere Anzeige (Nummer des Durchganges), um zu sehen, ob die Antwort registriert wurde. Wenn Sie eine Farbe gesehen haben, und auch darauf mit der Maustaste geantwortet haben, stellen Sie jetzt bitte die wahrgenommene Farbe mit Hilfe der Schieberegler so genau wie möglich ein. Lassen Sie sich dabei Zeit! Wenn Sie fertig sind, klicken Sie auf die entsprechende Taste. Warten Sie eventuell bis auf dem großen Bildschirm eine weitere Instruktion gegeben wird, und drücken Sie entsprechend eine Taste auf der großen Tastatur. Damit wird der nächste Flickerdurchgang gestartet, das heißt, Sie sollten sofort wieder in die Flickerbox schauen.

Das Ende der Untersuchung wird Ihnen über Kopfhörer angesagt. Dann können Sie vorsichtig den Kopf aus der Kinnstütze nehmen und die Kopfhörer abnehmen, auf den Tisch vor Ihnen legen und den Raum verlassen.

Sollten Sie während der Untersuchung ein Unwohlsein verspüren oder falls Sie aus anderen Gründen die Untersuchung abbrechen möchten, nehmen Sie bitte ebenfalls die Kopfhörer ab und verlassen Sie den Raum.

Instruction Experiment 7

Liebe Teilnehmerin, lieber Teilnehmer,

Vielen Dank für Ihre Teilnahme an unseren Untersuchungen!

Die Untersuchung teilt sich auf drei Termine auf, die jeweils eine Dauer von etwa 60 Minuten haben. Für die Dauer der Untersuchung werden Sie Kopfhörer tragen und Ihr Kinn auf einer Kinnstütze so ablegen, dass Sie bequem in die Untersuchungsvorrichtung blicken können. Bitte stellen Sie den Sitz der Geräte mit Hilfe des Versuchsleiters so ein, dass Sie diese bequem über einen längeren Zeitraum tragen können. Bitte verändern Sie den Sitz der Geräte danach nicht mehr. Als Brillenträger sollen Sie Ihre Brille aufbehalten. Die Untersuchung wird in einem abgedunkelten Raum durchgeführt.

Jede Sitzung beinhaltet 54 Durchgänge. Ihnen wird von Zeit zu Zeit angesagt, wieviel Durchgänge etwa noch verbleiben.

In jedem Durchgang wird Ihnen für 20 Sekunden flackerndes Licht gezeigt. Bitte halten Sie die Augen während der Präsentation des Lichtes auf jeden Fall geöffnet. Es ist am günstigsten, wenn Sie die Augen nicht direkt auf das Licht fokussieren, sondern durch die Box "hindurchsehen". Nach jedem Durchgang gibt es eine Pause von mindestens 10 Sekunden, während derer das Licht ausgeschaltet ist und Sie sich erholen können. Dabei können Sie auch kurz die Augen schließen.

Das flackernde Licht kann Illusionen von Farbe, Formen und Bewegungen hervorrufen. In diesem Versuch achten Sie bitte nur auf Formwahrnehmungen (Linien, Kreise, Wellen, radiale Muster, Waben, Punkte, Zickzack, Vierecke, Spiralen). Vor jedem Durchgang hören Sie per Kopfhörer, auf welche Form sie in diesem Durchgang achten sollen. Ihre Aufgabe besteht darin, sofort eine Taste der Maus zu drücken, wenn Sie diese Form wahrnehmen. Drücken Sie die Maustaste in jedem Durchgang dabei nur einmal (es kommt uns nur auf das erste Auftreten der Illusion an). Sollten Sie die Taste mehrmals drücken, ist das aber auch kein Problem. Wenn Sie die entsprechende Form nicht sehen, drücken Sie bitte keine Taste (es ist normal, dass man nicht in allen Durchgängen jede

Form sieht). Bitte denken Sie daran, dass es sich um Illusionen handelt, d.h. das die Formen unter Umständen nicht so deutlich. Antworten Sie aber bitte auch nicht auf Formen, die Sie schon bei konstantem Licht in der Box (wird vorher demonstriert) wahrnehmen (z.B. kann Ihnen das Licht insgesamt etwas rund angeordnet erscheinen; antworten Sie hier nicht auf Kreise, sondern warten Sie ob sich ein anderer Eindruck von Kreisen ergibt).

Wenn das Flackern beendet ist, wenden Sie sich bitte zu dem Schreibtisch, an welchem Sie die wahrgenommenen Formen zeichnen. Sollten Sie keine Form gesehen haben (also auch die Maustaste nicht gedrückt haben), kreuzen Sie bitte unter dem entsprechenden Feld "Keine Form gesehen" an. Haben Sie eine Form wahrgenommen, zeichnen Sie bitte die wahrgenommene Form, nach der Sie in dem Durchgang gefragt wurden, so genau wie möglich. Lassen Sie sich dabei Zeit! Für jeden Durchgang müssen Sie etwas auf dem Papier kennzeichnen - entweder, dass Sie nichts gesehen haben; oder das Gesehene zeichnen. Warten Sie eventuell bis auf dem Computer-Bildschirm eine weitere Instruktion gegeben wird, und drücken Sie entsprechend eine Taste auf der Tastatur. Damit wird der nächste Flickerdurchgang gestartet, das heißt, Sie sollten sofort wieder in die Flickerbox schauen.

Das Ende der Untersuchung wird Ihnen über Kopfhörer angesagt. Dann können Sie vorsichtig den Kopf aus der Kinnstütze nehmen und die Kopfhörer abnehmen, auf den Tisch vor Ihnen legen und den Raum verlassen.

Sollten Sie während der Untersuchung ein Unwohlsein verspüren oder falls Sie aus anderen Gründen die Untersuchung abbrechen möchten, nehmen Sie bitte ebenfalls die Kopfhörer ab und verlassen Sie den Raum.

Instruction Experiment 8

Liebe Teilnehmerin, lieber Teilnehmer,

Vielen Dank für Ihre Teilnahme an unseren Untersuchungen!

Die Untersuchung teilt sich auf zwei Termine auf, die jeweils eine Dauer von etwa 60 Minuten haben. Für die Dauer der Untersuchung werden Sie Kopfhörer tragen und Ihr Kinn auf einer Kinnstütze so ablegen, dass Sie bequem in die Untersuchungsvorrichtung blicken können. Bitte stellen Sie den Sitz der Geräte mit Hilfe des Versuchsleiters so ein, dass Sie diese bequem über einen längeren Zeitraum tragen können. Bitte verändern Sie den Sitz der Geräte danach nicht mehr. Als Brillenträger können Sie Ihre Brille aufbehalten. Die Untersuchung wird in einem abgedunkelten Raum durchgeführt.

Jede Sitzung besteht aus 64 Durchgängen. Das Experiment wird durch einen Tastendruck fortgesetzt.

Vor jedem Durchgang blicken Sie für 20 Sekunden in die dunkle Box. Hier messen wir das EEG als Vergleichsbedingung. Wir möchten Sie bitten, die Augen geöffnet zu halten, keine Augenbewegungen und möglichst keine anderen Bewegungen durchzuführen. Bitte sprechen Sie auch nicht während dieser Zeit. In jedem Durchgang wird Ihnen für maximal 20 Sekunden flackerndes Licht gezeigt. Bitte halten Sie die Augen während der Präsentation des Lichtes auf jeden Fall geöffnet. Nach jedem Durchgang gibt es eine Pause von beliebiger Zeitdauer, während derer das Licht ausgeschaltet ist und Sie sich erholen können. Dabei können Sie auch kurz die Augen schließen. Der Beginn des nächsten Durchgangs wird Ihnen durch die Kopfhörer angesagt. Bitte öffnen Sie bei dieser Ansage die Augen wieder. Es ist am günstigsten, wenn Sie die Augen nicht direkt auf das Licht fokussieren, sondern durch die Box "hindurchsehen".

Das flackernde Licht kann Illusionen von Farbe, Formen und Bewegungen hervorrufen. In diesem Versuch achten Sie bitte nur auf Farbwahrnehmungen. Vor jedem Durchgang, also schon vor dem dunklen Vergleichszeitraum, hören Sie per Kopfhörer, auf welche

Farbe sie in diesem Durchgang achten sollen. Ihre Aufgabe besteht darin, eine Taste der Maus zu drücken, wenn Sie diese Farbe wahrnehmen. Drücken Sie die Maustaste in jedem Durchgang dabei nur einmal. Nachdem Sie die Taste gedrückt haben, wird der Flicker automatisch beendet. Jetzt berichten Sie bitte dem Versuchsleiter, welche anderen Farben sie evtl. wahrgenommen haben. Er wird diese aufschreiben. Dann machen Sie sich für den nächsten Durchgang bereit und geben Sie dem Versuchsleiter ein Zeichen, wenn Sie fertig sind. Wenn Sie die entsprechende Farbe nicht sehen, drücken Sie bitte keine Taste (es ist normal, dass man nicht in allen Durchgängen jede Farbe sieht). Berichten Sie aber trotzdem dem Versuchsleiter andere wahrgenommene Farben. Bitte denken Sie daran, dass es sich um Illusionen handelt, d.h. das die Farben unter Umständen nicht so deutlich und klar sind, wie z.B. auf einem Bild. Antworten Sie aber bitte auch nicht auf Farben, die Sie gleich bei Beginn in der Box wahrnehmen (z.B. kann Ihnen das Licht insgesamt etwas grau erscheinen; antworten Sie hier nicht auf grau, sondern warten Sie ob sich ein anderer Eindruck von grau ergibt).

Das Ende der Untersuchung wird Ihnen über Kopfhörer angesagt.

Sollten Sie während der Untersuchung ein Unwohlsein verspüren oder falls Sie aus anderen Gründen die Untersuchung abbrechen möchten, nehmen Sie bitte ebenfalls die Kopfhörer ab und verlassen Sie den Raum.

Appendix C

Experiment 1 - Sizer plots

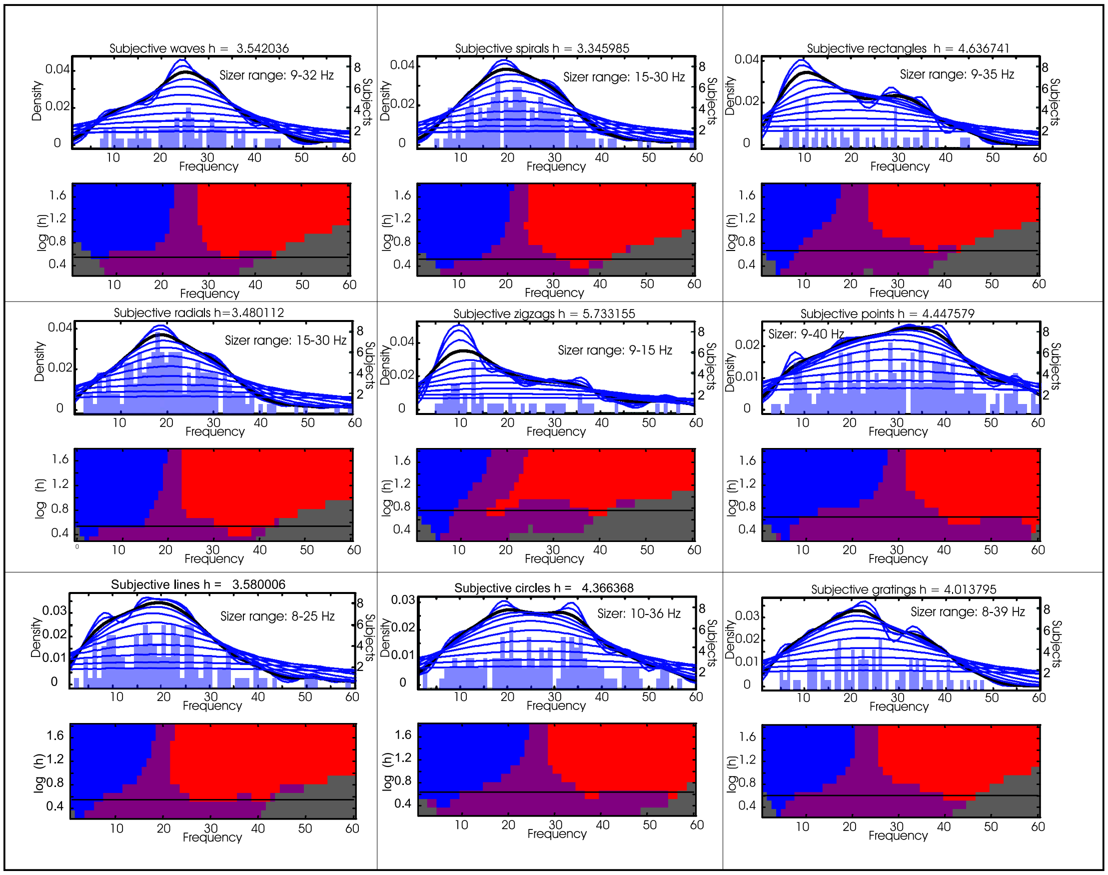


Figure C.1: Graphical representation of the SiZer analysis for subjective forms reported in Experiment 1. The upper part of each graph shows histograms denoting the number of participants reporting a given subjective form at a specific frequency and a family of density estimations with different smoothing parameters h, where the black line marks the smoothing with bandwidth h calculated by the Silverman algorithm (the numerical value of h being giving in the title of the graph). The lower part of each graph represents the actual SiZer analysis. While the flicker frequencies are plotted on the x-axis, the different bandwidths of the smoothing family are represented on the y-axis. Regions of a significant increase and decrease of the corresponding density curve are in blue and red colour, respectively, while regions of no significant changes of the density curve are plotted in purple. Grey regions mark regions with few observation which cannot be included in the SiZer analysis. Again, the critical Silverman bandwidth is marked in black. The relevant Sizer range, which corresponds to a range where a number of responses significantly differing from zero responses is given, is derived by reading the x-axis relative to this marked line and the colour of the plot.

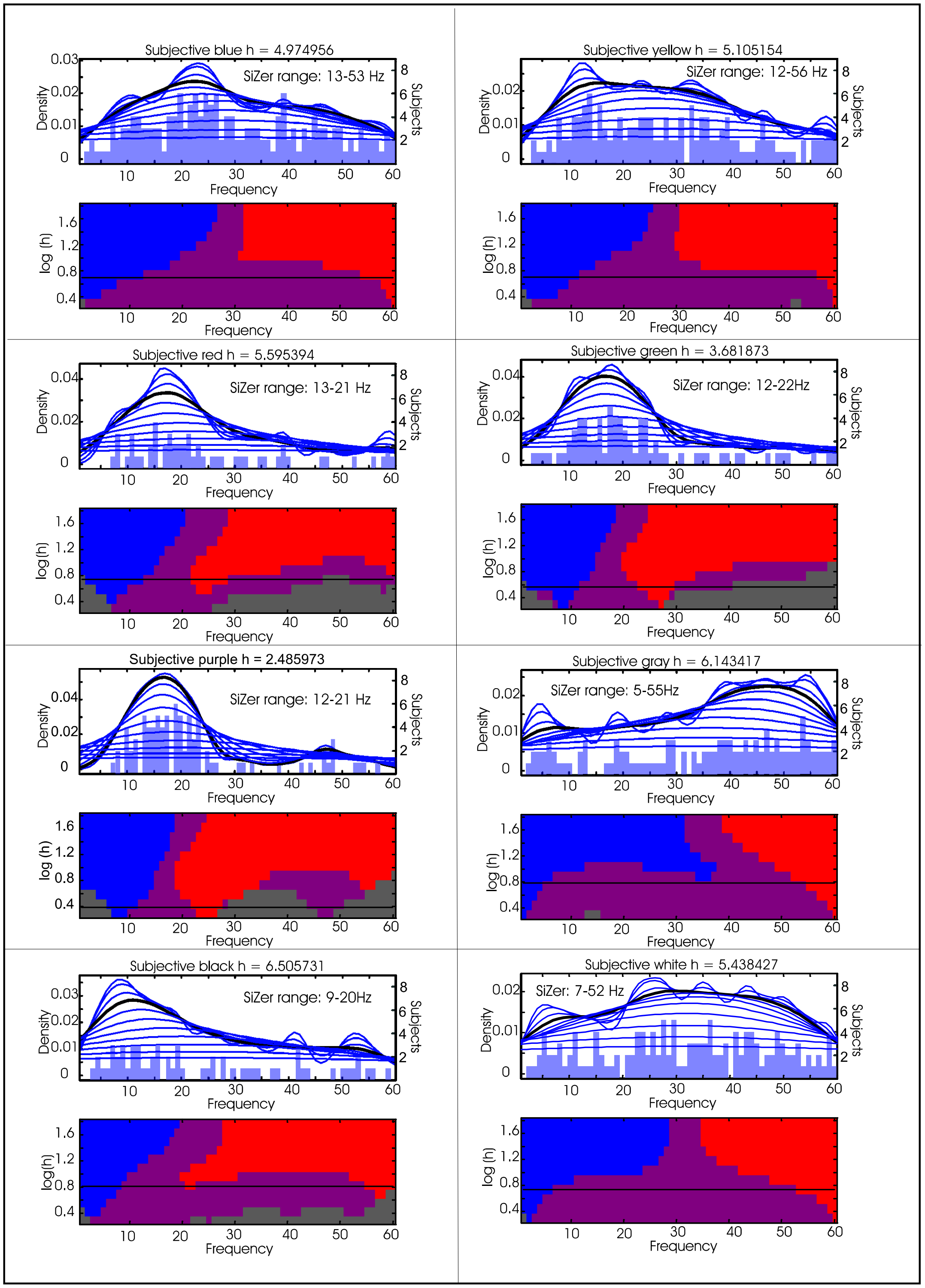


Figure C.2: Graphical representation of the SiZer analysis for subjective colours reported in Experiment 1. For further information see the caption of Figure C.1 and the text.

Appendix D

Experiment 1 - Kolmogorov-Smirnov-tests

Table D.1: Pairs of subjective experiences whose distributions differ significantly. D is the test statistic of a Kolmogorov-Smirnov-test. p was corrected for multiple comparisons between the 17 different subjective experiences ($p_{adj} < 0.05/136$). Pairs marked in italics were also shown to differ significantly in the analysis of Chapter 3, while pairs marked in bold face were shown to be significantly co-occurring in Chapter 3. Further information is given in the text.

		D	p			D	p
black	**grey**	0,3399	0,000198	**white**	**lines**	0,3699	0,000000
white	*green*	0,3858	0,000001	*white*	*radial*	0,3574	0,000000
white	*purple*	0,4407	0,000000	*white*	*grating*	0,2849	0,000268
grey	yellow	0,2605	0,000341	white	zigzag	0,3617	0,000197
grey	red	0,3638	0,000130	*white*	*spiral*	0,3441	0,000000
grey	green	0,4652	0,000000	grey	lines	0,4853	0,000000
grey	*purple*	0,4993	0,000000	*grey*	*circle*	0,3399	0,000002
blue	green	0,2908	0,000283	grey	wave	0,4284	0,000001
blue	*purple*	0,3567	0,000001	*grey*	*radial*	0,4831	0,000000
yellow	**purple**	0,3285	0,000017	*grey*	*grating*	0,4181	0,000000
				grey	zigzag	0,4204	0,000017
lines	point	0,3339	0,000000	grey	square	0,4706	0,000000
radial	point	0,2898	0,000003	*grey*	*spiral*	0,4729	0,000000
point	*spiral*	0,2753	0,000038	blue	lines	0,2753	0,000033
				blue	radial	0,2708	0,000019
				blue	spiral	0,2672	0,000075
				yellow	lines	0,2615	0,000183
				yellow	radial	0,2446	0,000313
				green	point	0,3472	0,000006
				purple	circle	0,3316	0,000027
				purple	*point*	0,4019	0,000000

Appendix E

Experiment 1 - Multidimensional scaling

Table E.1: Coordinates of the 3-dimensional scaling of subjective experiences for participant 1. Details are given in the text.

white	0.12	16.33	-5.90
black	-13.46	-16.46	25.30
grey	80.08	-10.24	-12.25
blue	4.25	20.01	-11.04
purple	-8.53	-10.64	-6.77
red	-20.55	-10.64	3.28
line	10.90	29.34	16.20
circle	-0.42	-3.24	4.42
wave	-23.46	23.30	-8.51
radial	-9.49	-5.39	-20.09
grating	-16.06	9.40	21.65
point	47.34	-11.50	14.82
zigzag	-9.21	-21.38	-2.64
rectangle	-32.02	-3.50	1.62
spiral	-9.49	-5.39	-20.09

Table E.2: Participant 1: Pairs of colour and form experiences exhibiting significantly small distances ($\alpha_{adj} = (.05/105)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	blue	line	grating	*white*	*line*
white	purple	circle	radial	white	circle
white	red	circle	grating	white	wave
black	purple	circle	zigzag	white	radial
black	*red*	circle	rectangle	white	grating
blue	purple	circle	spiral	white	spiral
purple	*red*	wave	radial	black	circle
		wave	*grating*	black	grating
		wave	rectangle	*black*	*zigzag*
		wave	spiral	black	rectangle
		radial	*zigzag*	blue	line
		radial	rectangle	blue	circle
		radial	*spiral*	blue	wave
		grating	*rectangle*	blue	radial
		zigzag	rectangle	blue	spiral
		zigzag	spiral	purple	circle
		rectangle	spiral	*purple*	*radial*
				purple	*grating*
				purple	*zigzag*
				purple	rectangle
				purple	*spiral*
				red	circle
				red	*radial*
				red	grating
				red	*zigzag*
				red	rectangle
				red	*spiral*

Table E.3: Participant 1: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/105)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	*grey*	line	radial	*white*	*point*
black	grey	line	point	black	wave
black	blue	line	zigzag	black	point
grey	blue	line	rectangle	grey	line
grey	*purple*	line	spiral	*grey*	*circle*
grey	red	wave	point	grey	wave
		radial	point	*grey*	*radial*
		grating	point	*grey*	*grating*
		point	zigzag	grey	zigzag
		point	*rectangle*	grey	rectangle
		point	*spiral*	*grey*	*spiral*
				blue	*point*
				purple	*point*
				red	*point*

Table E.4: Coordinates of the 3-dimensional scaling of subjective experiences for participant 2. Details are given in the text.

white	-7.07	-19.76	19.07
black	-31.75	5.08	30.71
grey	-19.47	26.26	5.05
blue	-13.62	-34.92	-19.66
purple	6.51	27.36	-17.11
red	-37.25	17.78	-13.07
green	-32.53	-30.50	1.87
yellow	-33.23	10.91	-7.53
line	29.79	8.97	23.80
circle	-18.33	-18.56	-36.52
wave	40.75	-9.80	-1.76
radial	42.36	-9.94	0.31
grating	19.57	35.72	-11.81
point	-6.71	-43.67	11.92
zigzag	38.56	10.94	1.95
rectangle	-20.17	27.36	15.17
spiral	42.61	-3.23	-2.40

Table E.5: Participant 2: Pairs of colour and form experiences exhibiting significantly small distances (α_{adj} = (.05/136)) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	black	line	wave	*white*	*line*
white	blue	*line*	*radial*	white	point
white	green	line	grating	white	rectangle
white	yellow	line	zigzag	black	rectangle
black	*grey*	line	spiral	grey	grating
black	*red*	wave	radial	grey	rectangle
black	green	*wave*	*zigzag*	blue	circle
black	yellow	wave	spiral	blue	point
grey	purple	*radial*	*zigzag*	*purple*	*grating*
grey	red	*radial*	*spiral*	*purple*	*zigzag*
grey	yellow	grating	zigzag	purple	rectangle
purple	*red*	*grating*	*rectangle*	red	circle
purple	*yellow*	grating	spiral	red	rectangle
red	yellow	zigzag	spiral	green	circle
green	*yellow*			green	point
				yellow	circle
				yellow	rectangle

Table E.6: Participant 2: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form	colour	form
black	blue	line	circle	*white*	*grating*	*purple*	*point*
black	purple	line	point	black	line	red	line
grey	blue	circle	wave	black	circle	red	wave
blue	*purple*	circle	radial	black	wave	red	radial
purple	green	circle	grating	black	radial	*red*	*point*
		circle	zigzag	black	grating	red	zigzag
		circle	rectangle	black	zigzag	red	spiral
		circle	spiral	black	spiral	green	line
		wave	rectangle	grey	wave	green	wave
		radial	rectangle	*grey*	*radial*	green	radial
		grating	point	*grey*	*point*	green	grating
		point	zigzag	*grey*	*spiral*	green	zigzag
		point	*rectangle*	blue	line	green	spiral
		point	*spiral*	*blue*	*wave*	yellow	line
		zigzag	rectangle	blue	radial	*yellow*	*wave*
		rectangle	spiral	*blue*	*grating*	yellow	radial
				blue	zigzag	*yellow*	*point*
				blue	rectangle	yellow	zigzag
				blue	spiral	yellow	spiral

Table E.7: Coordinates of the 3-dimensional scaling of subjective experiences for participant 3. Details are given in the text.

white	-44.75	4.37	-27.64
black	-12.54	-0.64	2.64
grey	-28.72	8.91	24.76
blue	23.44	25.17	2.95
purple	26.69	8.39	-5.36
red	-21.03	2.85	-13.74
green	-4.91	20.61	-2.47
yellow	28.14	14.57	5.87
line	-8.70	-9.72	9.79
circle	30.18	-24.71	-6.91
wave	-26.05	-8.81	-8.39
radial	9.64	-2.22	-9.96
grating	-6.71	-31.94	4.17
point	45.45	-18.74	7.38
zigzag	-8.65	12.60	13.74
rectangle	-9.88	-5.15	26.50
spiral	8.39	4.44	-23.31

Table E.8: Participant 3: Pairs of colour and form experiences exhibiting significantly small distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form	colour	form
white	red	line	wave	white	wave	red	line
black	*grey*	*line*	*radial*	black	line	*red*	*wave*
black	*red*	line	grating	*black*	*wave*	*red*	*radial*
black	green	line	zigzag	black	radial	*red*	*zigzag*
blue	purple	line	rectangle	black	grating	*red*	*spiral*
blue	green	circle	radial	*black*	*zigzag*	*green*	*line*
blue	yellow	circle	point	black	rectangle	green	wave
purple	*green*	wave	radial	black	spiral	*green*	*radial*
purple	*yellow*	*wave*	*grating*	grey	line	green	zigzag
red	*green*	*wave*	*zigzag*	grey	zigzag	*green*	*spiral*
green	*yellow*	radial	grating	grey	rectangle	yellow	radial
		radial	*zigzag*	blue	radial	yellow	spiral
		radial	*spiral*	blue	zigzag		
		grating	*rectangle*	blue	spiral		
		zigzag	rectangle	purple	circle		
				purple	*radial*		
				purple	point		
				purple	*spiral*		

Table E.9: Participant 3: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form	colour	form
white	*grey*	line	point	white	line	*blue*	*circle*
white	*blue*	circle	wave	white	circle	*blue*	*wave*
white	*purple*	circle	zigzag	*white*	*radial*	*blue*	*grating*
white	*green*	circle	rectangle	*white*	*grating*	*blue*	*point*
white	*yellow*	wave	point	*white*	*point*	blue	rectangle
grey	blue	grating	point	white	zigzag	purple	wave
grey	*purple*	point	zigzag	white	rectangle	purple	grating
grey	yellow	*point*	*rectangle*	*white*	*spiral*	purple	rectangle
blue	red	*point*	*spiral*	black	circle	red	circle
purple	red	rectangle	spiral	black	point	*red*	*point*
red	yellow			*grey*	*circle*	green	circle
				grey	*radial*	green	grating
				grey	*grating*	green	point
				grey	*point*	*yellow*	*wave*
				grey	*spiral*	yellow	grating

Table E.10: Coordinates of the 3-dimensional scaling of subjective experiences for participant 4. Details are given in the text.

white	-13.64	-3.84	40.84
black	17.34	-12.12	-7.03
grey	-36.38	3.02	15.46
blue	-40.02	-17.17	-3.42
purple	23.00	6.51	-2.12
red	29.96	10.39	4.60
yellow	-60.53	18.62	-25.95
line	-0.11	-12.37	21.19
circle	18.60	-18.17	-4.79
wave	20.86	-17.03	-10.69
radial	15.46	38.72	3.15
point	-10.06	-18.11	-16.17
zigzag	18.46	-15.05	-14.06
spiral	17.05	36.61	-1.02

Table E.11: Participant 4: Pairs of colour and form experiences exhibiting significantly small distances ($\alpha_{adj} = (.05/91)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	grey	line	circle	*white*	*line*
black	purple	line	wave	black	line
black	*red*	line	point	black	circle
grey	blue	line	zigzag	*black*	*wave*
purple	*red*	circle	wave	black	point
		circle	point	*black*	*zigzag*
		circle	zigzag	grey	line
		wave	point	blue	point
		wave	*zigzag*	purple	line
		radial	*spiral*	purple	circle
		point	zigzag	purple	wave
				purple	*radial*
				purple	*zigzag*
				purple	*spiral*
				red	circle
				red	*wave*
				red	*radial*
				red	*zigzag*
				red	*spiral*

Table E.12: Participant 4: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/91)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	*red*	radial	point	white	wave
white	*yellow*	*point*	*spiral*	*white*	*radial*
black	grey			*white*	*point*
black	yellow			white	zigzag
grey	*purple*			*white*	*spiral*
grey	red			*grey*	*circle*
blue	*purple*			grey	wave
blue	red			*grey*	*radial*
purple	yellow			grey	zigzag
red	yellow			*grey*	*spiral*
				blue	*circle*
				blue	*wave*
				blue	radial
				blue	zigzag
				blue	spiral
				yellow	line
				yellow	circle
				yellow	*wave*
				yellow	radial
				yellow	*point*
				yellow	zigzag
				yellow	spiral

Table E.13: Coordinates of the 3-dimensional scaling of subjective experiences for participant 5. Details are given in the text.

white	32.98	-24.67	-21.75
black	32.59	1.74	-8.25
grey	37.11	5.79	3.51
blue	25.43	-0.98	9.44
purple	-21.33	28.71	-5.72
red	29.09	15.76	-2.99
green	-13.07	18.44	-6.53
yellow	-42.79	-4.90	-2.70
line	-21.97	-11.26	-20.21
circle	21.48	-14.29	18.57
wave	31.13	14.11	11.91
radial	-27.20	11.54	5.65
grating	-12.23	-26.31	7.76
point	-48.25	-22.21	4.52
spiral	-22.97	8.53	6.80

Table E.14: Participant 5: Pairs of colour and form experiences exhibiting significantly small distances ($\alpha_{adj} = (.05/105)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	black	*line*	*radial*	black	circle
white	grey	line	grating	*black*	*wave*
white	blue	line	point	grey	circle
black	*grey*	line	spiral	grey	wave
black	blue	circle	wave	blue	circle
black	*red*	circle	grating	blue	wave
grey	blue	radial	point	*purple*	*radial*
grey	red	*radial*	*spiral*	*purple*	*spiral*
blue	red	grating	point	red	circle
purple	*green*	grating	spiral	*red*	*wave*
purple	*yellow*	point	spiral	*green*	*line*
green	*yellow*			*green*	*radial*
				green	*spiral*
				yellow	line
				yellow	radial
				yellow	grating
				yellow	point
				yellow	spiral

Table E.15: Participant 5: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/105)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	*purple*	line	circle	white	line
white	*green*	line	wave	*white*	*radial*
white	*yellow*	circle	radial	*white*	*point*
black	purple	circle	point	*white*	*spiral*
black	yellow	wave	radial	black	line
grey	*purple*	wave	grating	black	radial
grey	yellow	wave	point	black	grating
blue	*purple*			black	point
blue	yellow			black	spiral
red	yellow			grey	line
				grey	*radial*
				grey	*grating*
				grey	*point*
				grey	*spiral*
				blue	line
				blue	*point*
				purple	circle
				purple	wave
				purple	grating
				purple	*point*
				red	line
				red	radial
				red	grating
				red	*point*
				yellow	circle
				yellow	*wave*

Table E.16: Coordinates of the 3-dimensional scaling of subjective experiences for participant 6. Details are given in the text.

white	35.79	50.19	9.69
black	-10.42	22.89	-10.87
grey	-29.17	12.50	-11.49
blue	-4.71	4.58	-19.08
purple	-16.13	-15.49	5.40
red	-10.94	-7.08	25.09
green	-8.77	-27.80	1.76
yellow	-0.16	-10.69	-10.78
line	5.98	-18.81	23.32
circle	31.30	-11.21	10.12
wave	-20.50	14.68	21.09
radial	-16.84	-16.22	-10.55
grating	35.49	-5.35	-18.51
point	47.08	-16.08	-4.57
zigzag	-23.41	14.32	-2.78
rectangle	3.59	23.35	3.25
spiral	-18.16	-13.76	-11.09

Table E.17: Participant 6: Pairs of colour and form experiences exhibiting significantly small distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form	colour	form
black	*grey*	line	circle	*black*	*wave*	red	line
black	blue	circle	grating	*black*	*zigzag*	*red*	*wave*
black	yellow	circle	point	black	rectangle	*red*	*radial*
grey	blue	*wave*	*zigzag*	black	spiral	*red*	*zigzag*
grey	purple	wave	rectangle	grey	wave	*red*	*spiral*
grey	yellow	*radial*	*zigzag*	grey	radial	*green*	*line*
blue	purple	*radial*	*spiral*	grey	zigzag	*green*	*radial*
blue	green	grating	point	grey	rectangle	*green*	*spiral*
blue	yellow	zigzag	rectangle	grey	spiral	yellow	line
purple	*red*	zigzag	spiral	blue	radial	yellow	circle
purple	*green*			blue	zigzag	yellow	radial
purple	*yellow*			blue	rectangle	yellow	grating
red	*green*			blue	spiral	yellow	zigzag
red	yellow			purple	line	yellow	rectangle
green	*yellow*			purple	wave	yellow	spiral
				purple	*radial*		
				purple	*zigzag*		
				purple	*spiral*		

Table E.18: Participant 6: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	black	line	grating	white	line
white	*grey*	line	zigzag	white	circle
white	*blue*	circle	wave	white	wave
white	*purple*	circle	radial	*white*	*radial*
white	*red*	circle	zigzag	*white*	*grating*
white	*green*	circle	spiral	*white*	*point*
white	*yellow*	wave	grating	white	zigzag
black	green	wave	point	*white*	*spiral*
		radial	grating	black	line
		radial	point	black	circle
		grating	zigzag	black	grating
		grating	spiral	black	point
		point	zigzag	grey	line
		point	*rectangle*	*grey*	*circle*
		point	*spiral*	*grey*	*grating*
				grey	*point*
				blue	*point*
				purple	grating
				purple	*point*
				red	grating
				red	*point*
				green	grating
				green	point
				green	rectangle

Table E.19: Coordinates of the 3-dimensional scaling of subjective experiences for participant 7. Details are given in the text.

white	-2.64	21.36	34.30
black	-15.72	-17.98	16.70
grey	-27.04	-12.34	-4.06
blue	-22.65	52.25	-23.05
purple	14.12	-17.23	-8.65
red	-21.68	-10.37	-18.23
green	9.98	-13.10	-10.55
yellow	20.90	-15.74	-10.59
line	12.58	7.63	20.36
circle	45.41	11.51	-7.94
wave	-36.35	-9.08	-5.95
radial	36.61	-1.87	1.64
grating	-19.64	-19.59	5.47
point	-37.92	17.99	-5.20
zigzag	-7.84	-15.46	23.95
rectangle	15.44	25.32	-6.90
spiral	36.43	-3.31	-1.30

Table E.20: Participant 7: Pairs of colour and form experiences exhibiting significantly small distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form	colour	form
black	*grey*	*line*	*radial*	*white*	*line*	*red*	*wave*
black	purple	line	zigzag	white	zigzag	red	grating
black	*red*	line	rectangle	black	line	red	point
black	green	line	spiral	*black*	*wave*	*green*	*line*
grey	red	circle	radial	black	grating	*green*	*radial*
grey	green	circle	rectangle	*black*	*zigzag*	green	grating
purple	*red*	circle	spiral	grey	wave	green	zigzag
purple	*green*	*wave*	*grating*	grey	grating	green	rectangle
purple	*yellow*	wave	point	grey	point	*green*	*spiral*
red	*green*	radial	rectangle	grey	zigzag	yellow	line
green	*yellow*	*radial*	*spiral*	blue	point	yellow	circle
		grating	zigzag	purple	line	yellow	radial
		rectangle	spiral	*purple*	*radial*	yellow	rectangle
				purple	*grating*	yellow	spiral
				purple	*zigzag*		
				purple	*spiral*		

Table E.21: Participant 7: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	*grey*	line	wave	white	circle
white	*blue*	line	point	white	wave
white	*purple*	circle	wave	*white*	*radial*
white	*red*	circle	grating	*white*	*spiral*
white	*green*	circle	point	black	circle
white	*yellow*	circle	zigzag	black	radial
black	blue	wave	radial	black	rectangle
grey	blue	wave	rectangle	black	spiral
blue	*purple*	wave	spiral	*grey*	*circle*
blue	red	radial	grating	*grey*	*radial*
blue	green	radial	point	grey	rectangle
blue	yellow	grating	rectangle	*grey*	*spiral*
		grating	spiral	blue	line
		point	*rectangle*	*blue*	*circle*
		point	*spiral*	*blue*	*wave*
		zigzag	rectangle	blue	radial
				blue	*grating*
				blue	zigzag
				blue	spiral
				purple	*point*
				red	line
				red	circle
				red	radial
				red	spiral
				green	point
				yellow	*wave*
				yellow	*point*

Table E.22: Coordinates of the 3-dimensional scaling of subjective experiences for participant 8. Details are given in the text.

white	-15.62	37.38	1.14
black	-0.36	38.64	-0.18
grey	-61.29	-13.13	-8.94
blue	-70.84	-12.58	1.13
purple	19.59	-18.39	-6.76
red	17.75	-15.20	-3.12
green	23.70	-4.52	2.41
yellow	-31.70	-3.16	38.10
line	-1.78	37.09	10.52
circle	-7.01	12.65	-34.16
wave	3.21	-30.43	2.21
radial	21.06	15.96	-8.92
grating	15.80	-9.53	24.03
point	20.82	-11.47	10.28
zigzag	12.48	-8.81	-22.57
rectangle	31.01	-7.43	0.71
spiral	23.17	-7.04	-5.87

Table E.23: Participant 8: Pairs of colour and form experiences exhibiting significantly small distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	black	*line*	*radial*	*white*	*line*
grey	blue	circle	radial	black	line
purple	*red*	circle	zigzag	black	radial
purple	*green*	*wave*	*grating*	purple	wave
red	*green*	wave	point	*purple*	*radial*
		wave	*zigzag*	*purple*	*grating*
		wave	rectangle	purple	point
		wave	spiral	*purple*	*zigzag*
		radial	grating	purple	rectangle
		radial	point	*purple*	*spiral*
		radial	*zigzag*	*red*	*wave*
		radial	rectangle	*red*	*radial*
		radial	*spiral*	red	grating
		grating	point	red	point
		grating	*rectangle*	*red*	*zigzag*
		grating	spiral	red	rectangle
		point	zigzag	*red*	*spiral*
		point	rectangle	green	wave
		point	spiral	*green*	*radial*
		zigzag	rectangle	green	grating
		zigzag	spiral	green	point
		rectangle	spiral	green	zigzag
				green	rectangle
				green	*spiral*

Table E.24: Participant 8: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/136)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form	colour	form
white	*grey*	line	wave	white	wave	blue	line
white	*blue*	line	zigzag	*white*	*grating*	*blue*	*circle*
white	*purple*	circle	grating	*white*	*point*	*blue*	*wave*
white	*red*			white	zigzag	blue	radial
black	grey			white	rectangle	*blue*	*grating*
black	blue			*white*	*spiral*	*blue*	*point*
black	purple			black	wave	blue	zigzag
black	yellow			grey	line	blue	rectangle
grey	*purple*			*grey*	*circle*	blue	spiral
grey	red			grey	wave	purple	line
grey	green			*grey*	*radial*	yellow	circle
blue	*purple*			*grey*	*grating*	yellow	radial
blue	red			*grey*	*point*	*yellow*	*point*
blue	green			grey	zigzag	yellow	zigzag
purple	yellow			grey	rectangle	yellow	rectangle
red	yellow			*grey*	*spiral*	yellow	spiral
green	yellow						

Table E.25: Coordinates of the 3-dimensional scaling of subjective experiences for participant 9. Details are given in the text.

white	46.10	28.07	2.14
blue	-43.45	6.63	-5.55
purple	2.17	-24.12	15.52
red	-12.37	-17.39	-6.42
green	0.64	-3.39	7.06
yellow	13.21	11.38	-29.99
line	0.19	27.73	1.07
circle	24.12	-10.91	17.27
wave	20.26	-6.58	9.14
radial	-30.17	2.54	-2.69
grating	18.17	-15.86	-15.10
point	-17.16	20.55	30.96
rectangle	0.28	-9.75	-31.13
spiral	-21.97	-8.90	7.72

Table E.26: Participant 9: Pairs of colour and form experiences exhibiting significantly small distances ($\alpha_{adj} = (.05/91)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
purple	*red*	line	point	blue	radial
purple	*green*	circle	wave	blue	spiral
red	*green*	circle	grating	purple	circle
		wave	*grating*	purple	wave
		radial	*spiral*	*purple*	*grating*
		grating	*rectangle*	*purple*	*spiral*
		point	spiral	*red*	*wave*
				red	*radial*
				red	grating
				red	rectangle
				red	*spiral*
				green	*line*
				green	circle
				green	wave
				green	*radial*
				green	grating
				green	point
				green	rectangle
				green	*spiral*
				yellow	line
				yellow	grating
				yellow	rectangle

Table E.27: Participant 9: Pairs of colour and form experiences exhibiting significantly large distances ($\alpha_{adj} = (.05/91)$) in the MDS model compared to the mean distance between experiences in the model. Italic writing marks pairs that co-occur significantly in at least 50% of all participants. Details are given in the text.

colour	colour	form	form	colour	form
white	*blue*	circle	radial	white	radial
white	*purple*	circle	point	*white*	*grating*
white	*red*	circle	rectangle	*white*	*point*
white	*green*	wave	radial	white	rectangle
blue	*purple*	radial	grating	*white*	*spiral*
blue	yellow	grating	point	*blue*	*circle*
purple	yellow	*point*	*rectangle*	*blue*	*wave*
				blue	*grating*
				blue	rectangle
				purple	line
				red	*point*
				yellow	circle
				yellow	radial
				yellow	*point*
				yellow	spiral

Appendix F

Experiment 2 and 3 - Circular plots

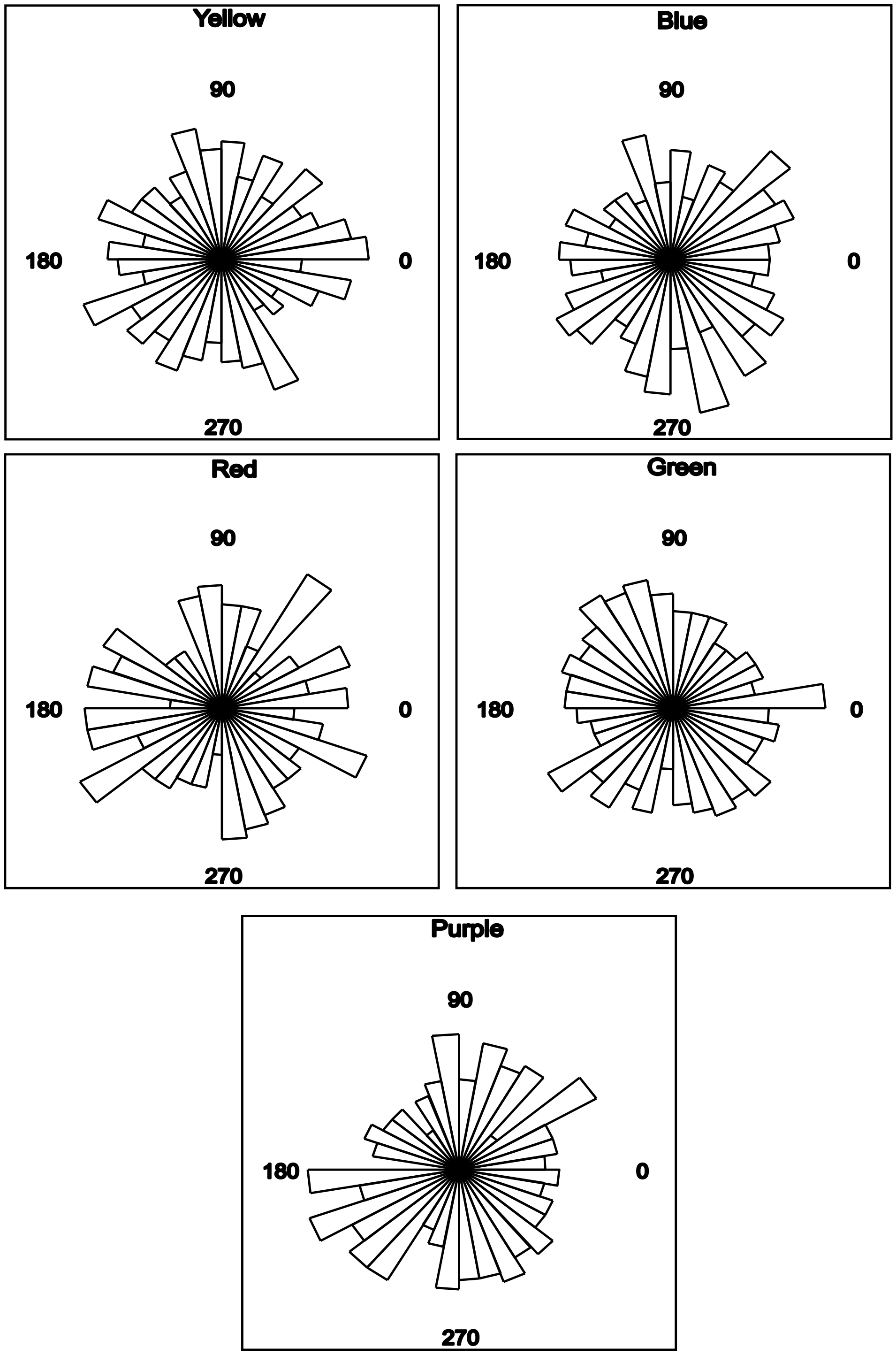


Figure F.1: Experiment 2: Circular diagrams indicating the distribution of response times to subjective colours expressed in terms of phase in the flicker frequency cycle. 360 degrees on the circle (in counter-clockwise direction) correspond to one flicker frequency cycle.

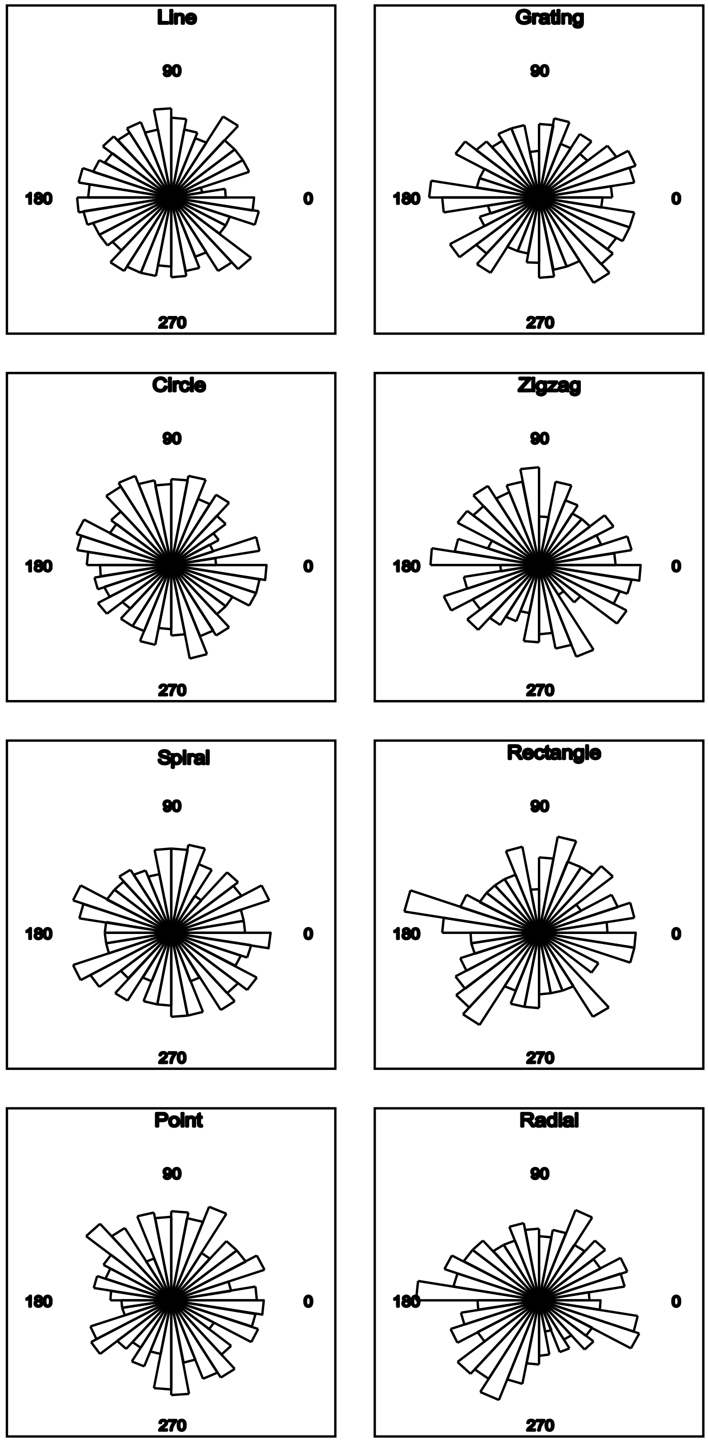


Figure F.2: Experiment 3: Circular diagrams indicating the distribution of response times to subjective forms expressed in terms of phase in the flicker frequency cycle. 360 degrees on the circle (in counter-clockwise direction) correspond to one flicker frequency cycle.

Appendix G

Experiment 4 and 5 - SiZer plots

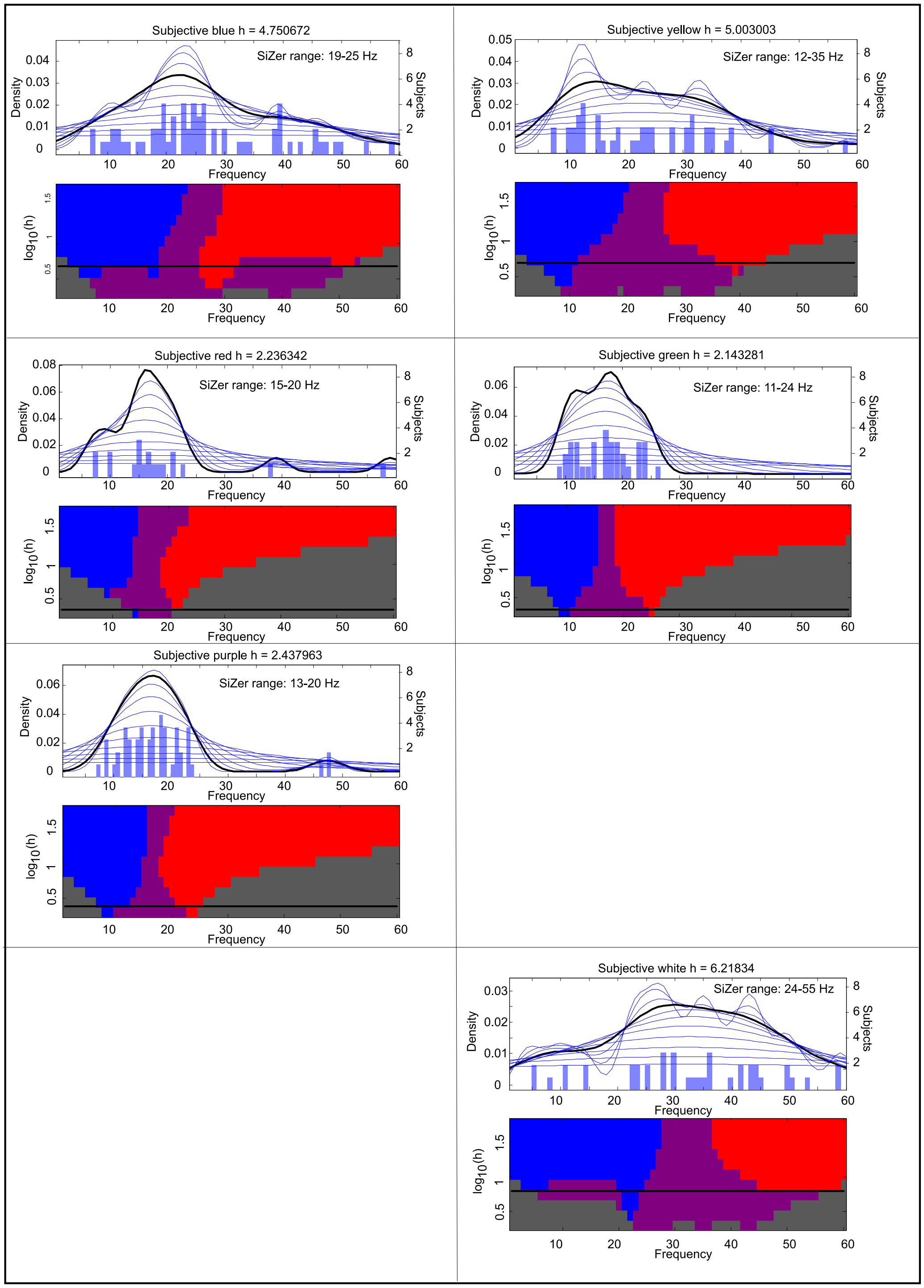


Figure G.1: Graphical representation of the SiZer analysis for subjective colours reported in Experiment 1 corrected by the reports of the free report trial in Experiment 4. SiZer plots for black and grey did not need correction and can be found in Figure C.2. For further information see the caption of Figure C.1 and the text.

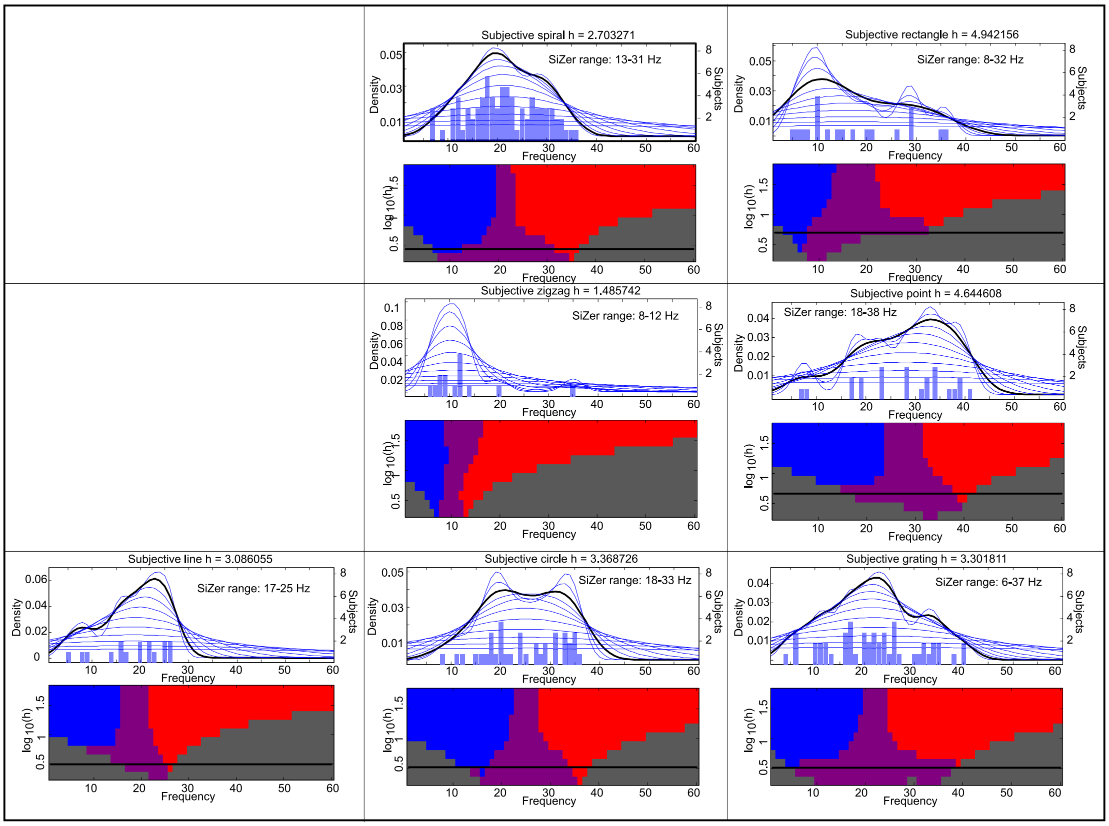


Figure G.2: Graphical representation of the SiZer analysis for subjective forms reported in Experiment 1 corrected by the reports of the free report trial in Experiment 5. SiZer plots for radials and waves did not need correction and can be found in Figure C.1. For further information see the caption of Figure C.1 and the text.

Appendix H

Experiment 7 - Drawings of subjective forms

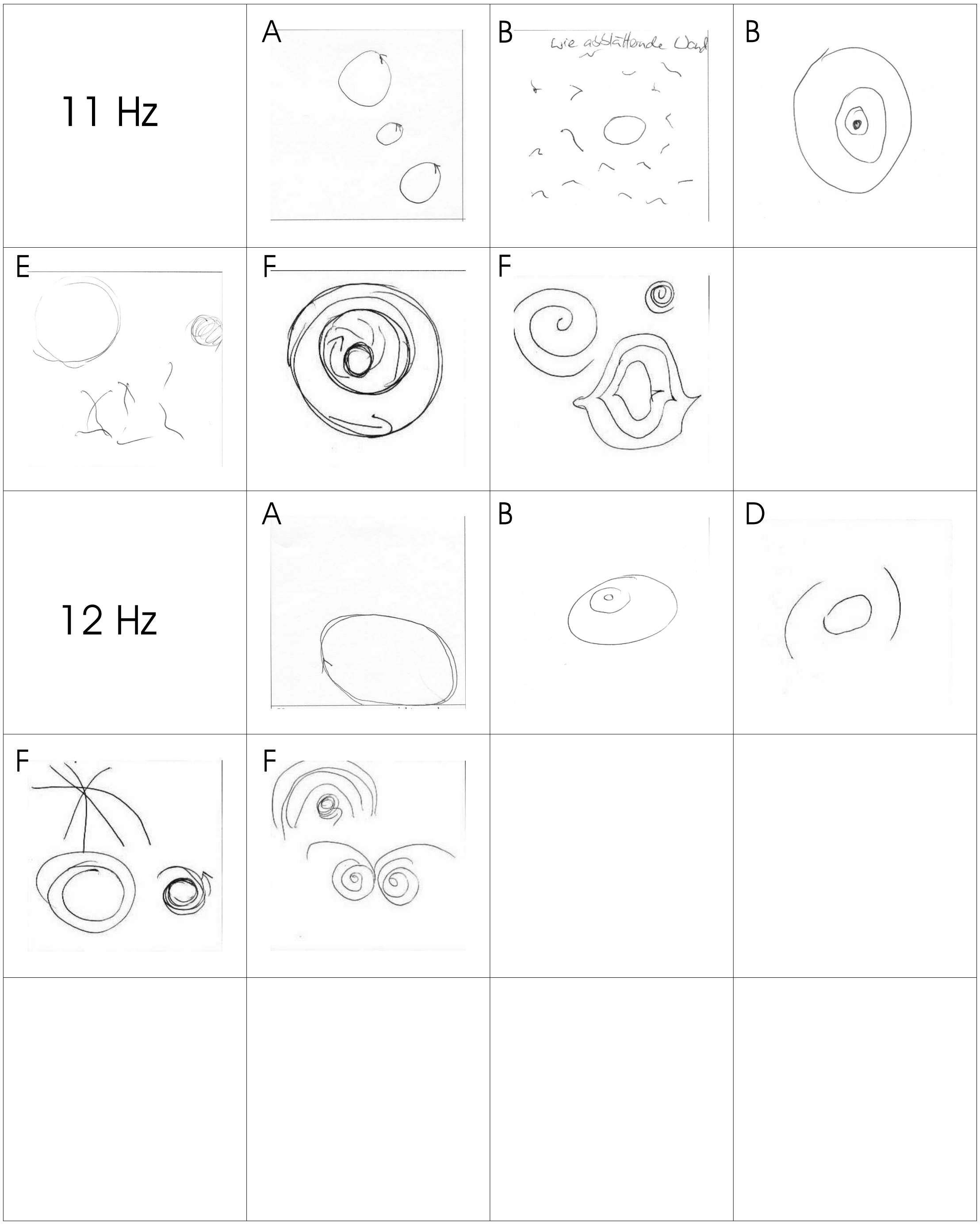


Figure H.1: Subjective experiences of circles as drawn by the participants following stimulation.

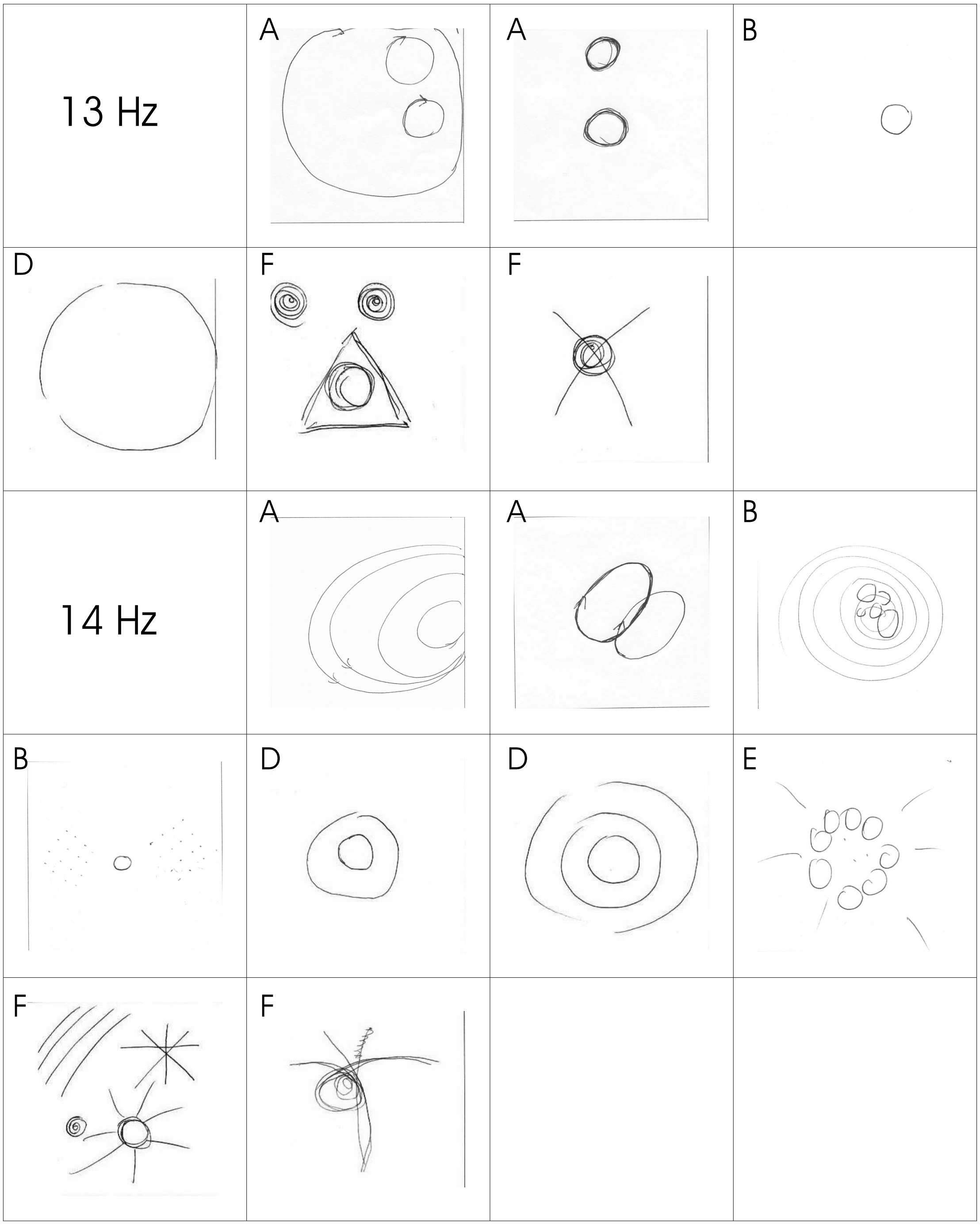


Figure H.2: Subjective experiences of circles as drawn by the participants following stimulation.

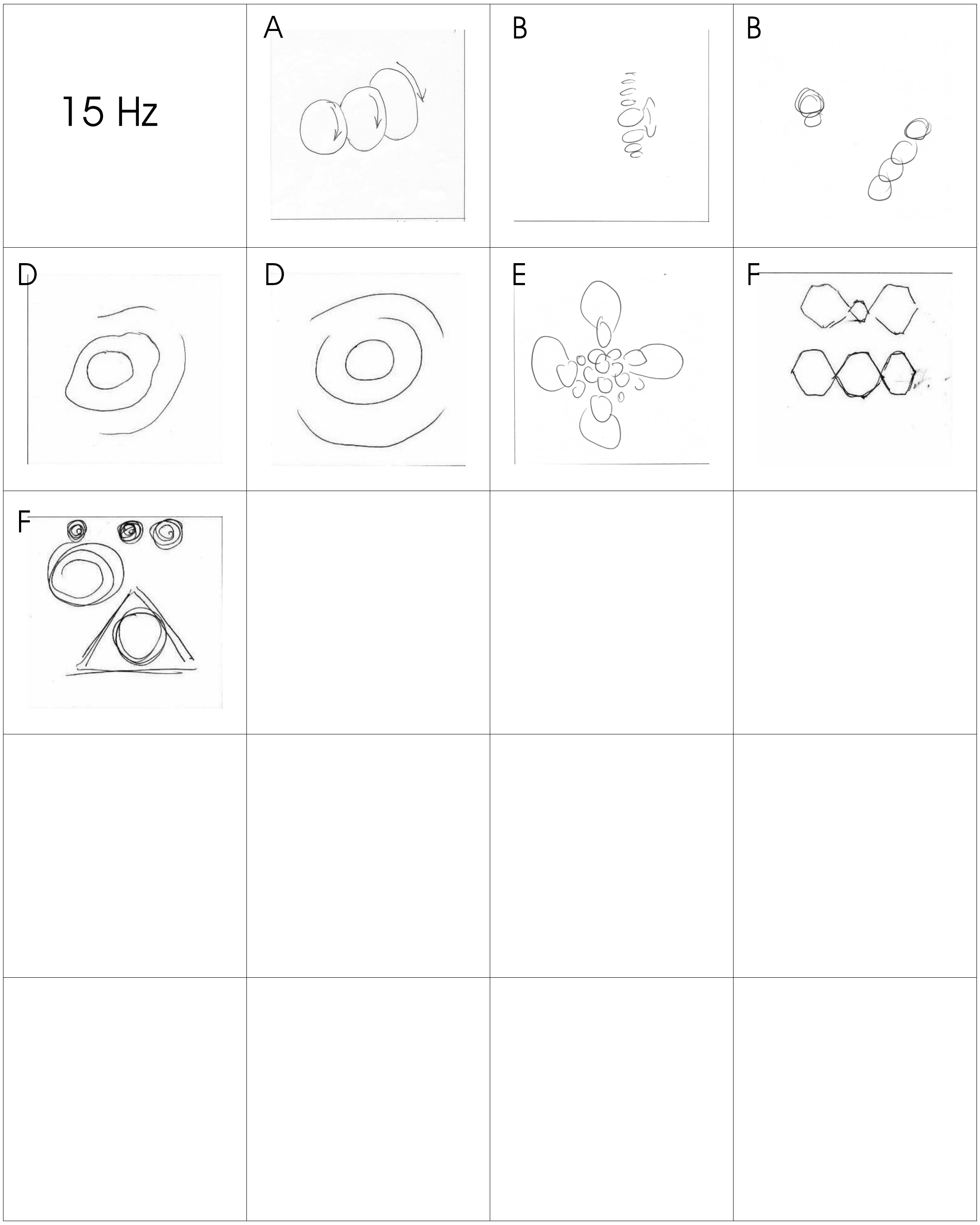


Figure H.3: Subjective experiences of circles as drawn by the participants following stimulation.

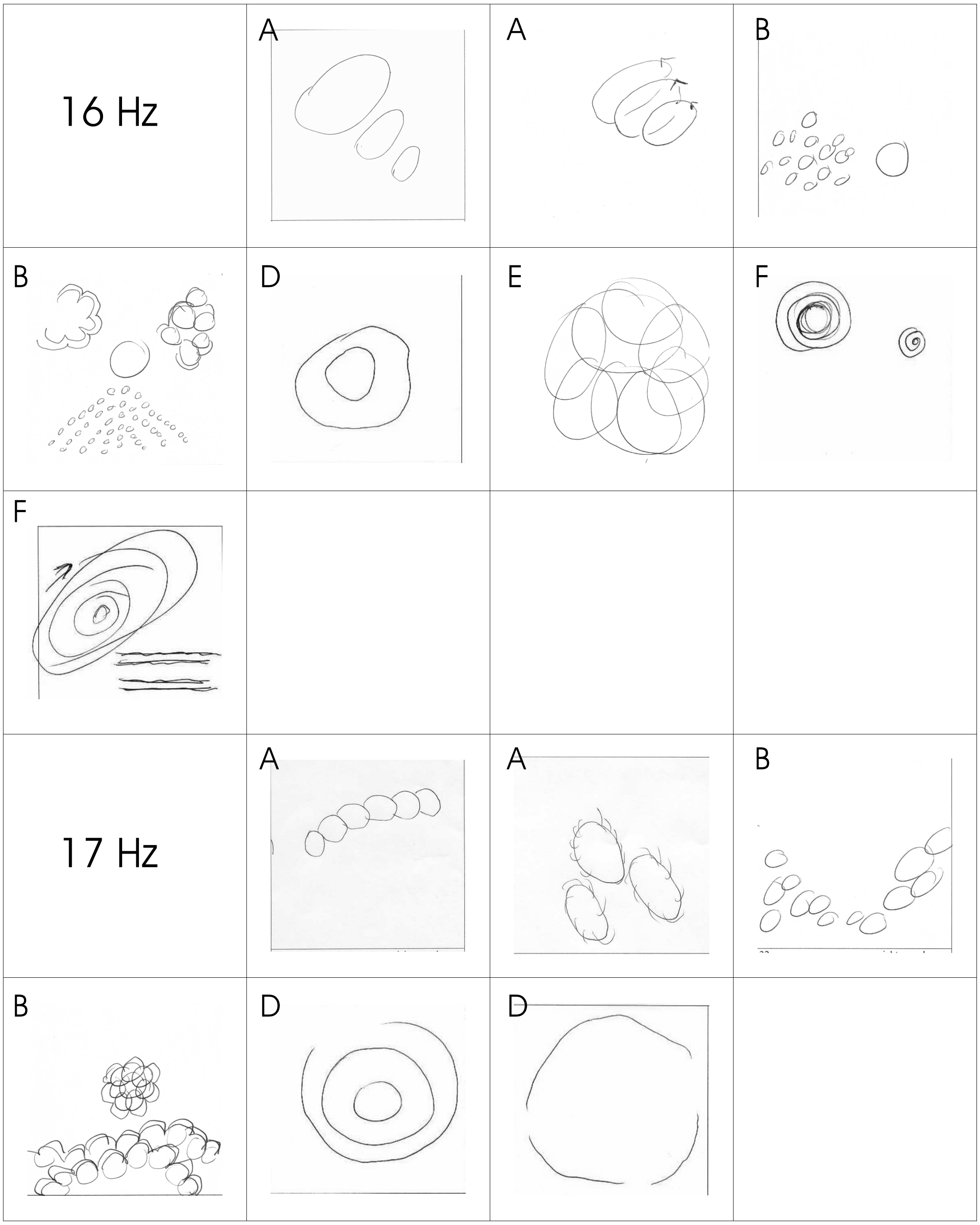


Figure H.4: Subjective experiences of circles as drawn by the participants following stimulation.

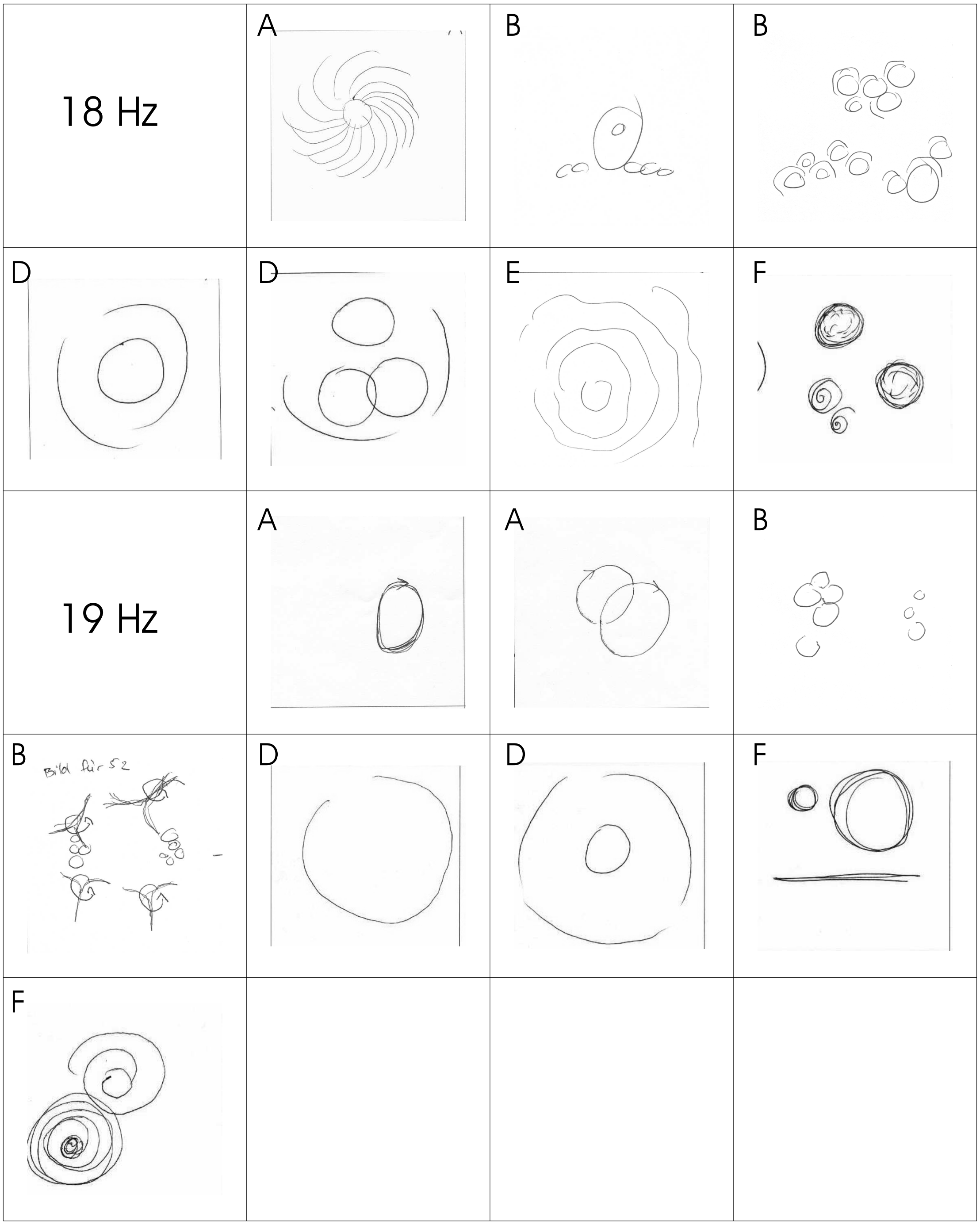


Figure H.5: Subjective experiences of circles as drawn by the participants following stimulation.

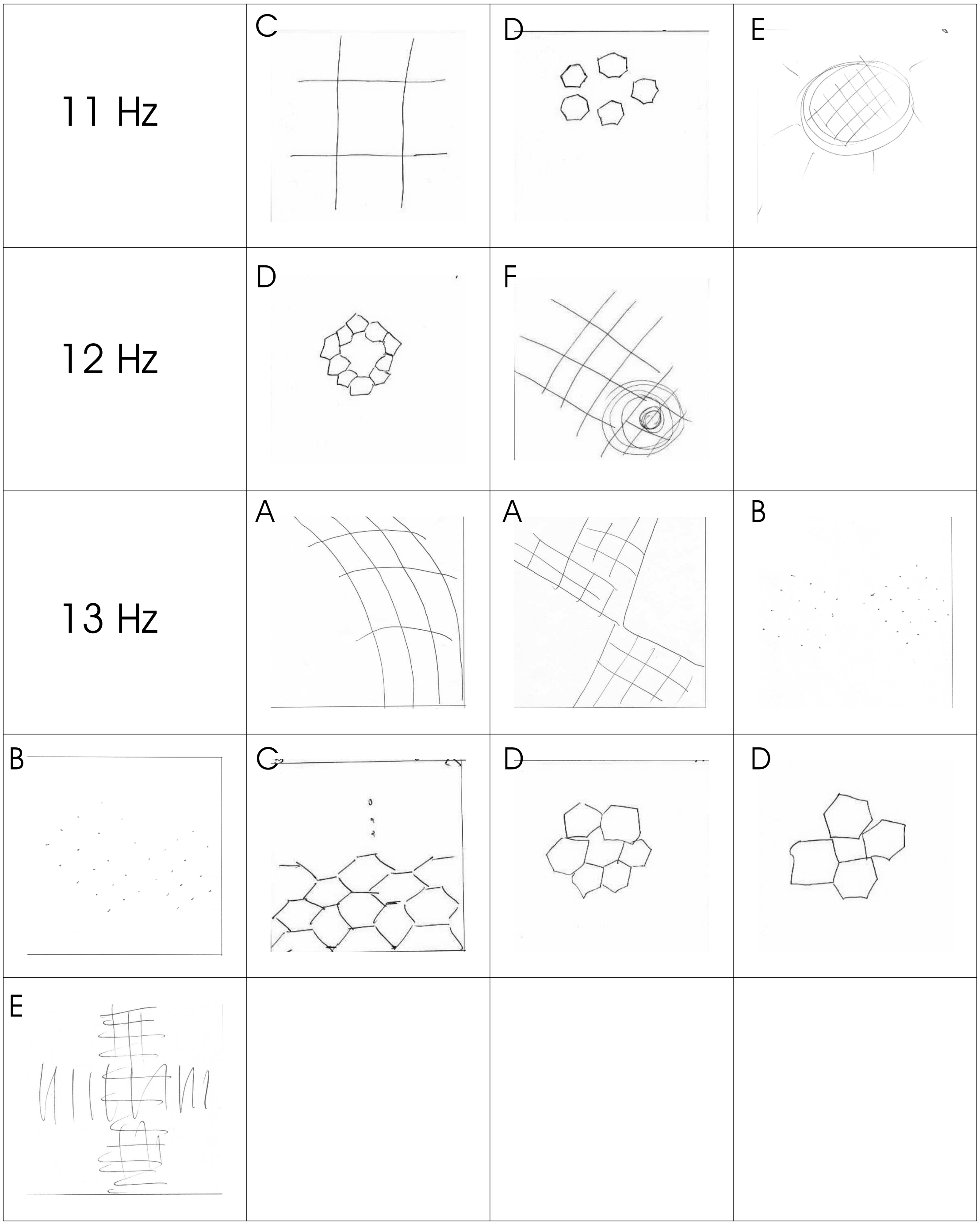


Figure H.6: Subjective experiences of gratings as drawn by the participants following stimulation.

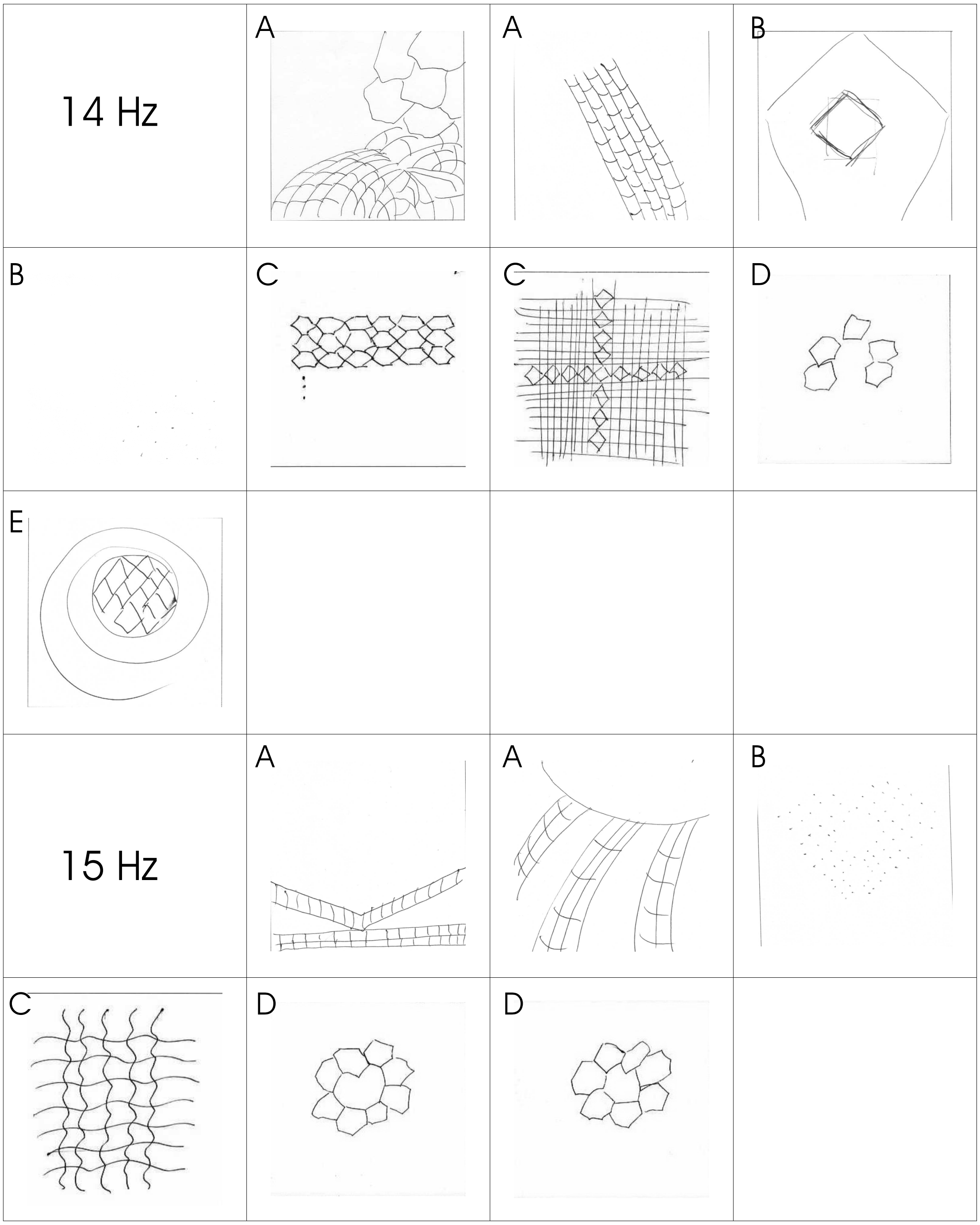


Figure H.7: Subjective experiences of gratings as drawn by the participants following stimulation.

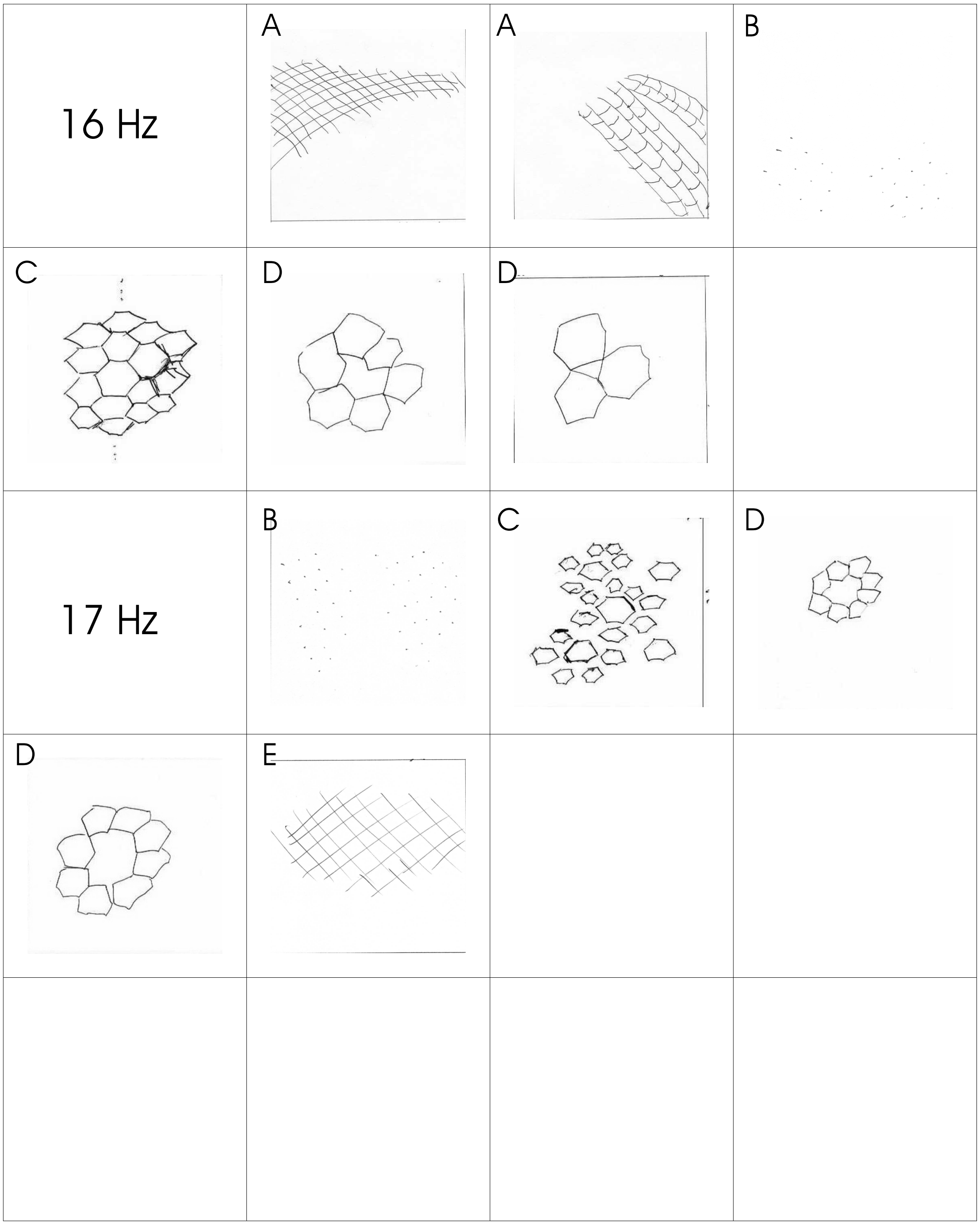


Figure H.8: Subjective experiences of gratings as drawn by the participants following stimulation.

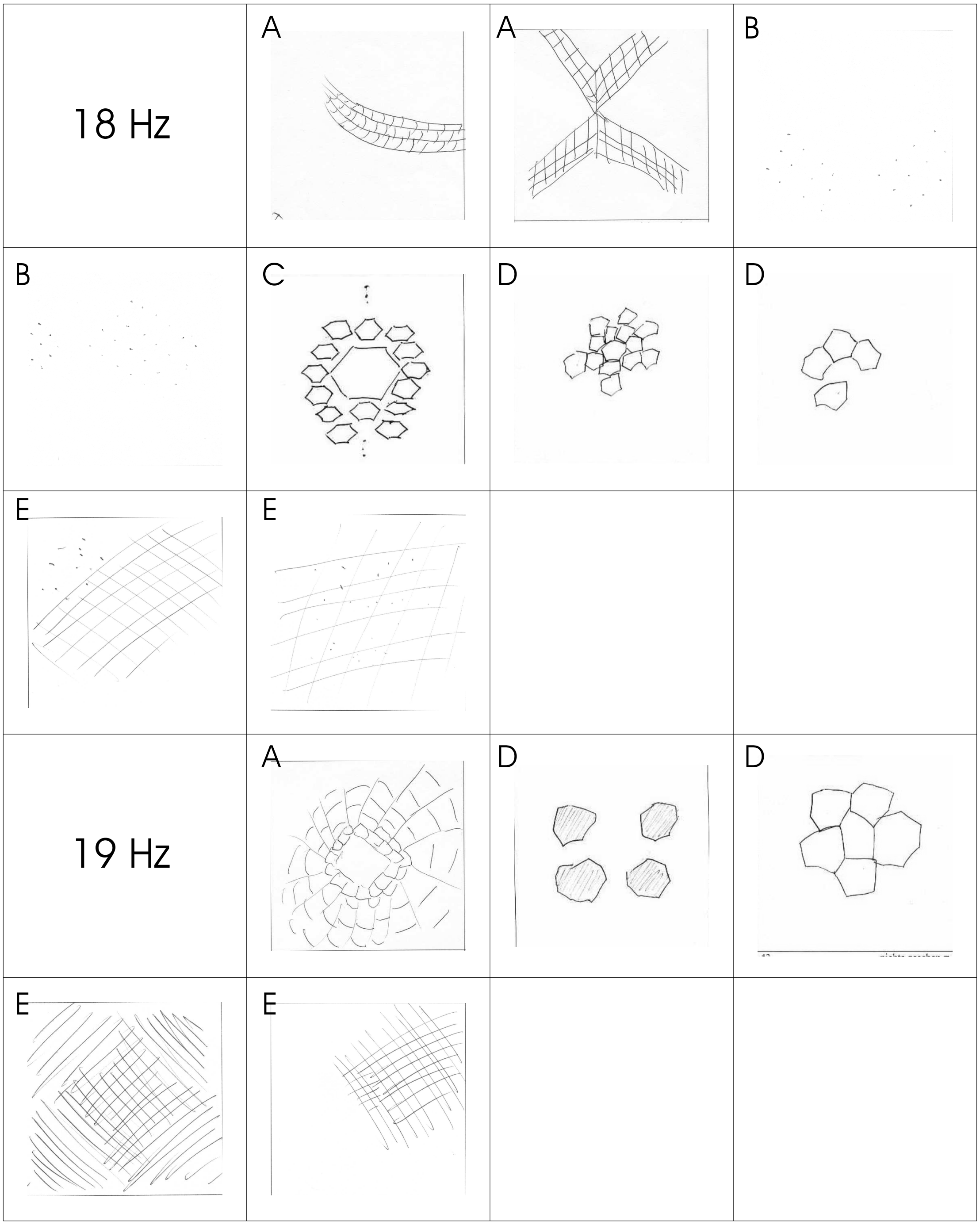


Figure H.9: Subjective experiences of gratings as drawn by the participants following stimulation.

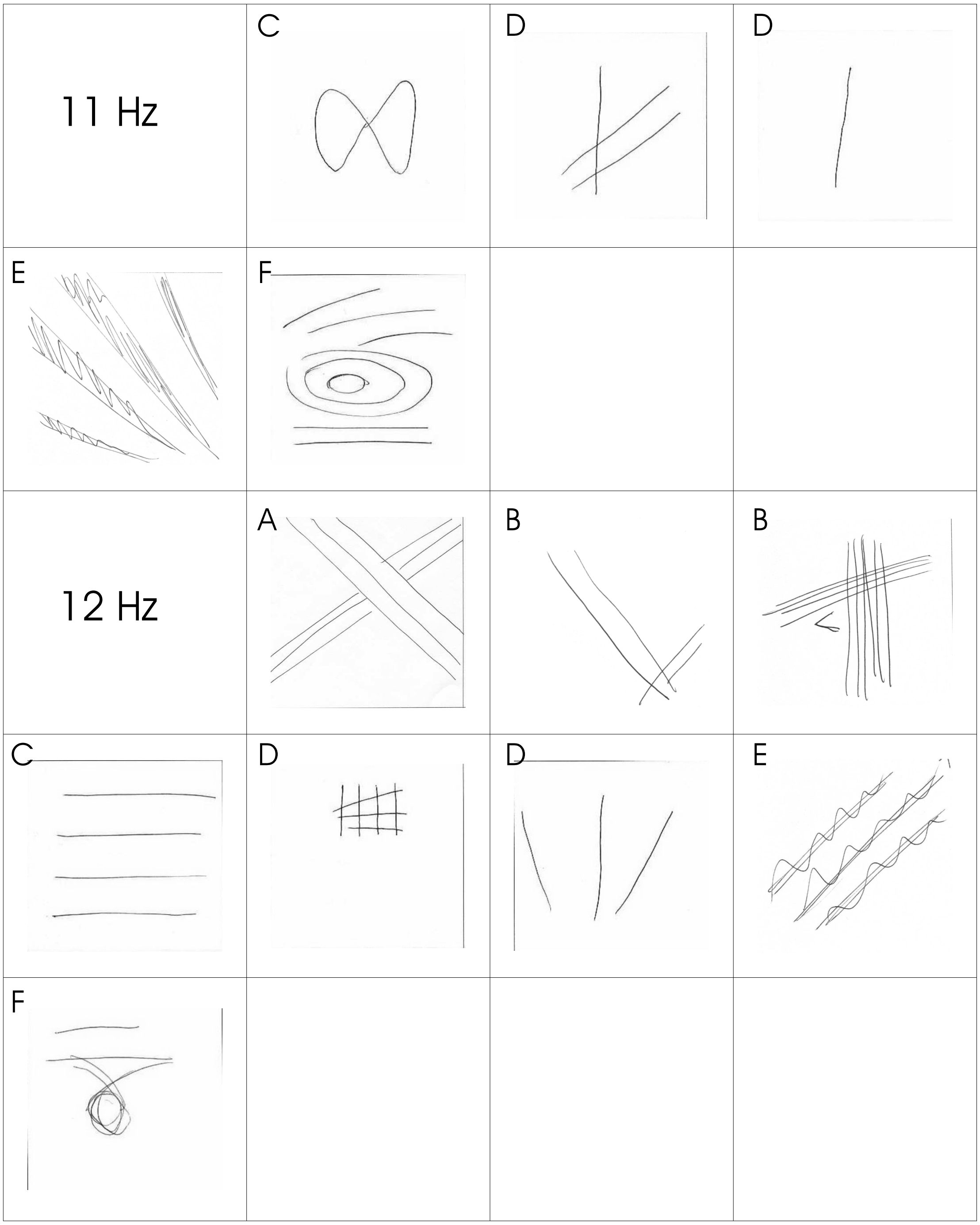


Figure H.10: Subjective experiences of lines as drawn by the participants following stimulation.

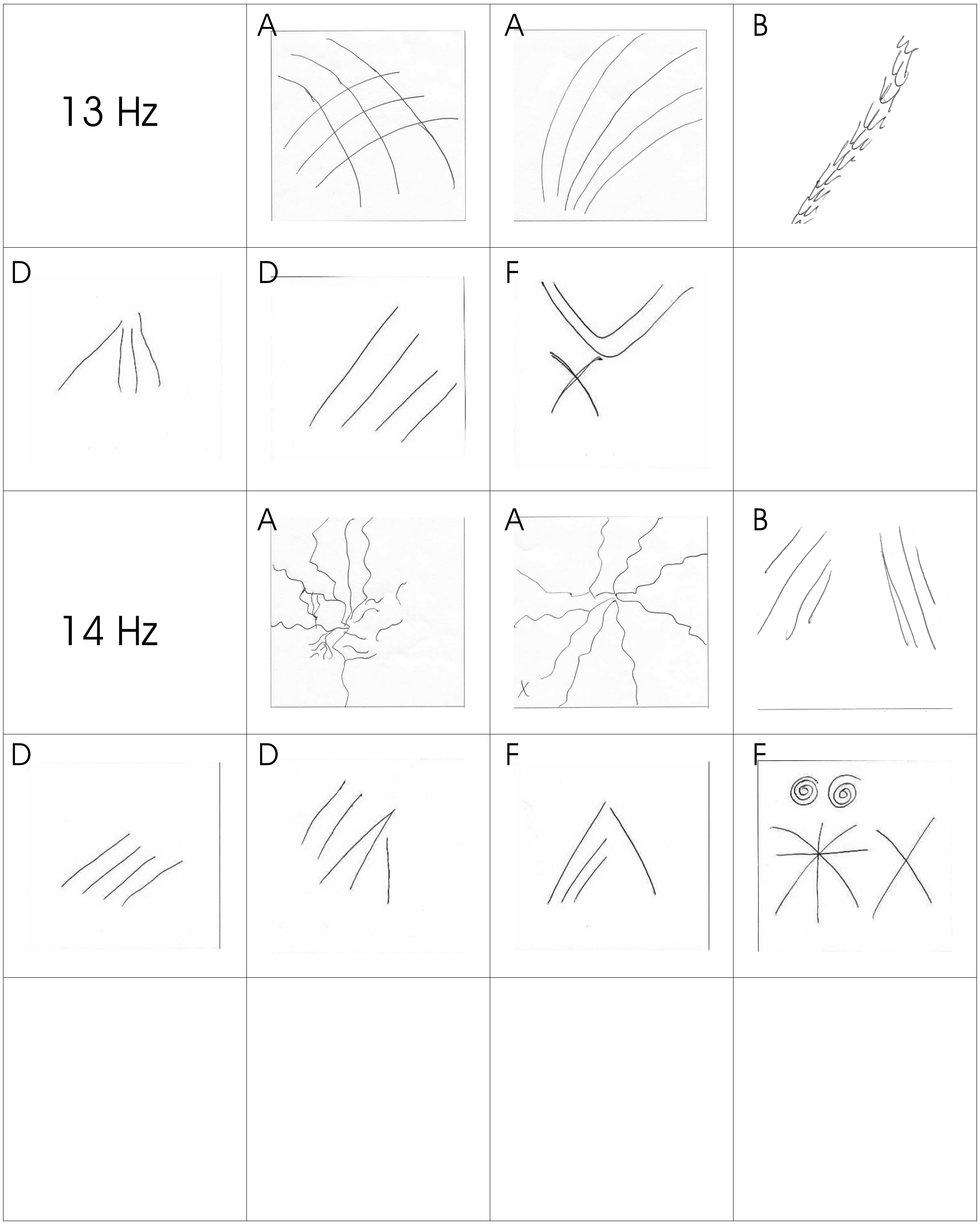


Figure H.11: Subjective experiences of lines as drawn by the participants following stimulation.

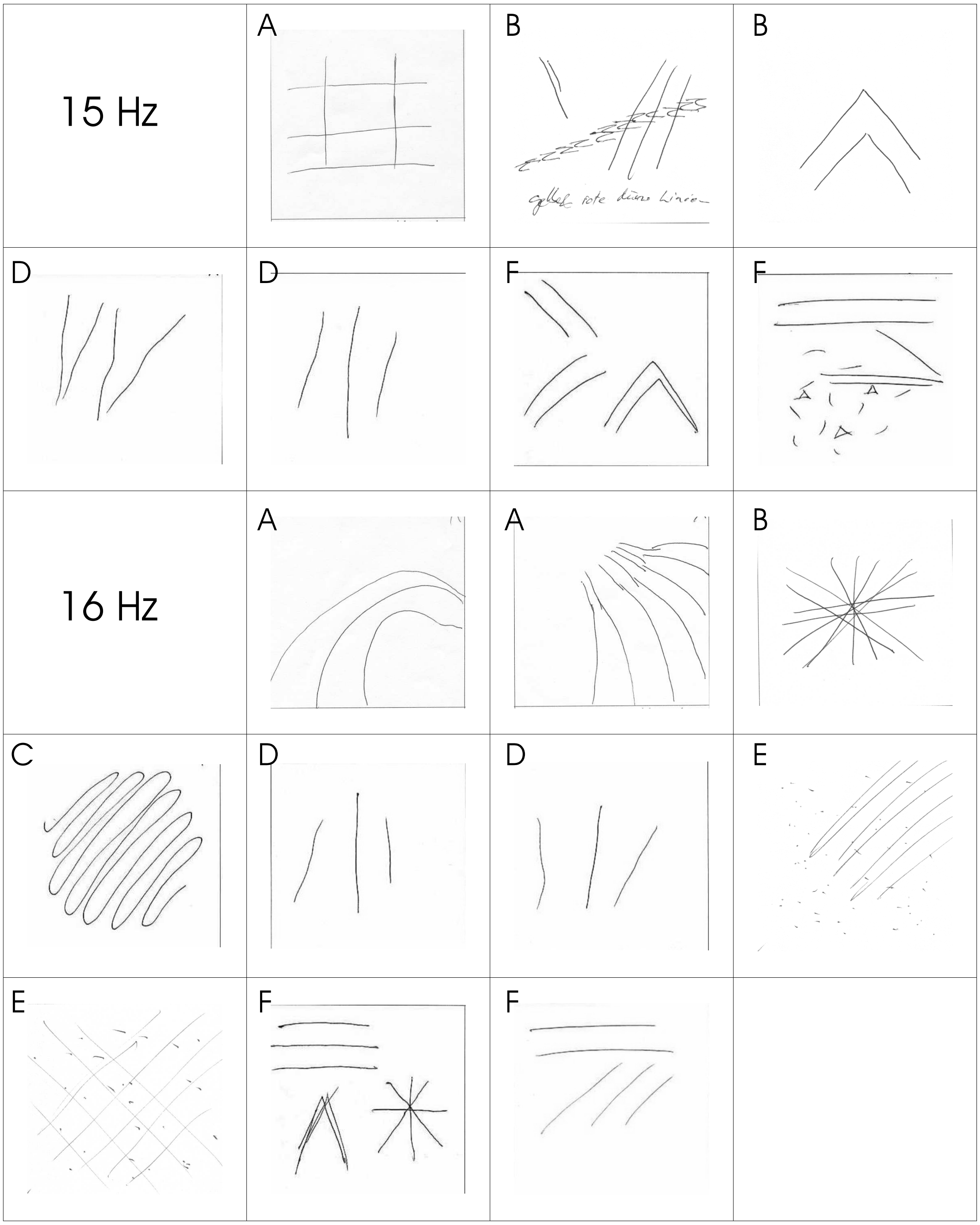


Figure H.12: Subjective experiences of lines as drawn by the participants following stimulation.

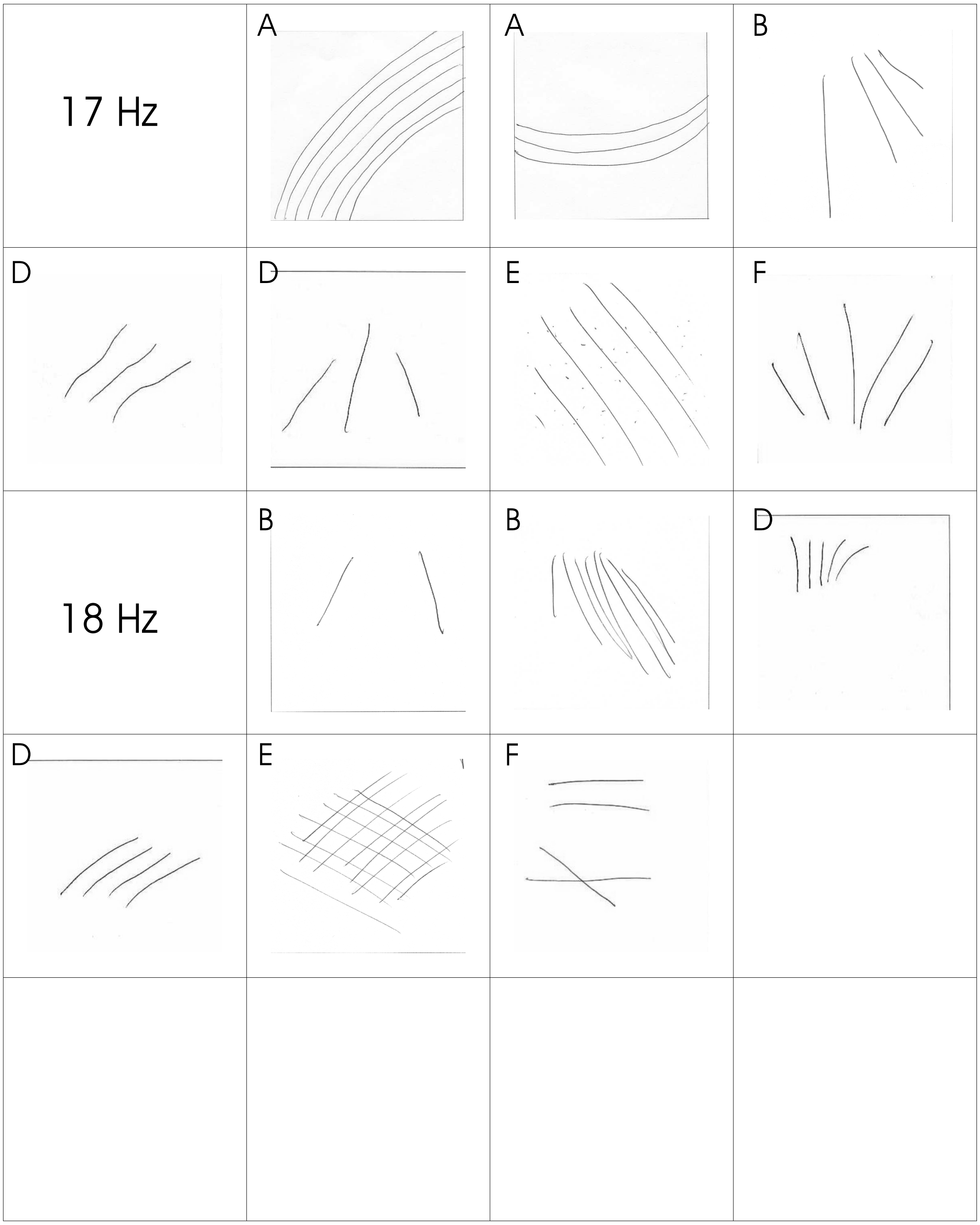


Figure H.13: Subjective experiences of lines as drawn by the participants following stimulation.

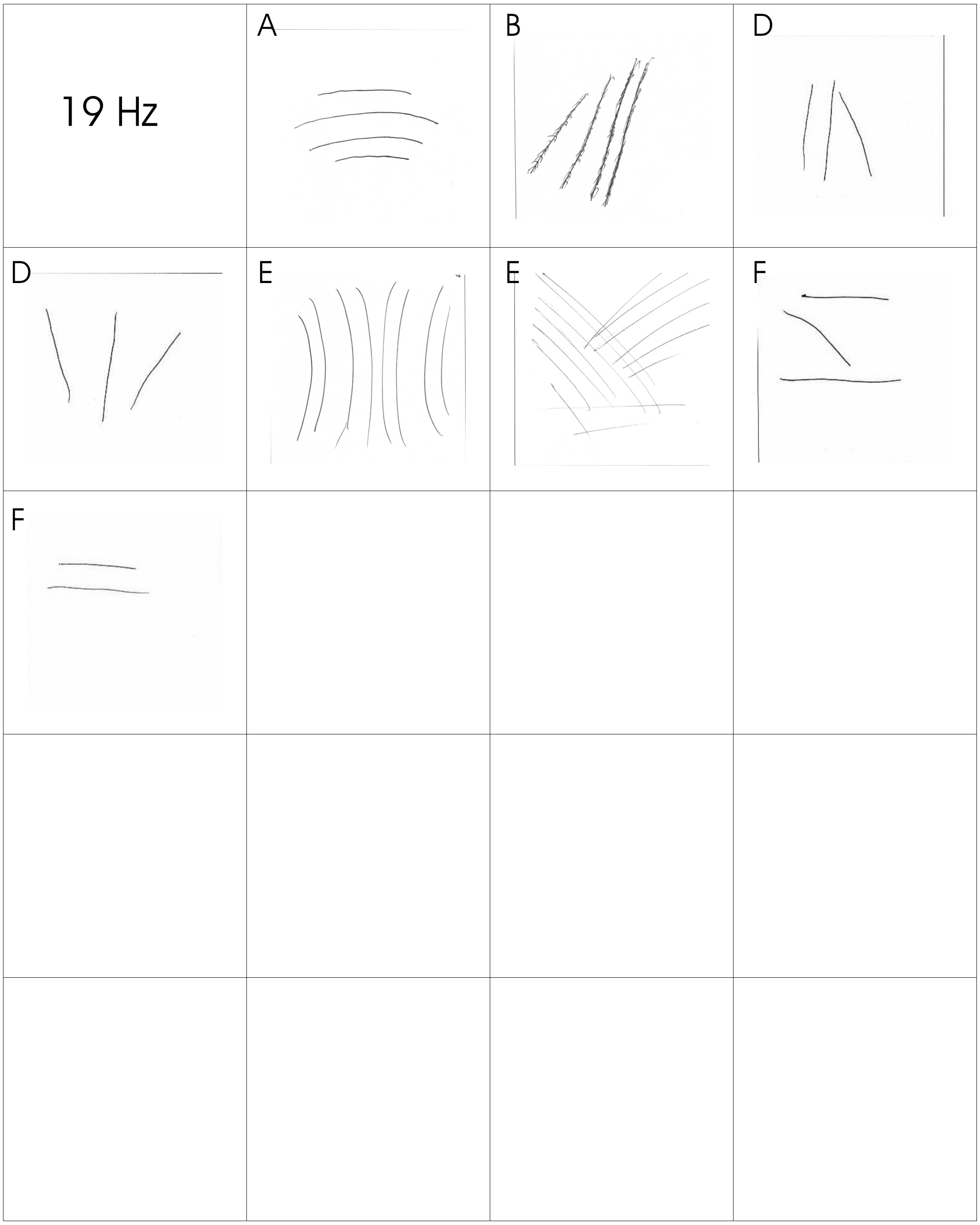


Figure H.14: Subjective experiences of lines as drawn by the participants following stimulation.

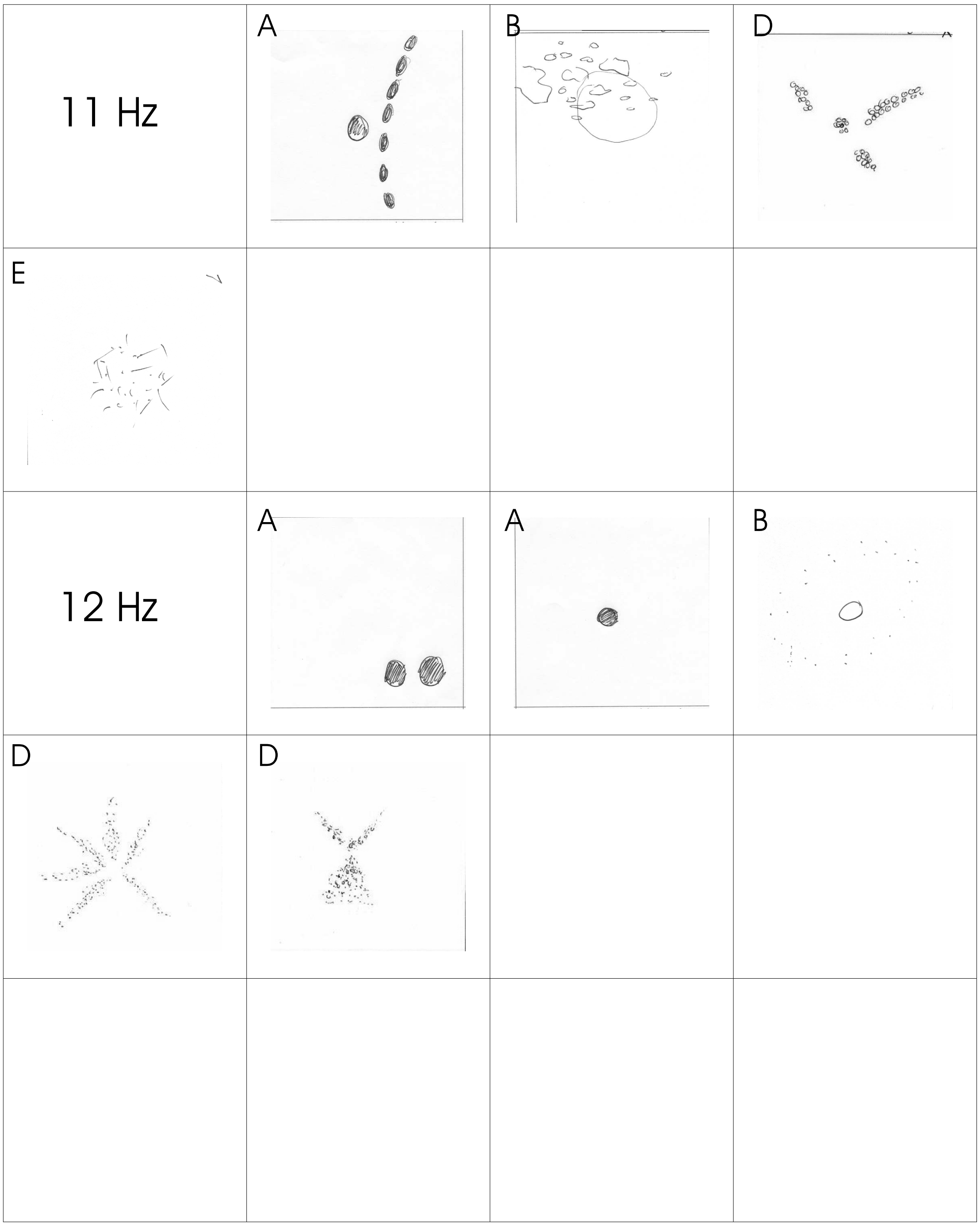


Figure H.15: Subjective experiences of points as drawn by the participants following stimulation.

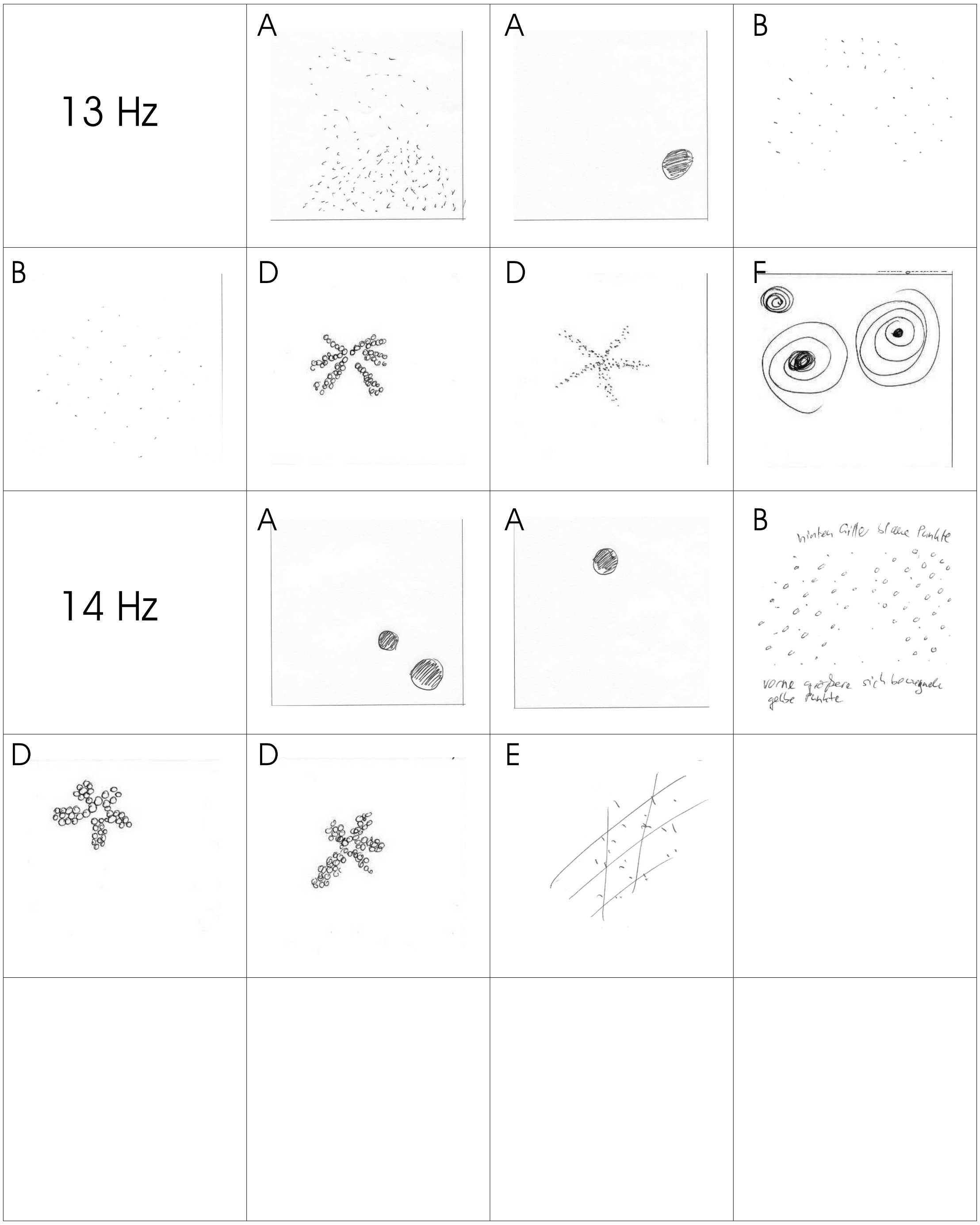


Figure H.16: Subjective experiences of points as drawn by the participants following stimulation.

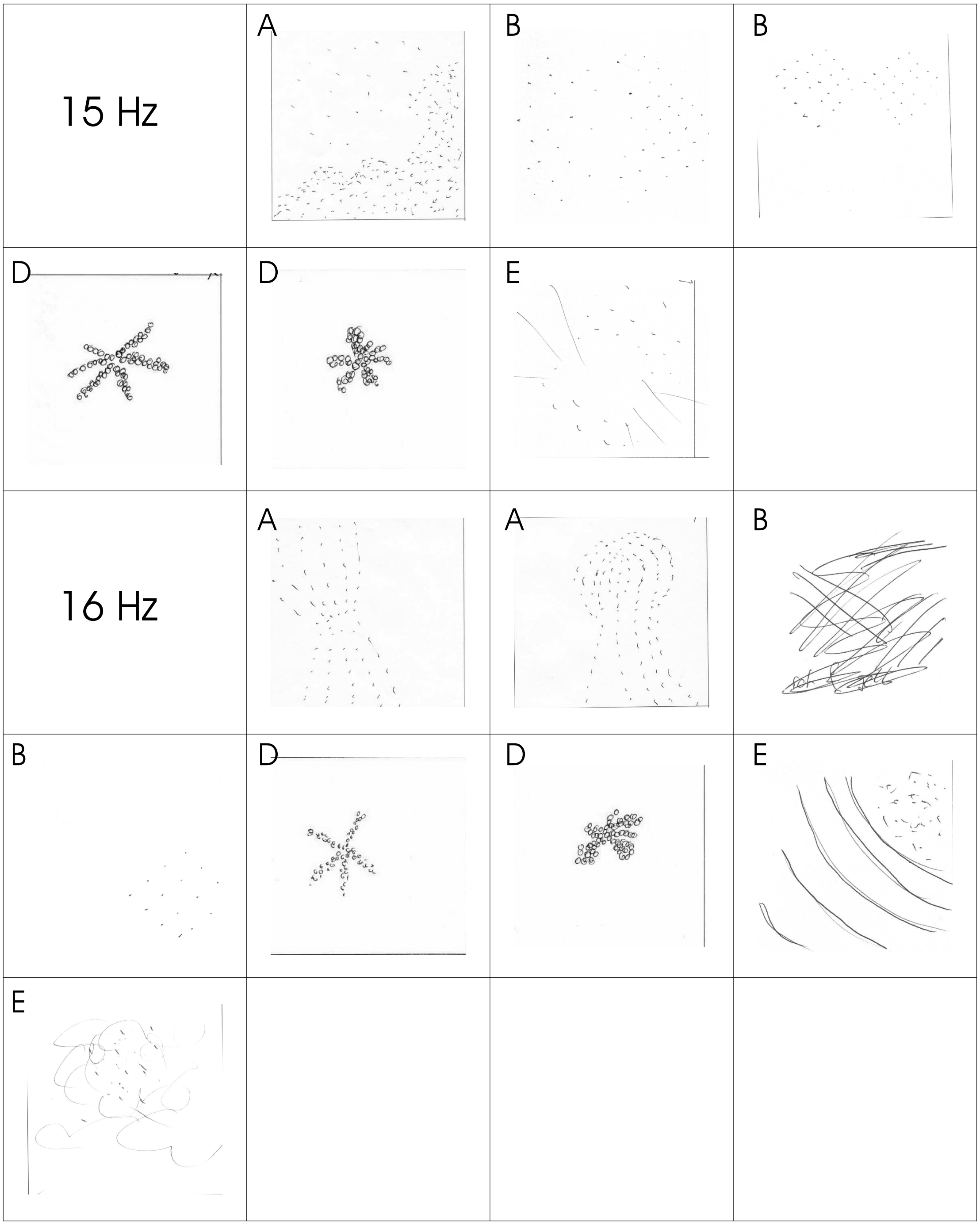


Figure H.17: Subjective experiences of points as drawn by the participants following stimulation.

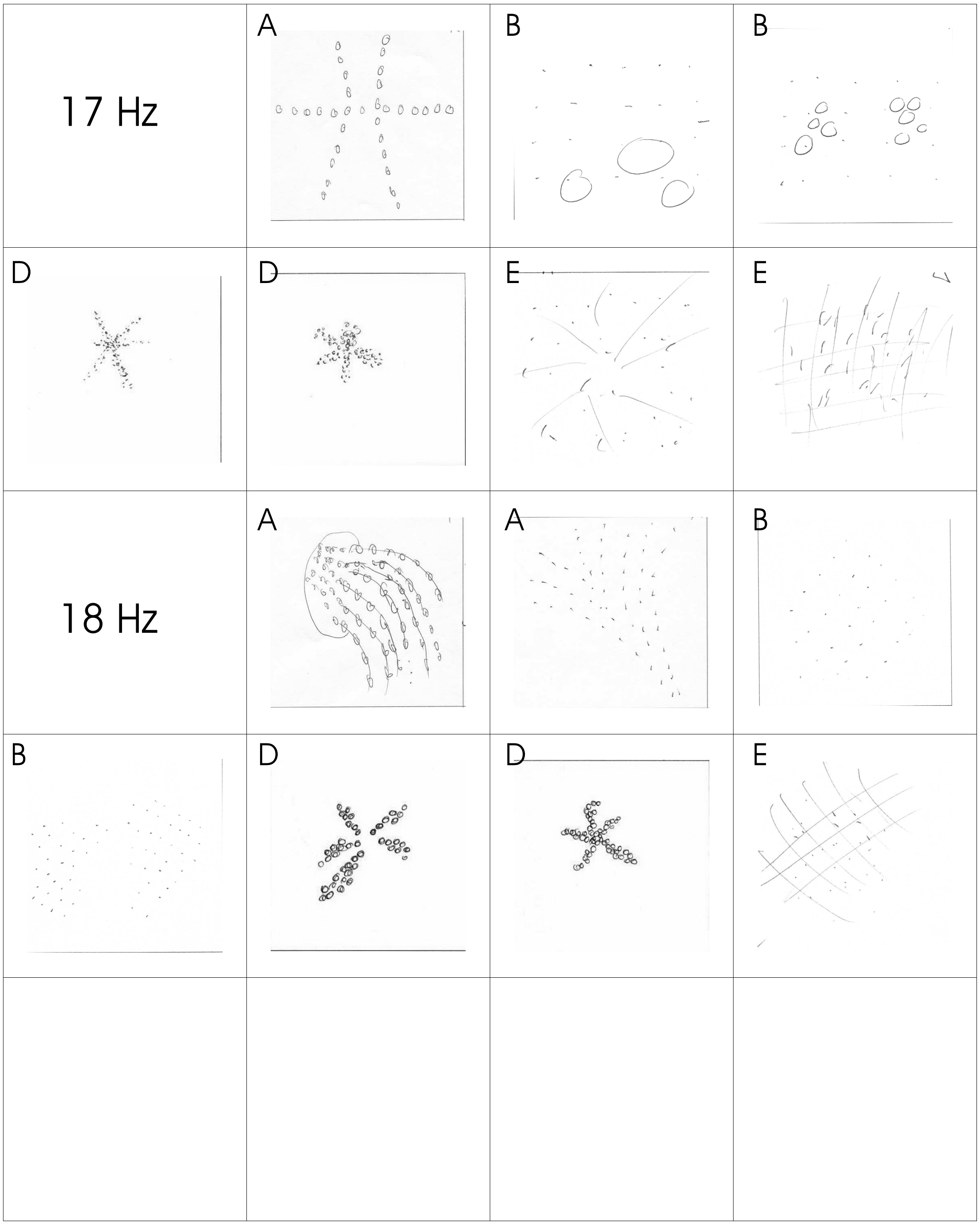


Figure H.18: Subjective experiences of points as drawn by the participants following stimulation.

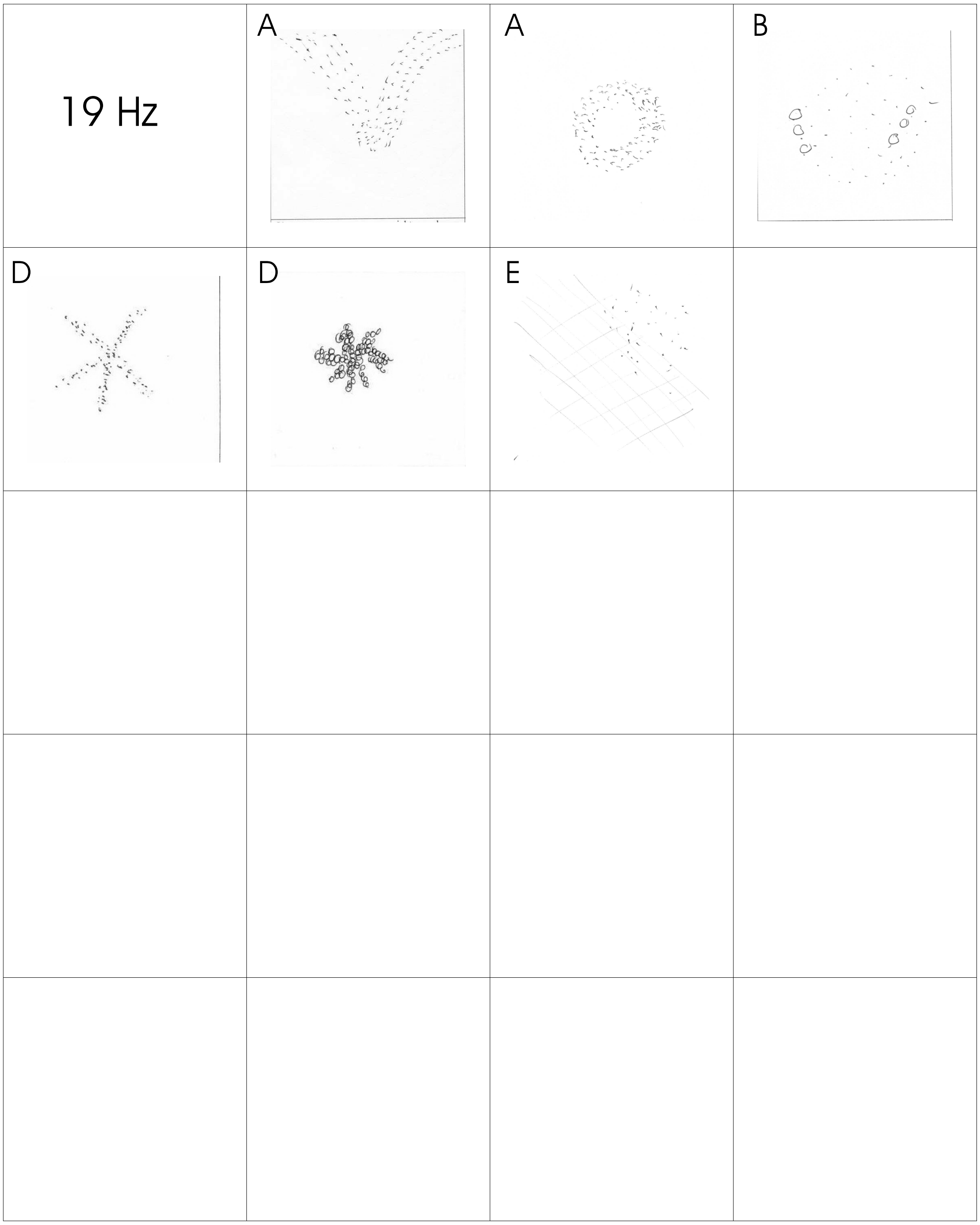


Figure H.19: Subjective experiences of points as drawn by the participants following stimulation.

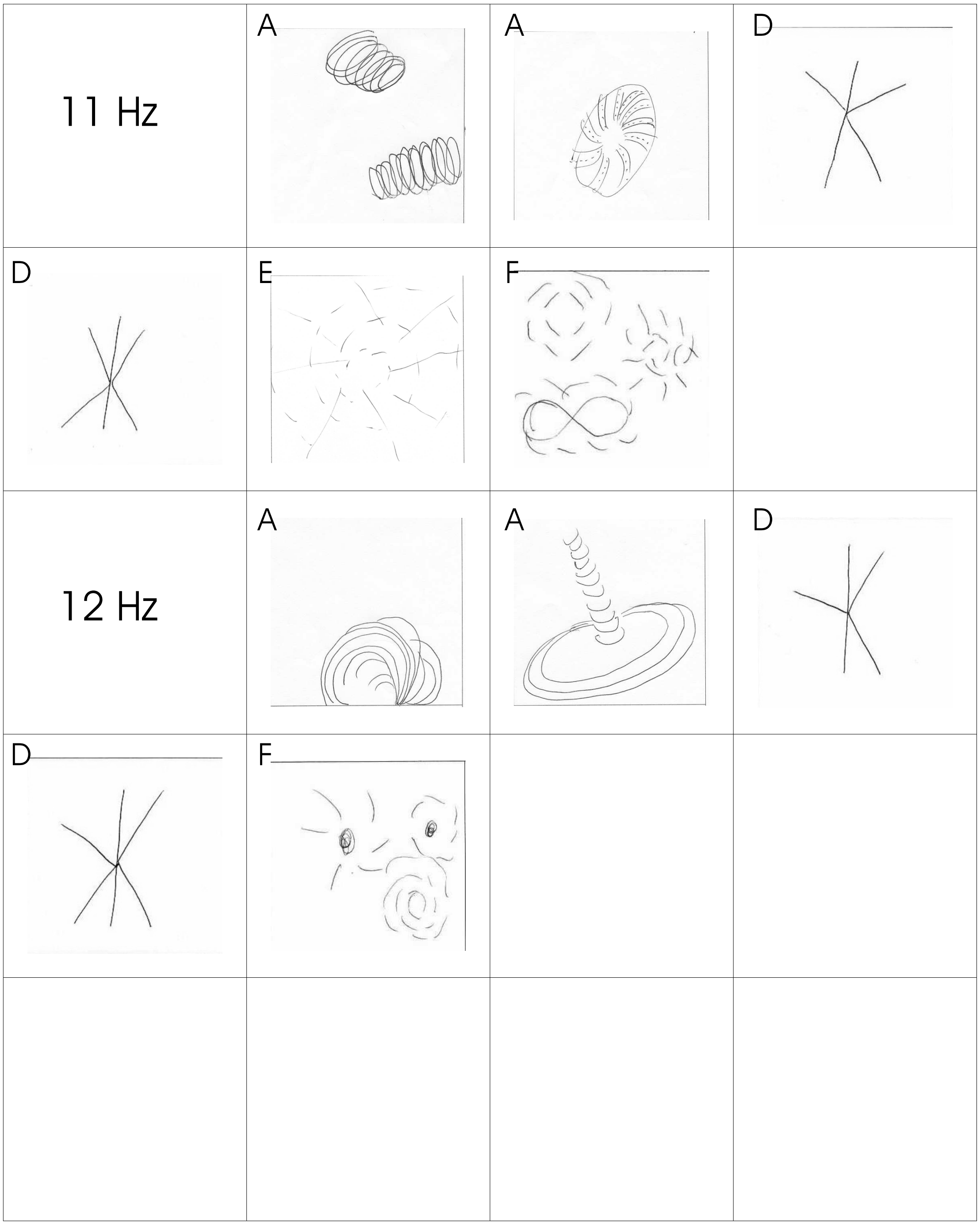


Figure H.20: Subjective experiences of radial patterns as drawn by the participants following stimulation.

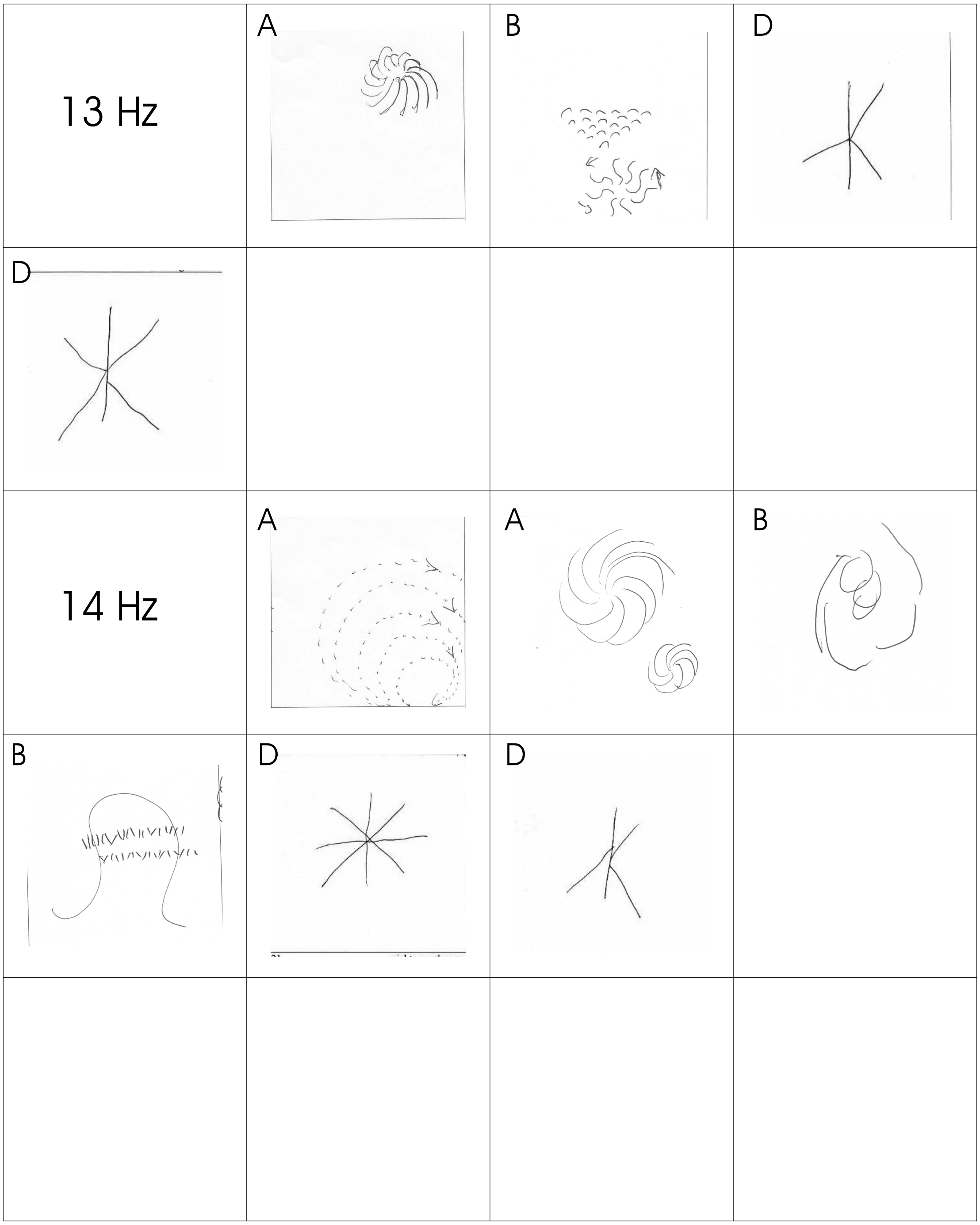


Figure H.21: Subjective experiences of radial patterns as drawn by the participants following stimulation.

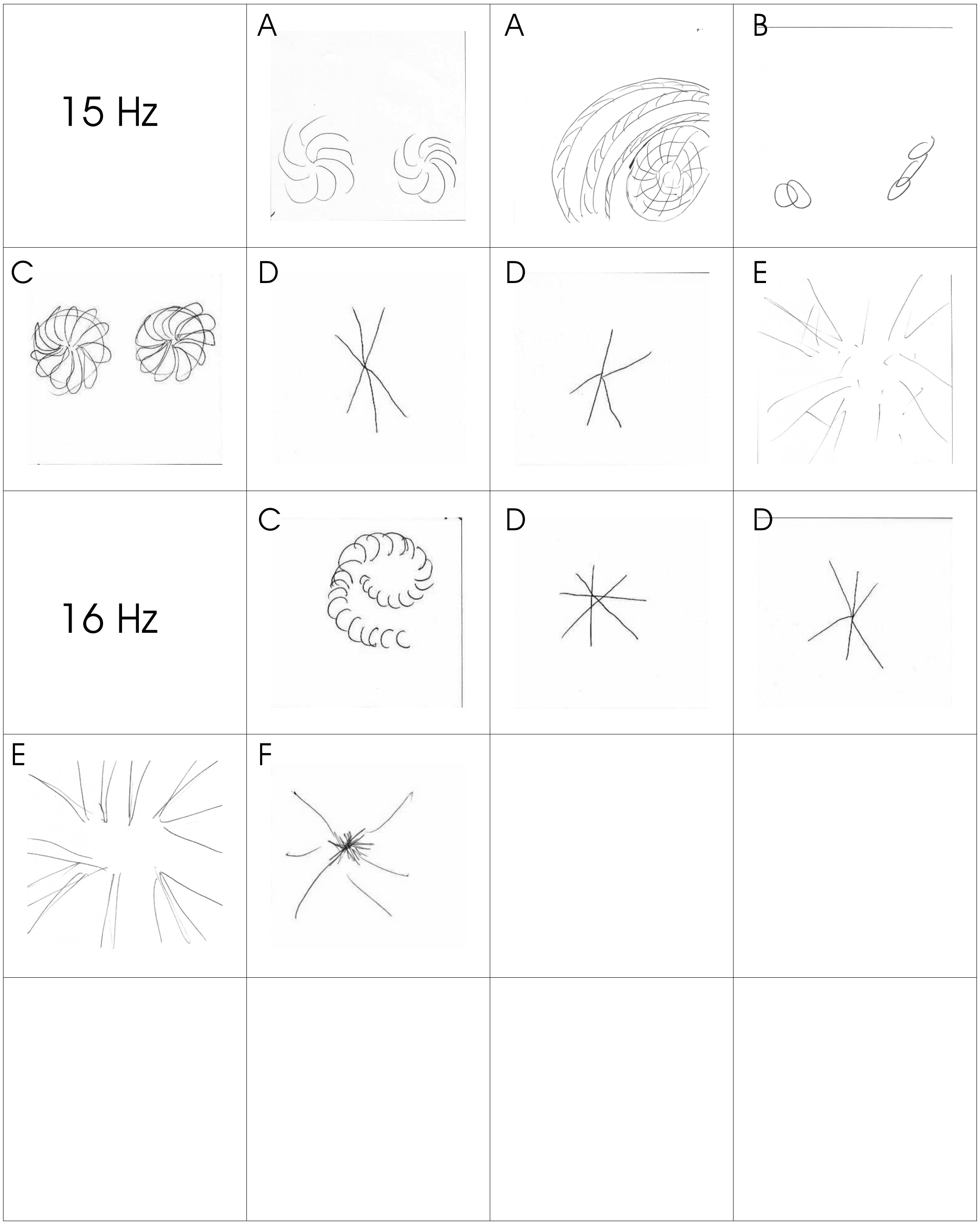


Figure H.22: Subjective experiences of radial patterns as drawn by the participants following stimulation.

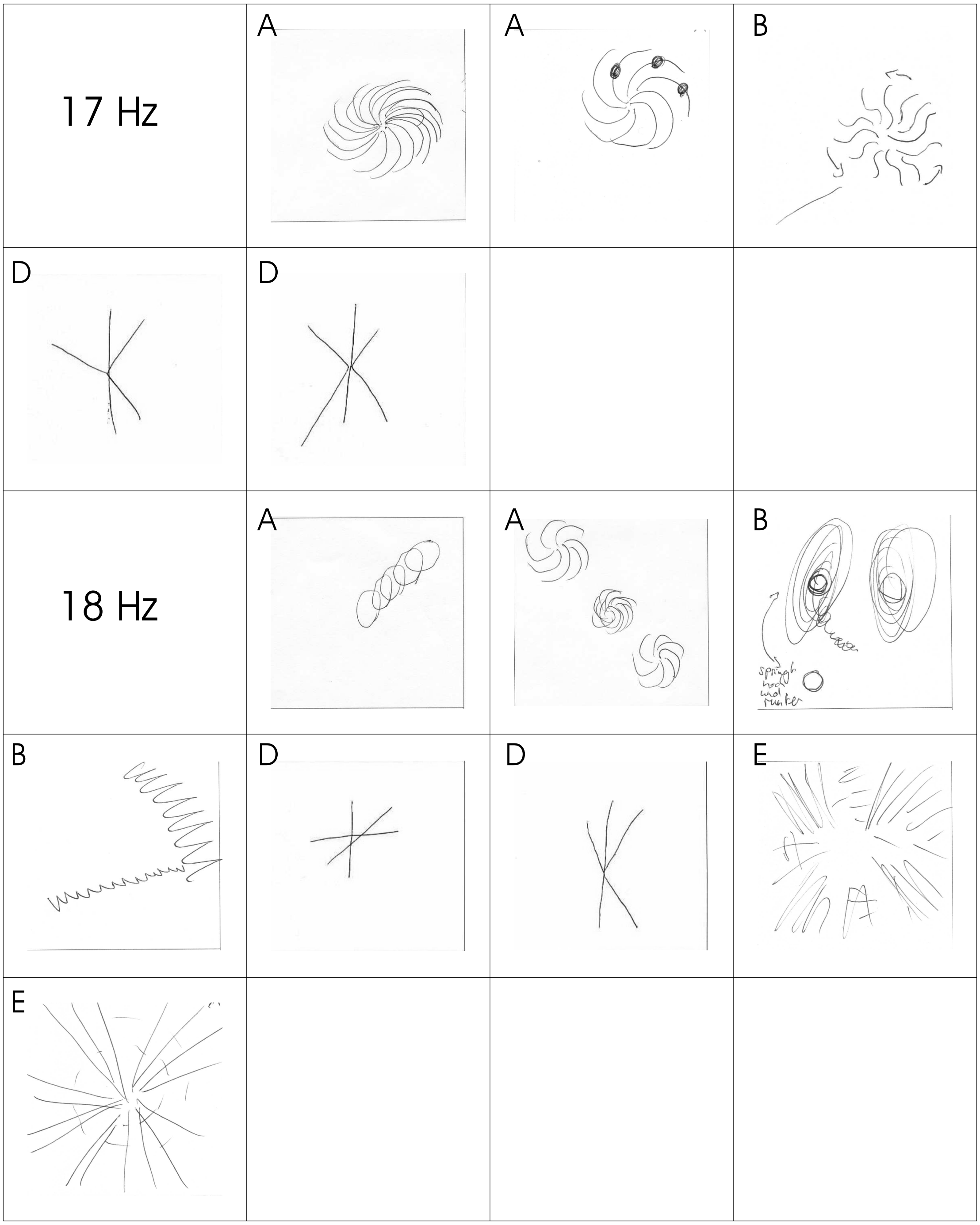


Figure H.23: Subjective experiences of radial patterns as drawn by the participants following stimulation.

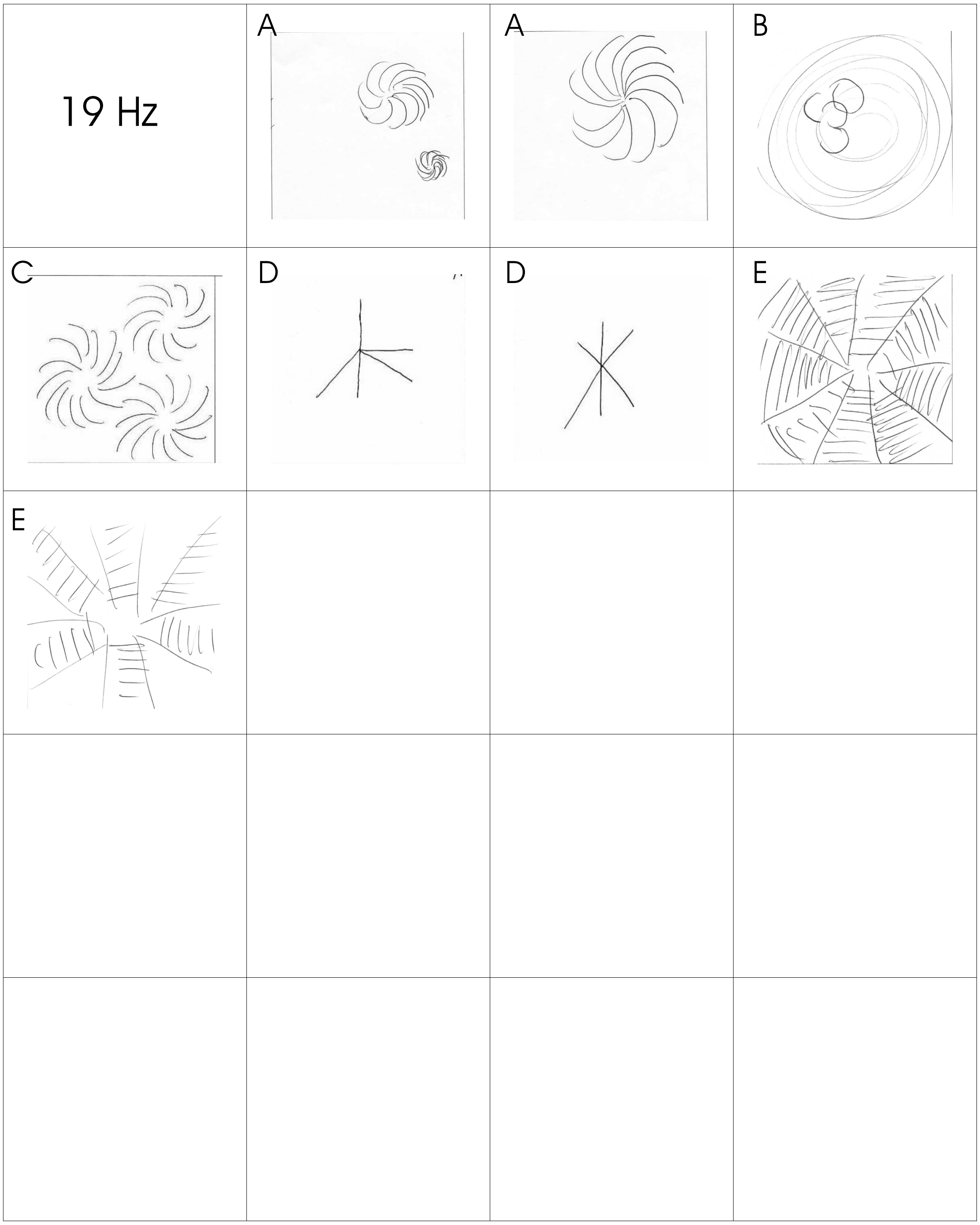


Figure H.24: Subjective experiences of radial patterns as drawn by the participants following stimulation.

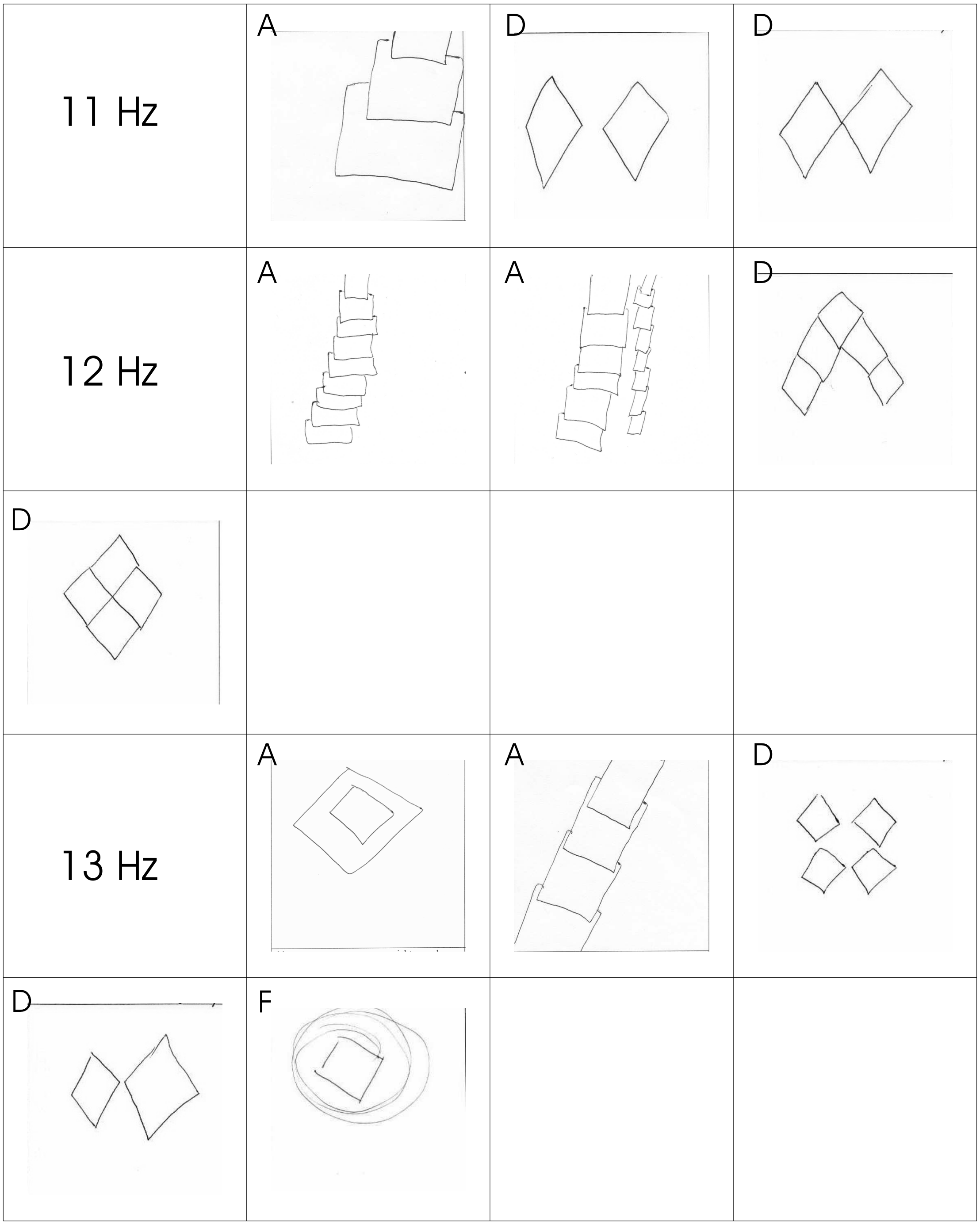


Figure H.25: Subjective experiences of rectangles as drawn by the participants following stimulation.

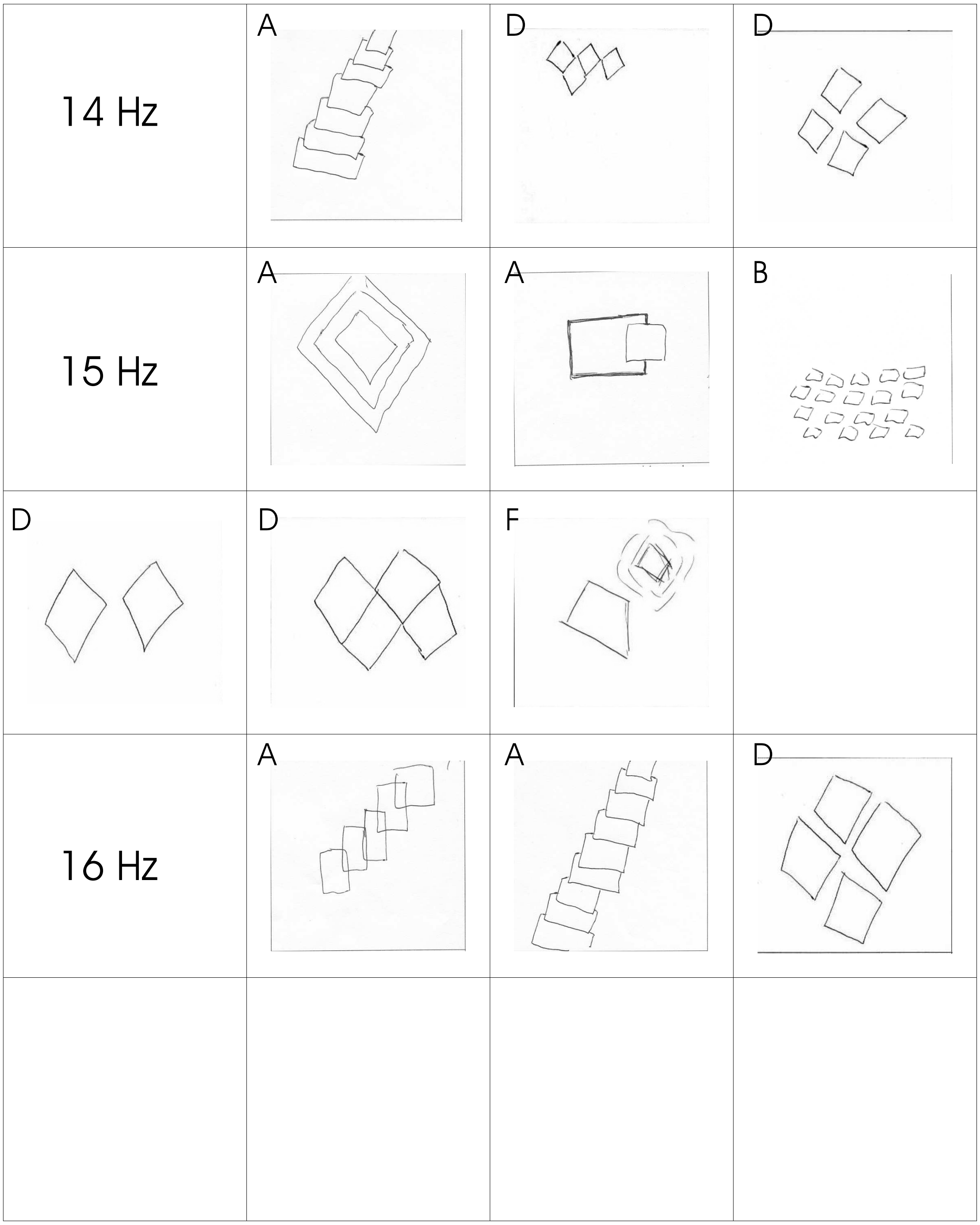


Figure H.26: Subjective experiences of rectangles as drawn by the participants following stimulation.

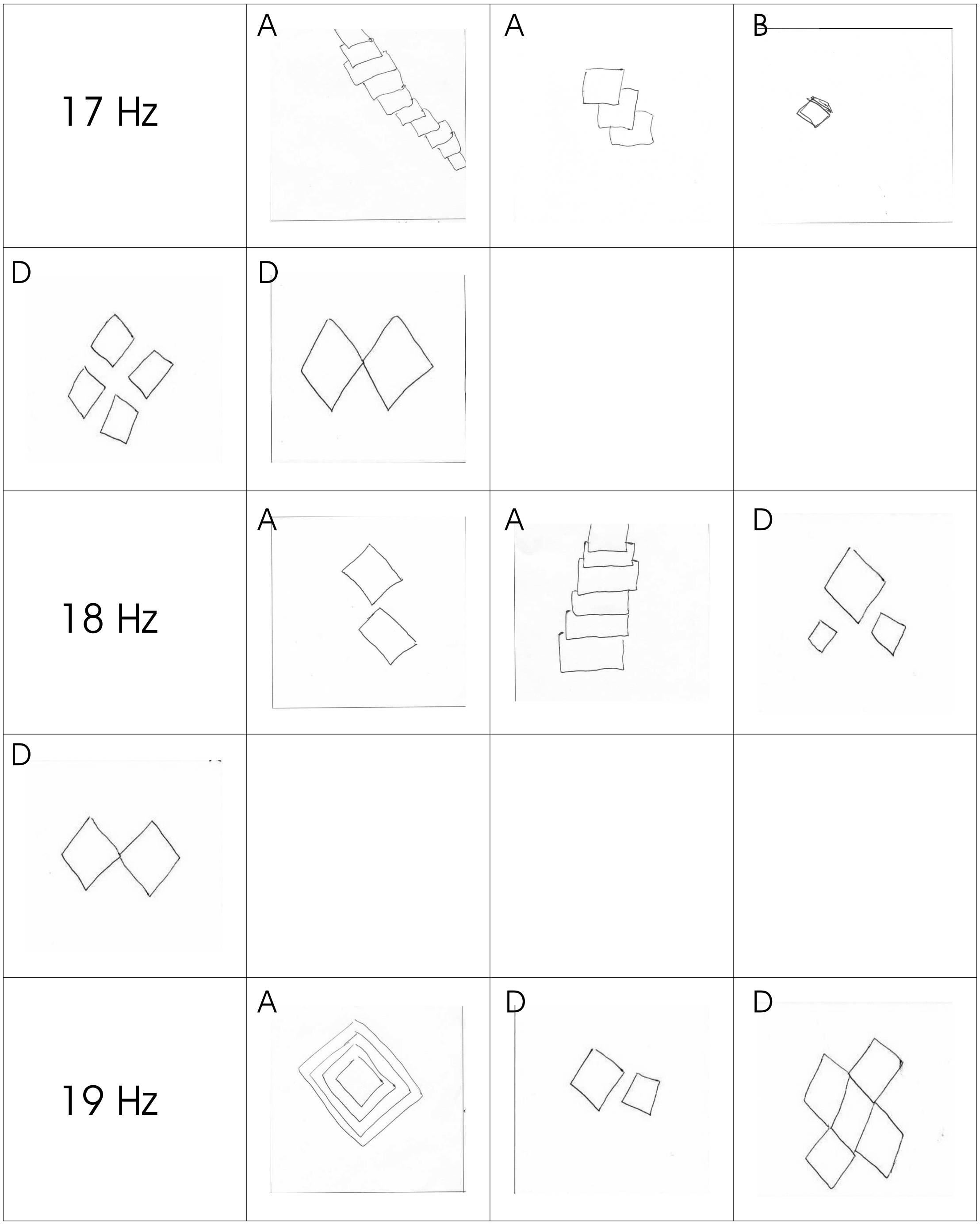


Figure H.27: Subjective experiences of rectangles as drawn by the participants following stimulation.

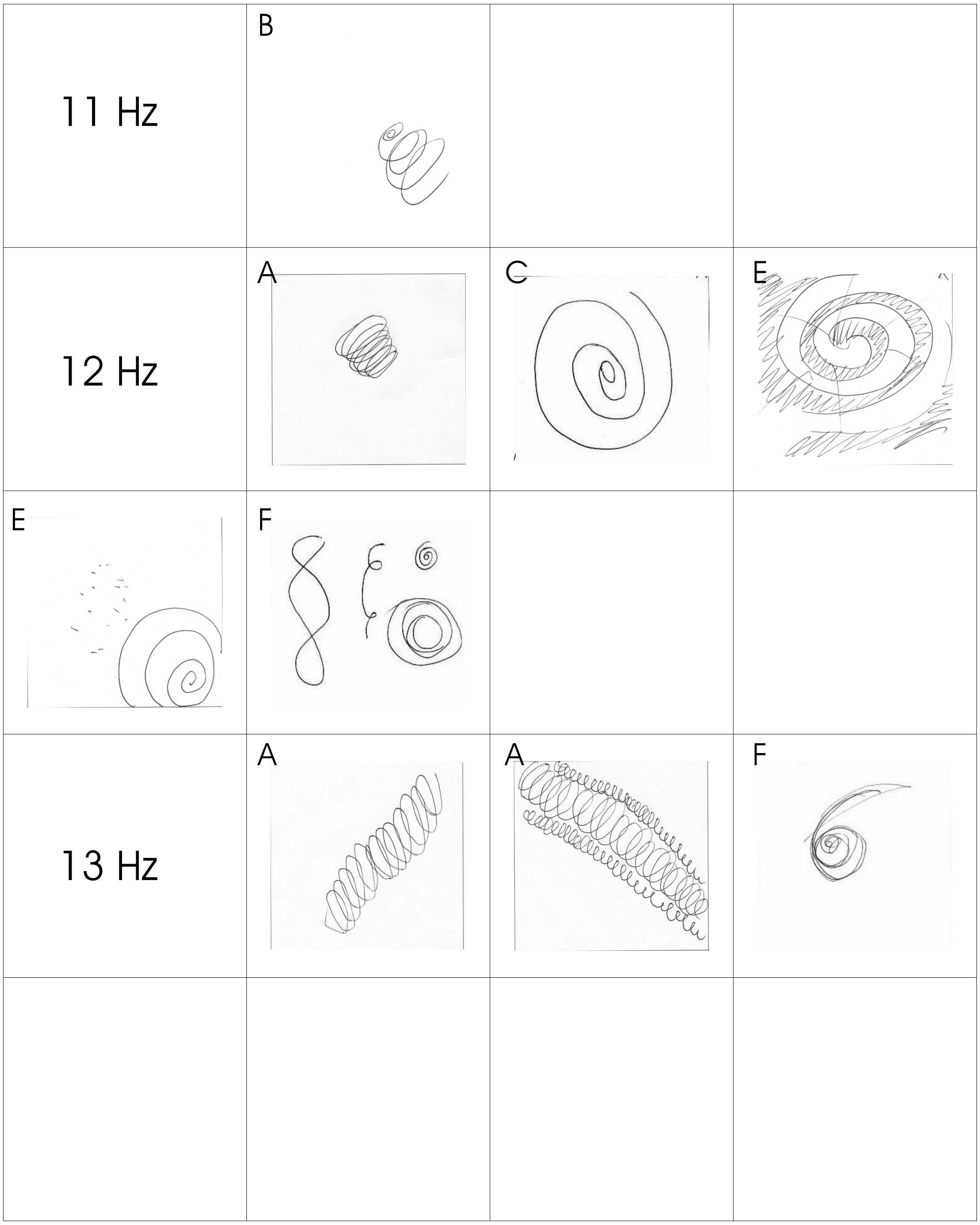


Figure H.28: Subjective experiences of spirals as drawn by the participants following stimulation.

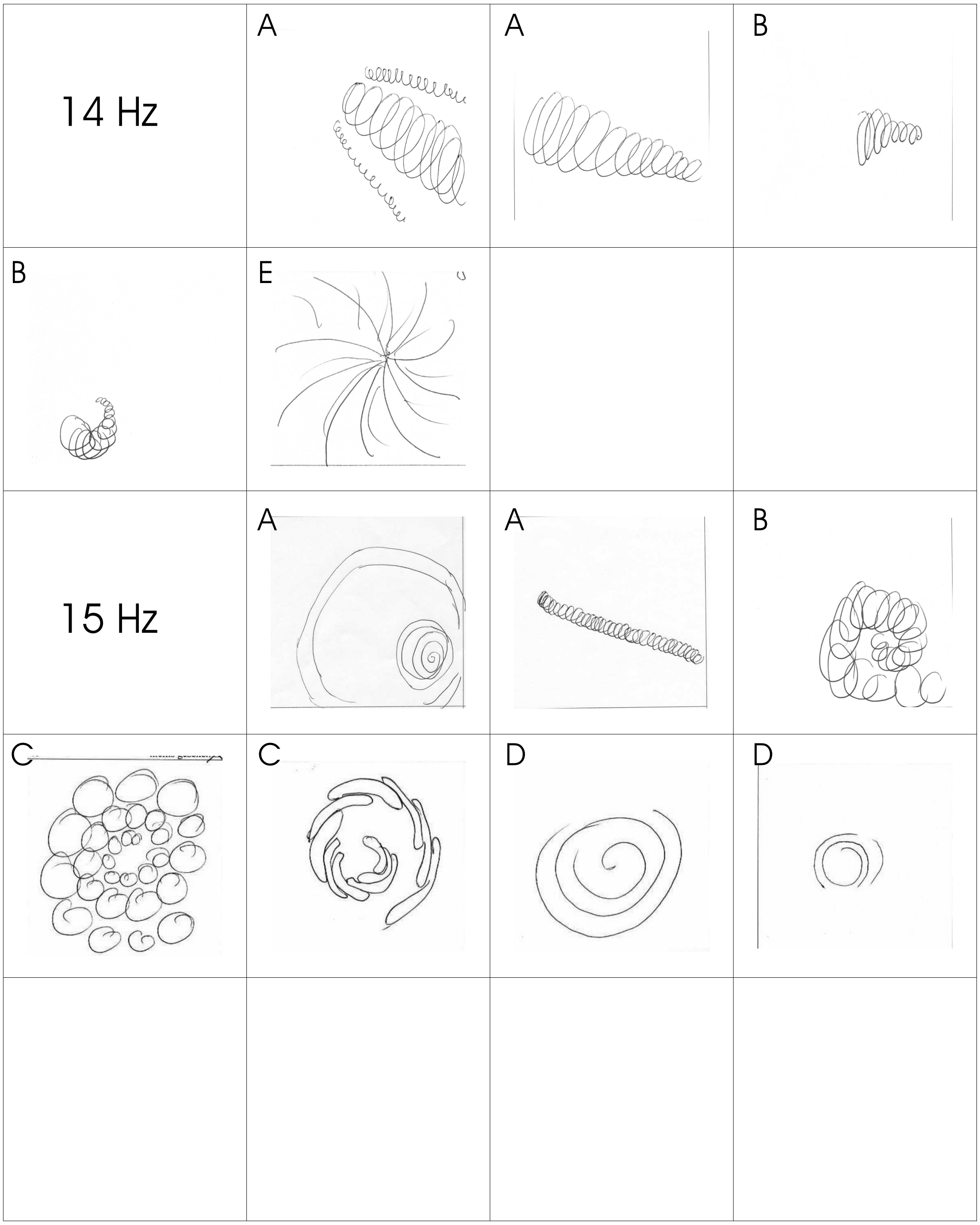


Figure H.29: Subjective experiences of spirals as drawn by the participants following stimulation.

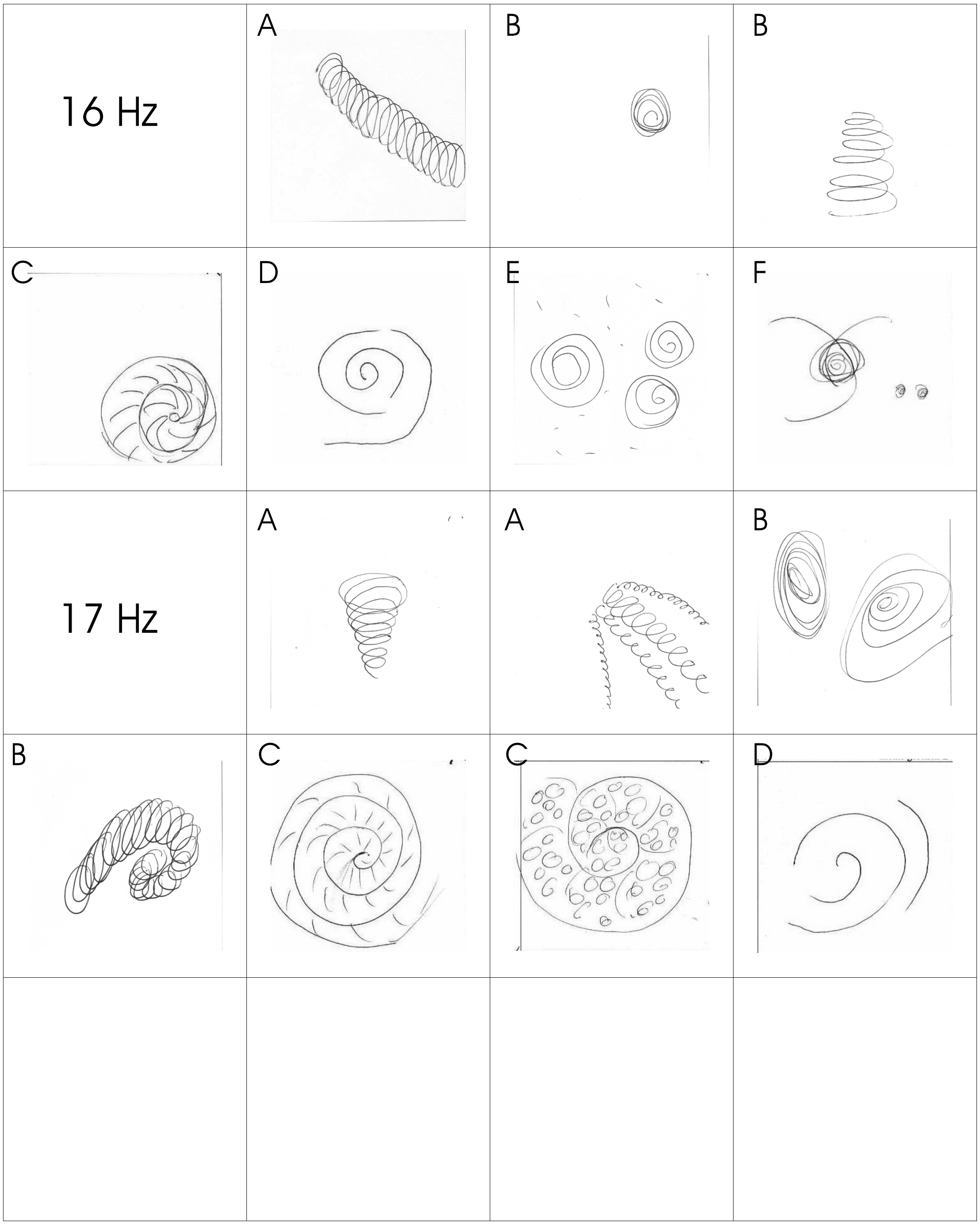


Figure H.30: Subjective experiences of spirals as drawn by the participants following stimulation.

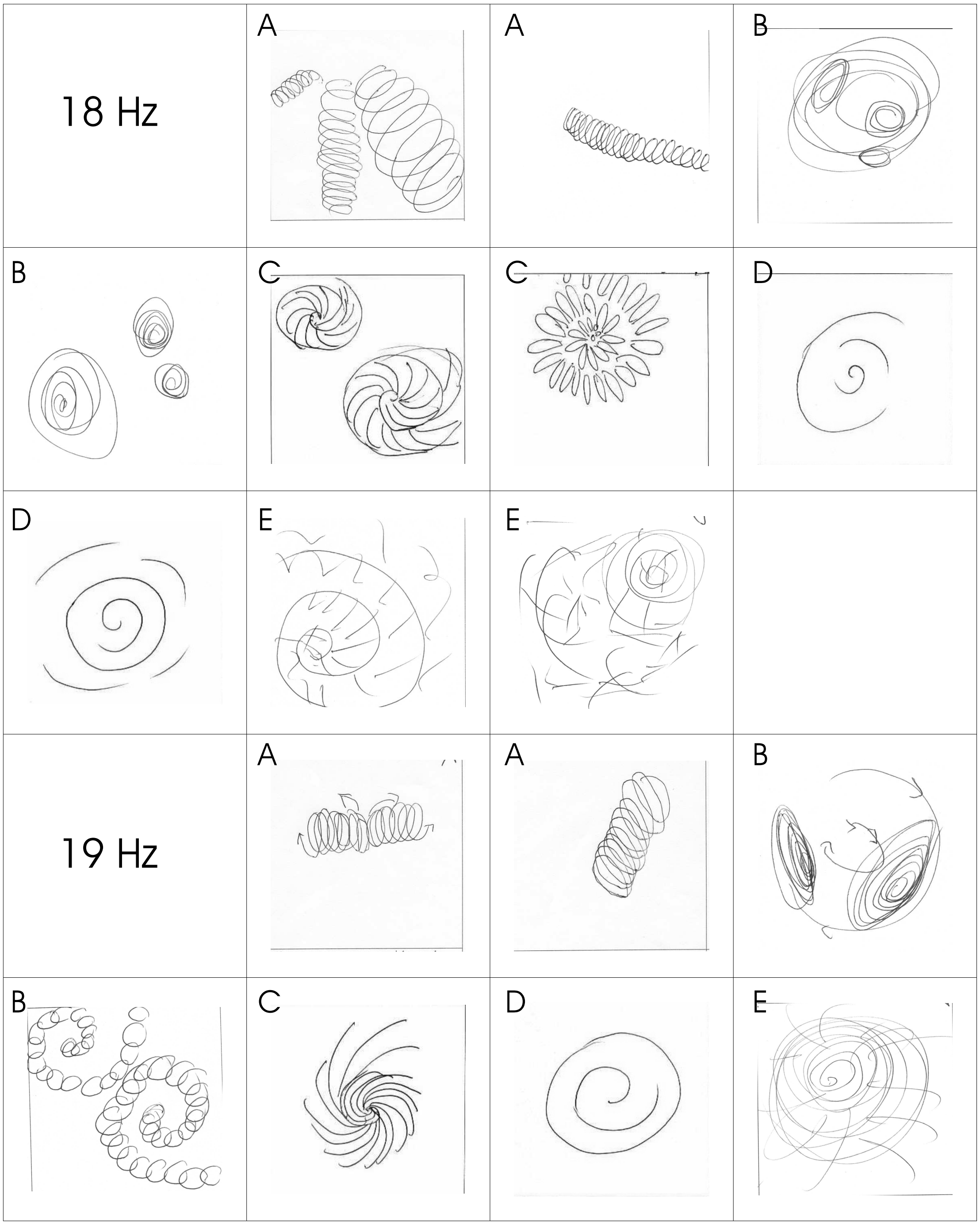


Figure H.31: Subjective experiences of spirals as drawn by the participants following stimulation.

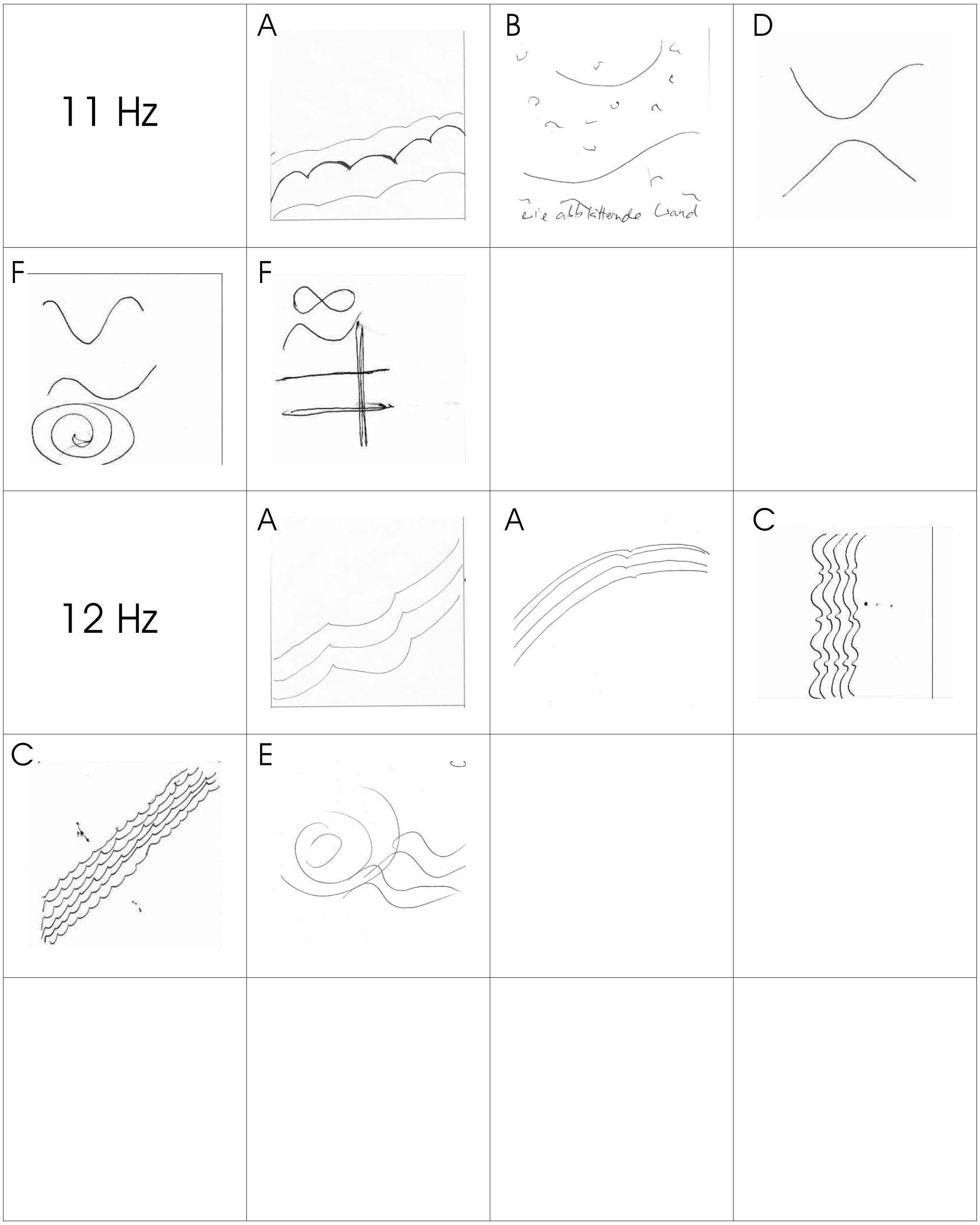


Figure H.32: Subjective experiences of waves as drawn by the participants following stimulation.

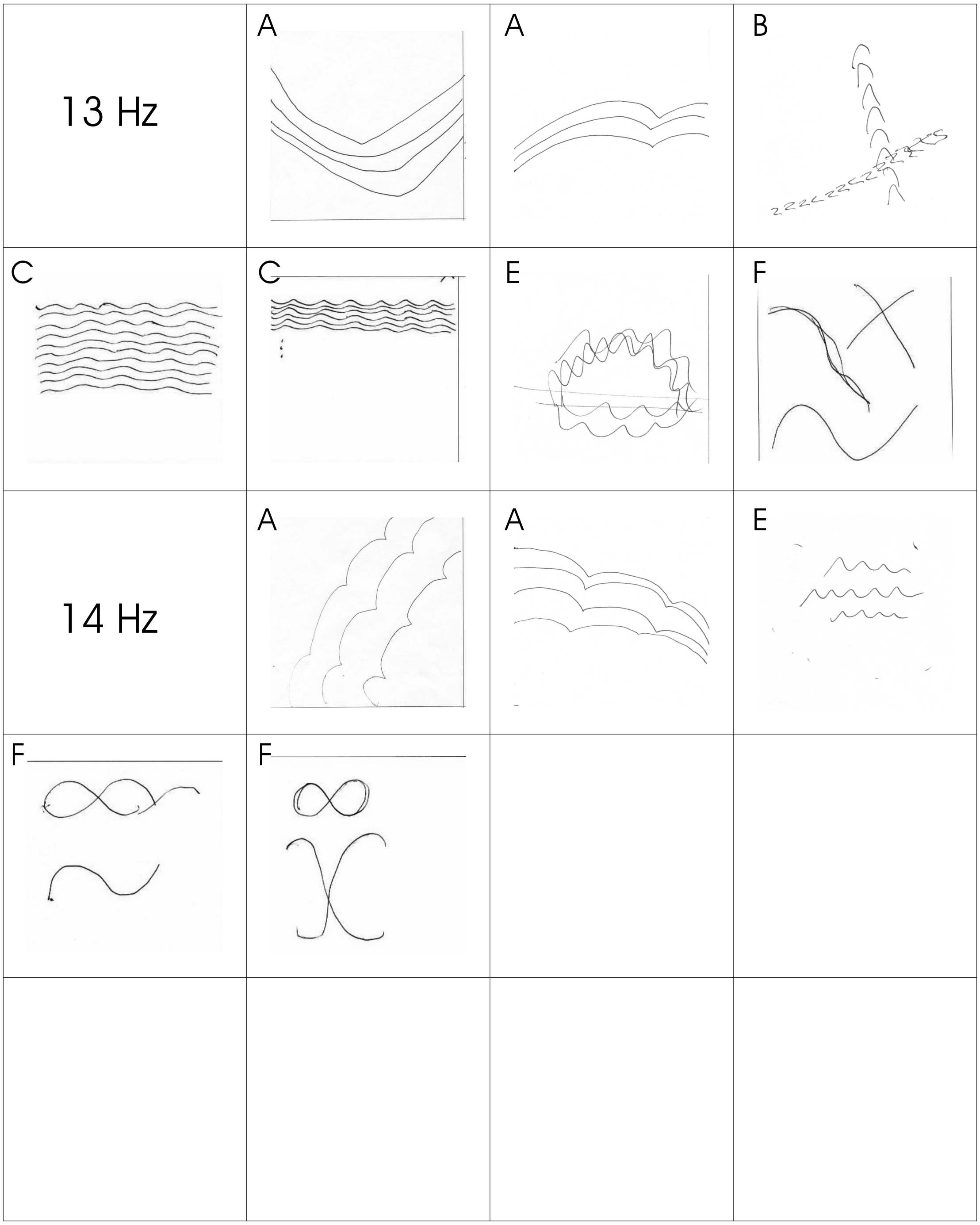


Figure H.33: Subjective experiences of waves as drawn by the participants following stimulation.

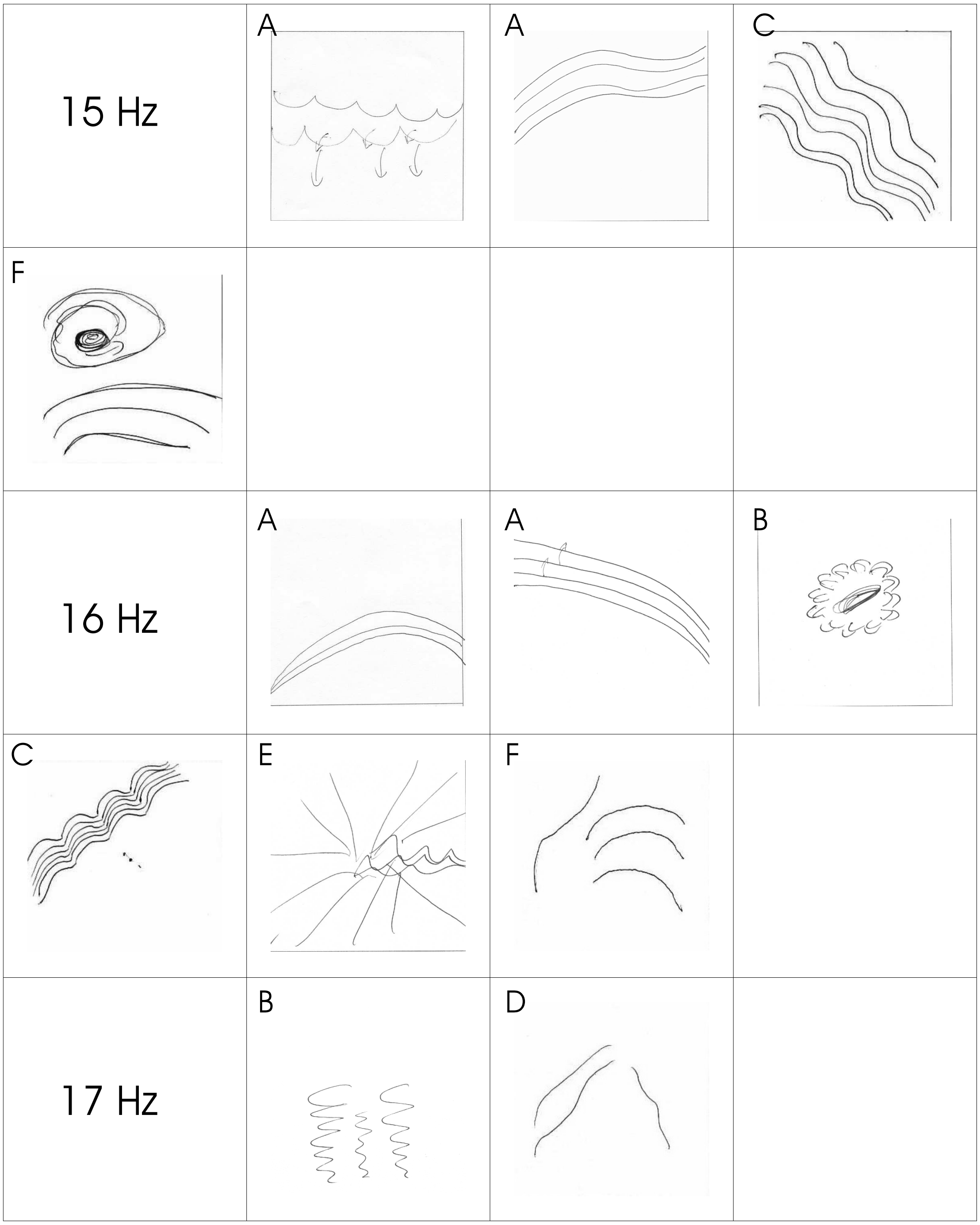


Figure H.34: Subjective experiences of waves as drawn by the participants following stimulation.

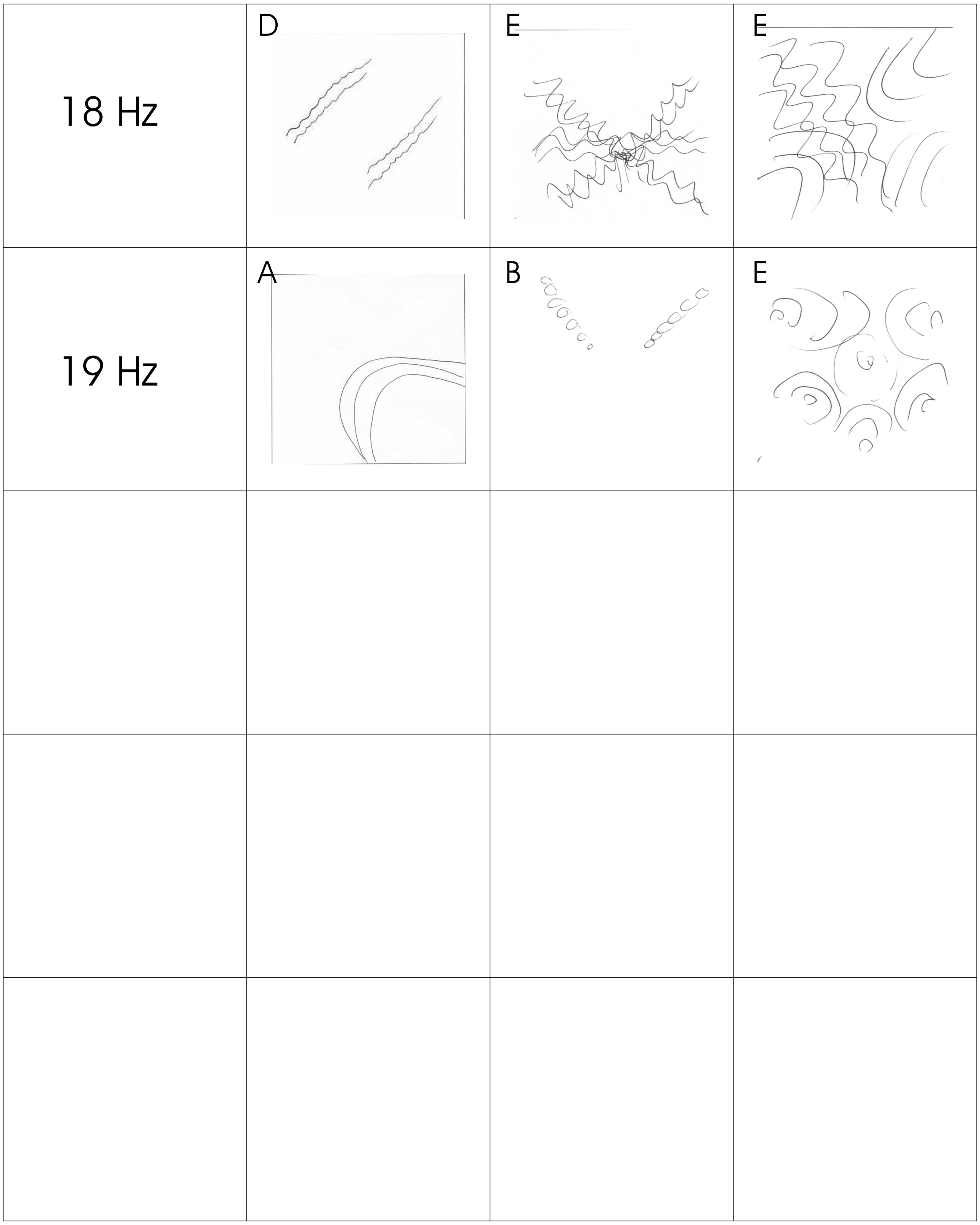


Figure H.35: Subjective experiences of waves as drawn by the participants following stimulation.

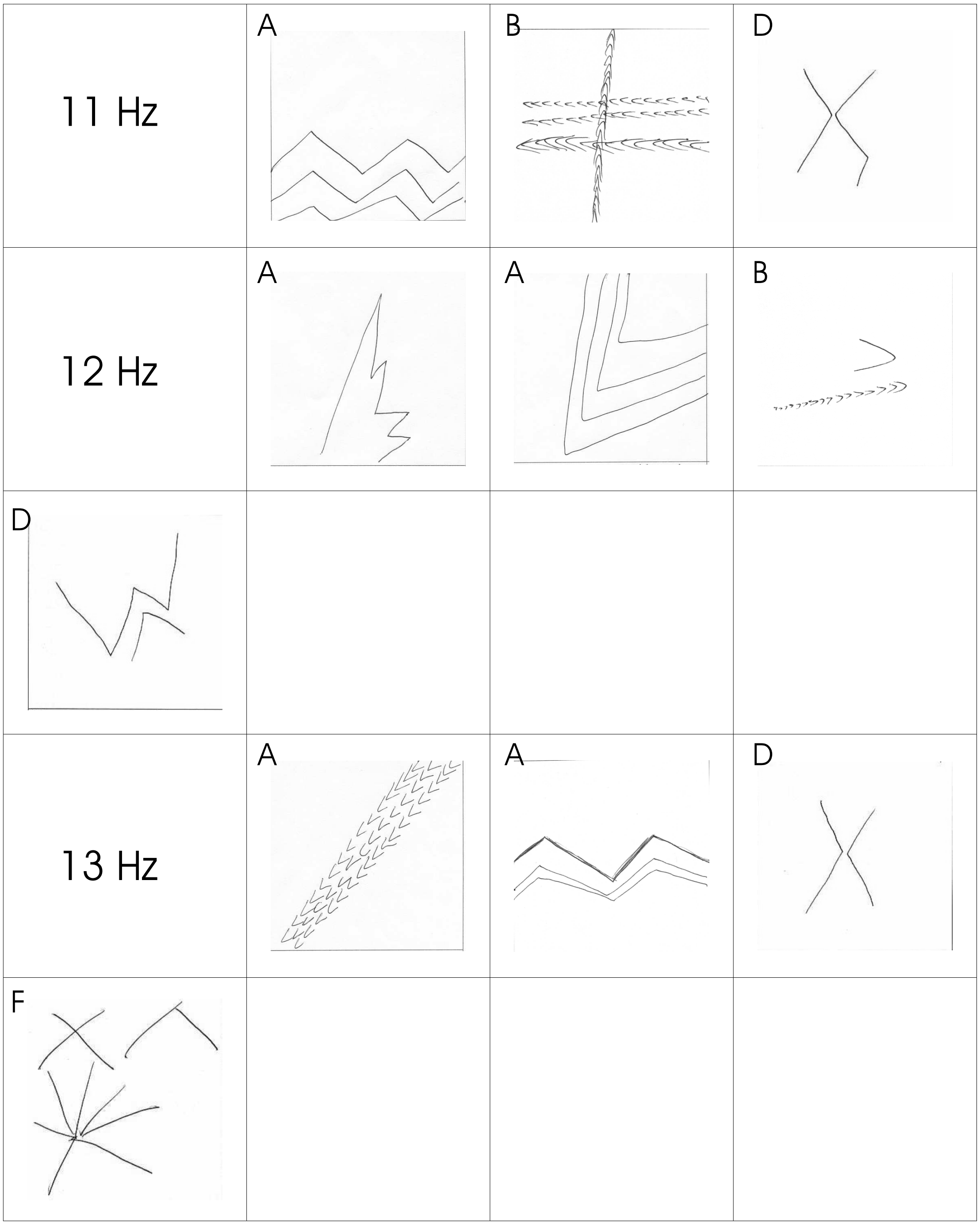


Figure H.36: Subjective experiences of zigzag patterns as drawn by the participants following stimulation.

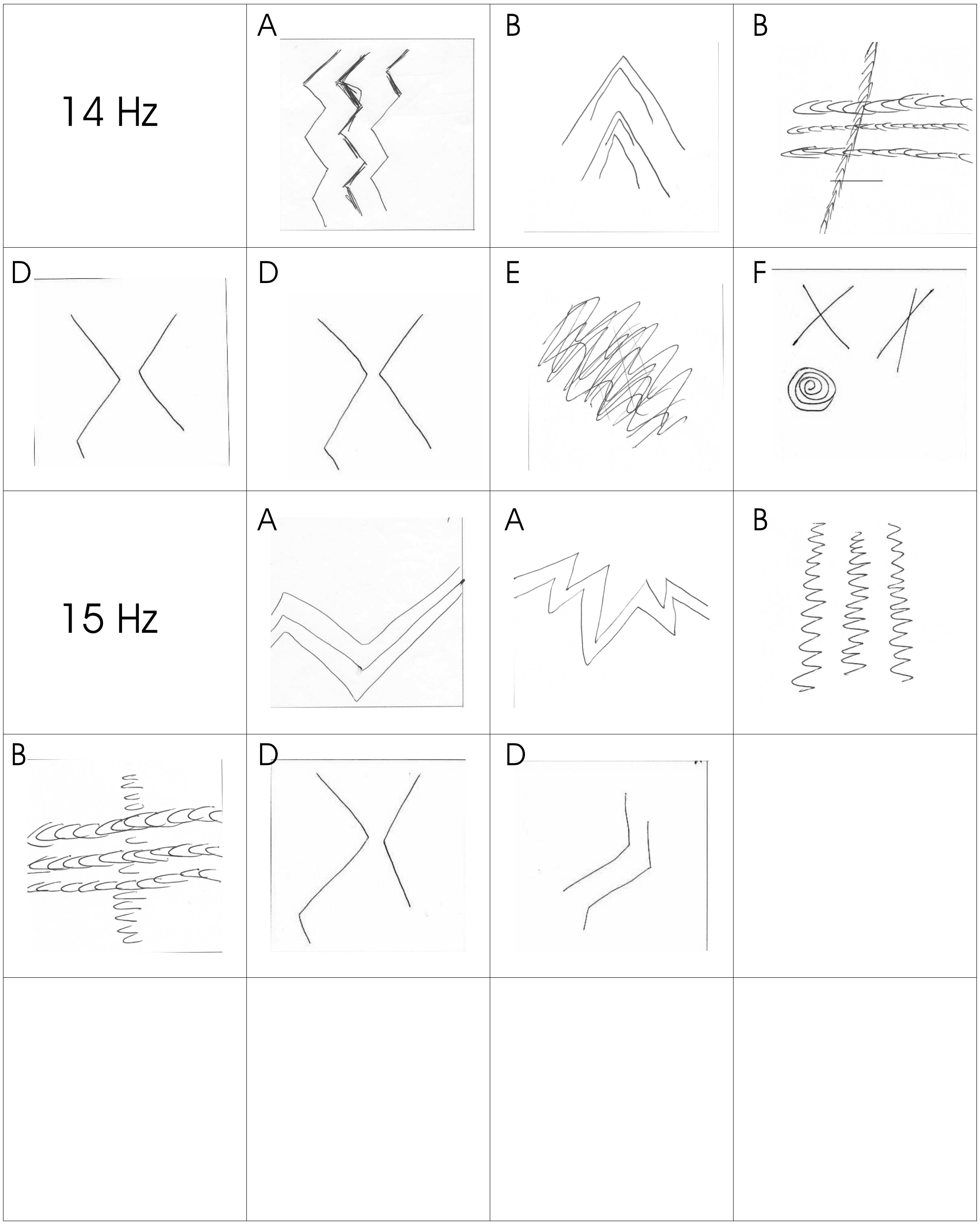


Figure H.37: Subjective experiences of zigzag patterns as drawn by the participants following stimulation.

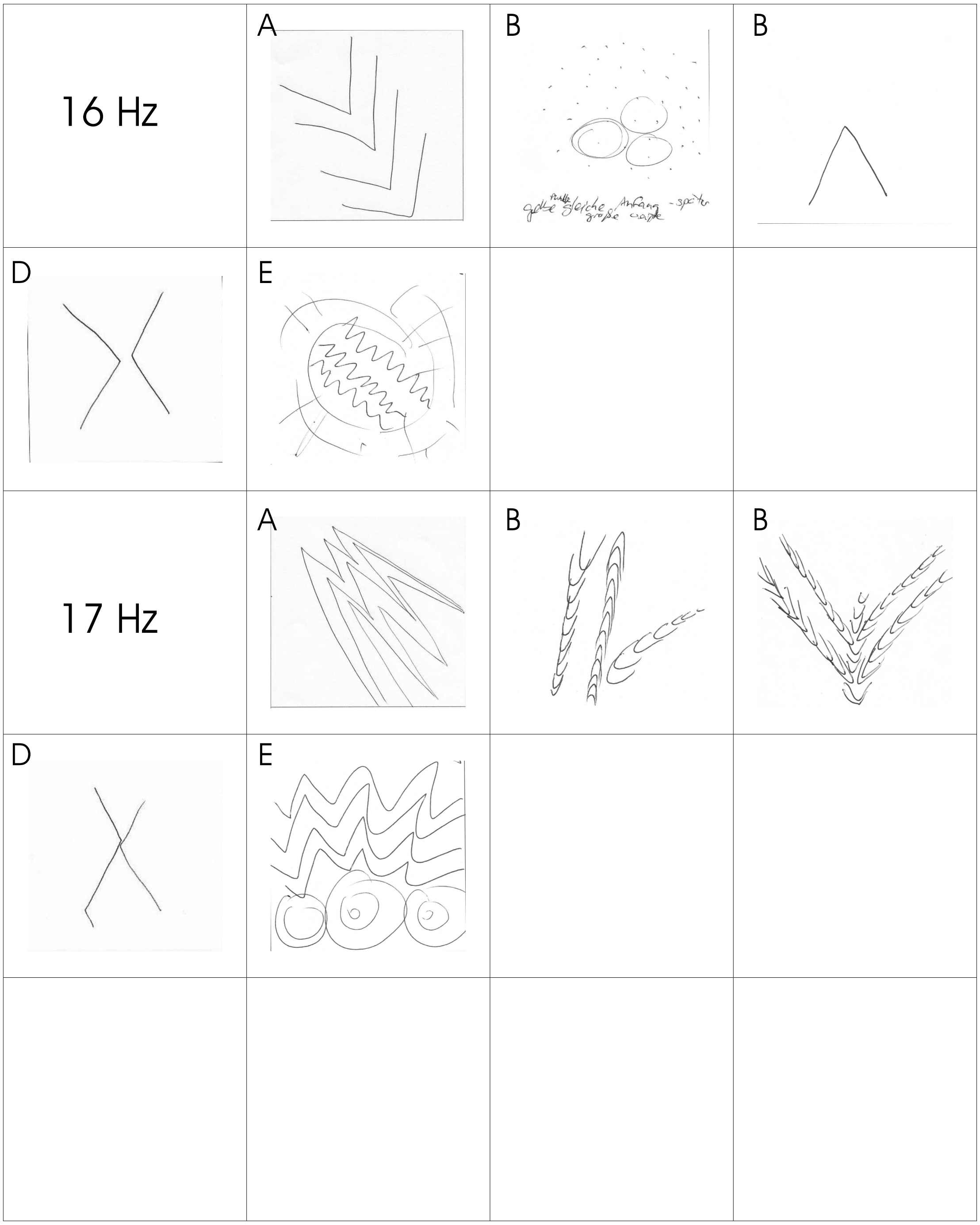


Figure H.38: Subjective experiences of zigzag patterns as drawn by the participants following stimulation.

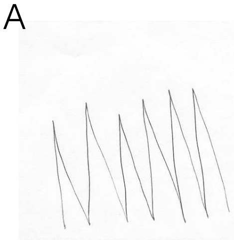
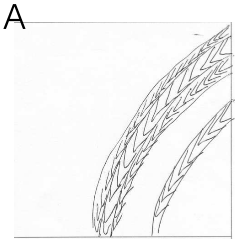
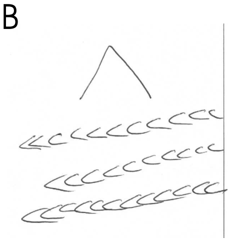
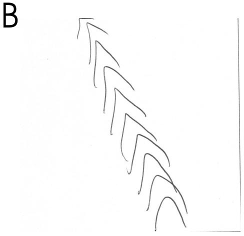
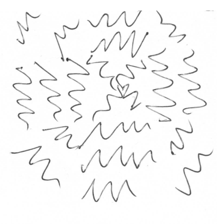
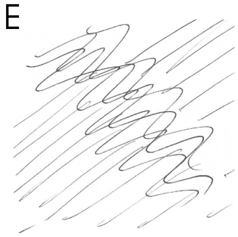
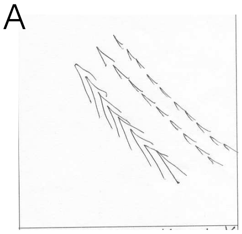
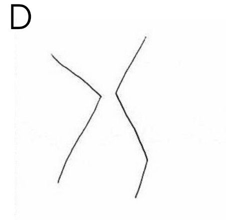
18 Hz	A 	A 	B 
B 	E 	E 	
19 Hz	A 	A 	D 

Figure H.39: Subjective experiences of zigzag patterns as drawn by the participants following stimulation.

Appendix I

Experiment 8 - EEG regression formulas

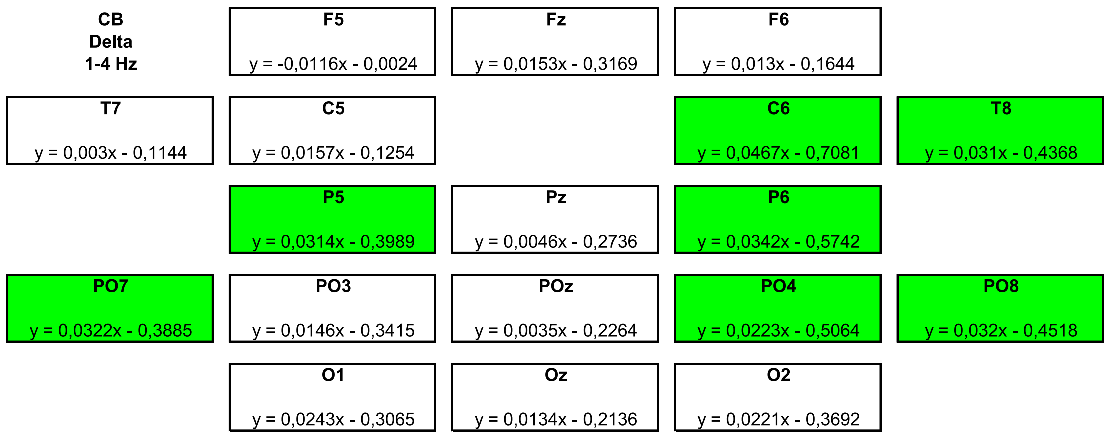


Figure I.1: Formulas of the regressions of corrected EEG power over time at different electrodes. The participant and its individual EEG bandwidth are given in the upper left of the figure. Significance of the regression slopes is indicated by colour: green colour represents electrodes at which a significant increase in EEG power over time was found, red colour represents a significant decrease of EEG power over time. Further information is given in the text.

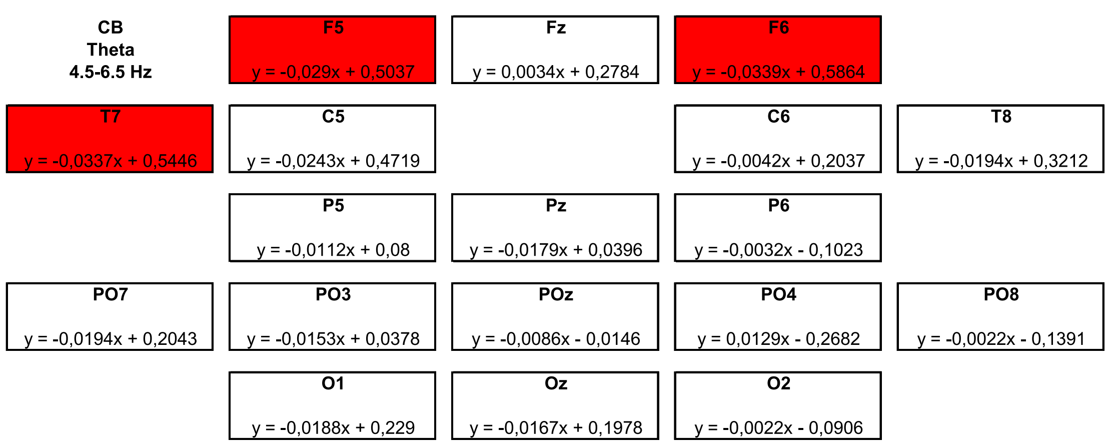


Figure I.2: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.1 and the text.

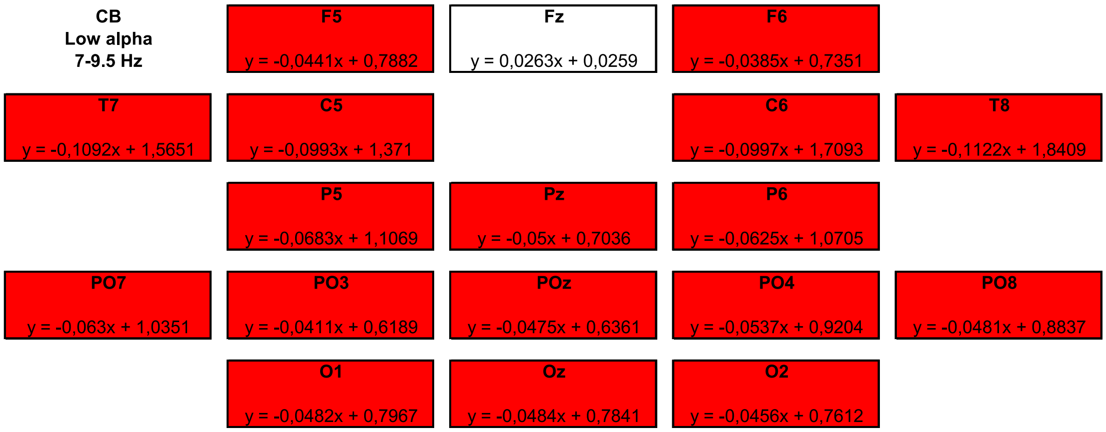


Figure I.3: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.1 and the text.

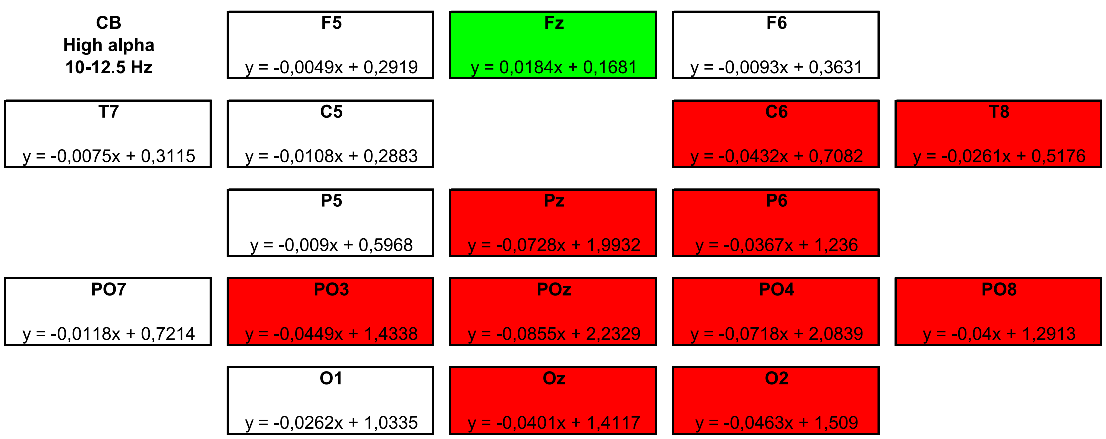


Figure I.4: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.1 and the text.

Figure I.5: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.1 and the text.

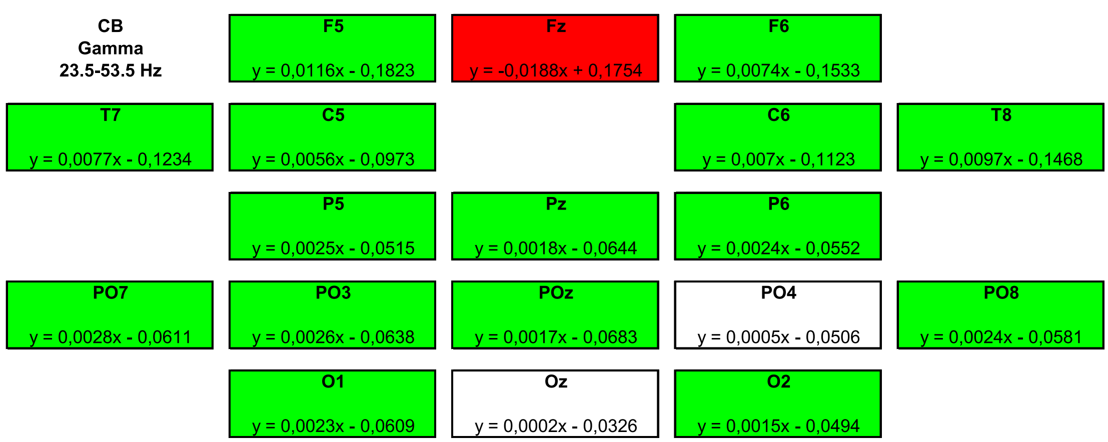


Figure I.6: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.1 and the text.

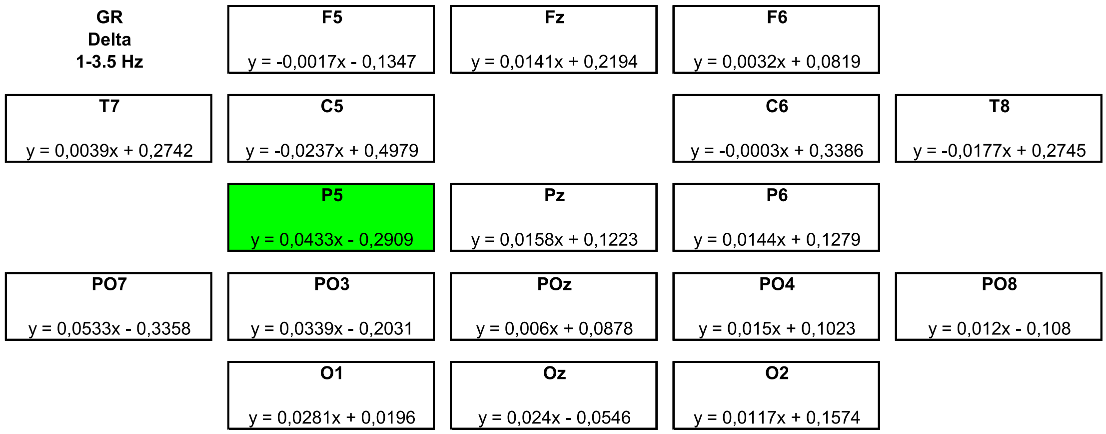


Figure I.7: Formulas of the regressions of corrected EEG power over time at different electrodes. The participant and its individual EEG bandwidth are given in the upper left of the figure. Significance of the regression slopes is indicated by colour: green colour represents electrodes at which a significant increase in EEG power over time was found, red colour represents a significant decrease of EEG power over time. Further information is given in the text.

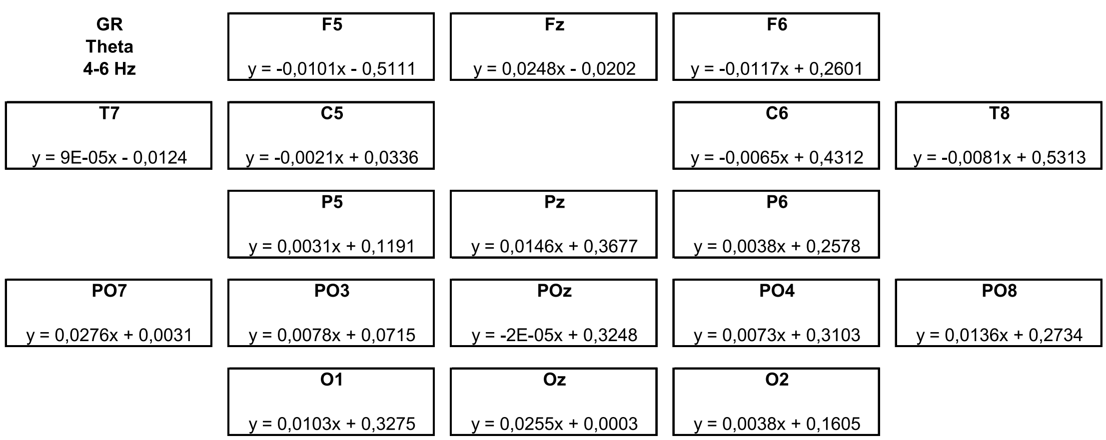


Figure I.8: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.7 and the text.

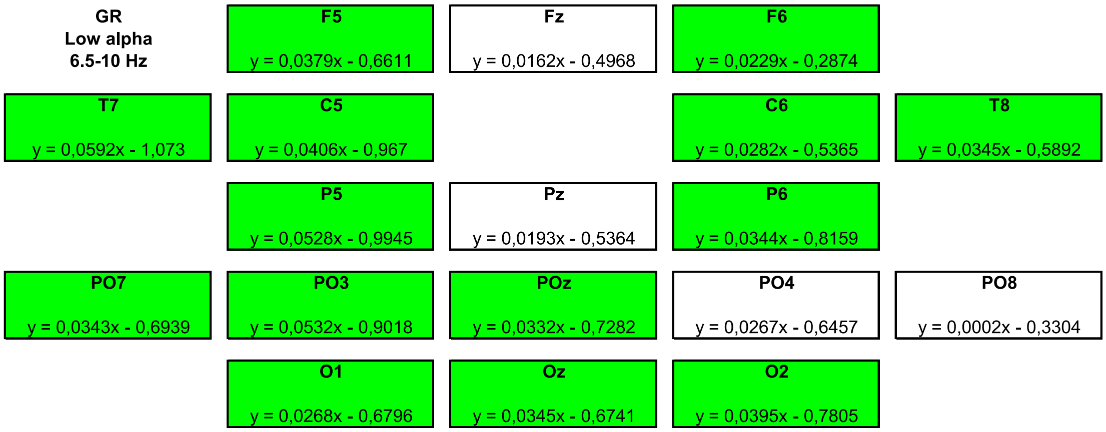


Figure I.9: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.7 and the text.

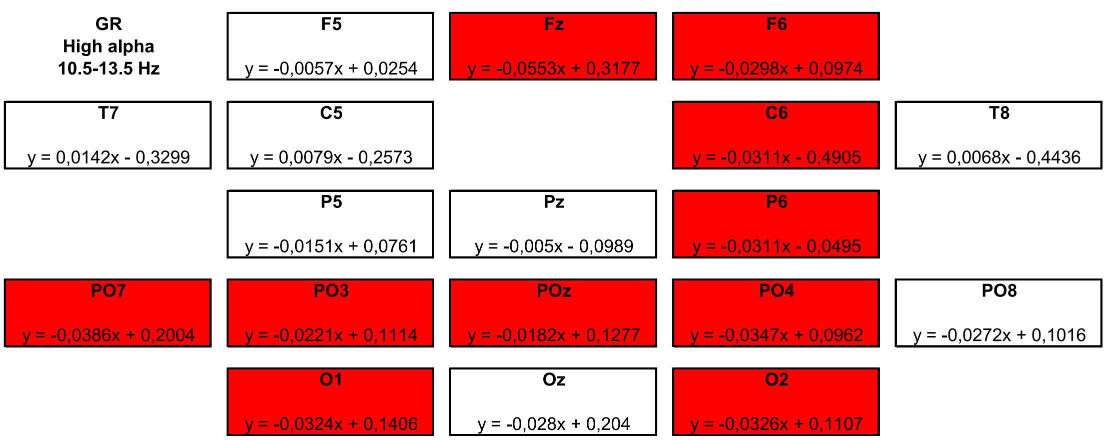


Figure I.10: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.7 and the text.

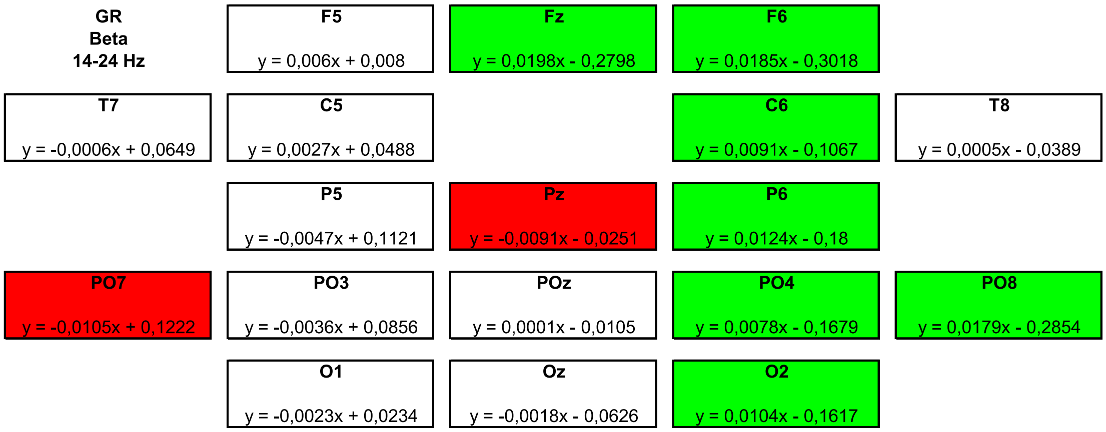


Figure I.11: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.7 and the text.

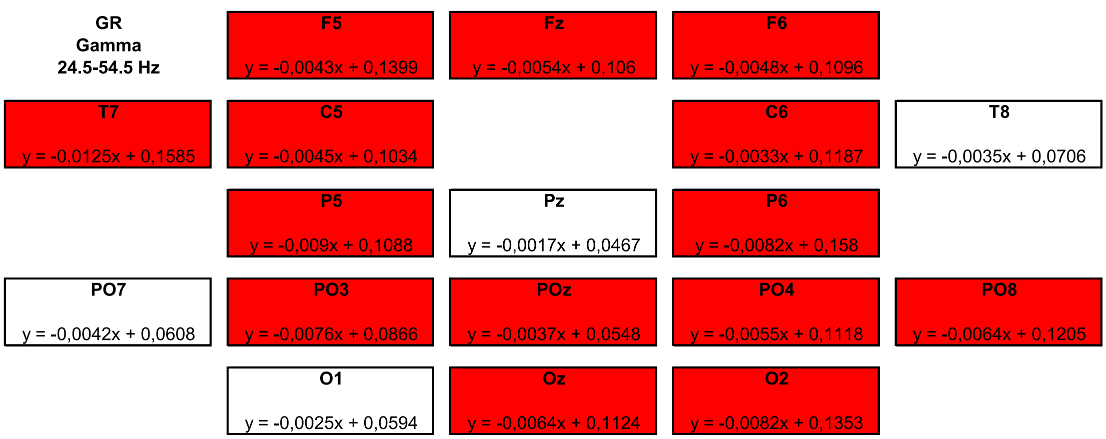


Figure I.12: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.7 and the text.

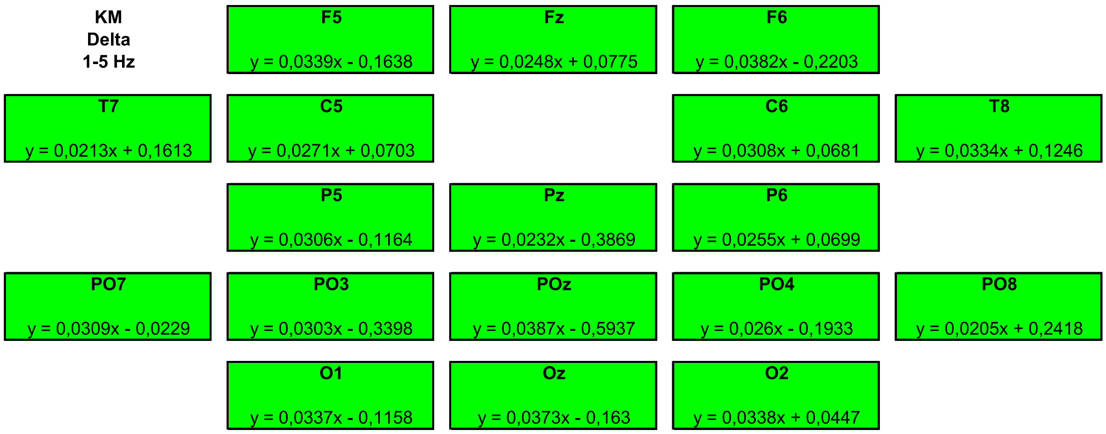


Figure I.13: Formulas of the regressions of corrected EEG power over time at different electrodes. The participant and its individual EEG bandwidth are given in the upper left of the figure. Significance of the regression slopes is indicated by colour: green colour represents electrodes at which a significant increase in EEG power over time was found, red colour represents a significant decrease of EEG power over time. Further information is given in the text.

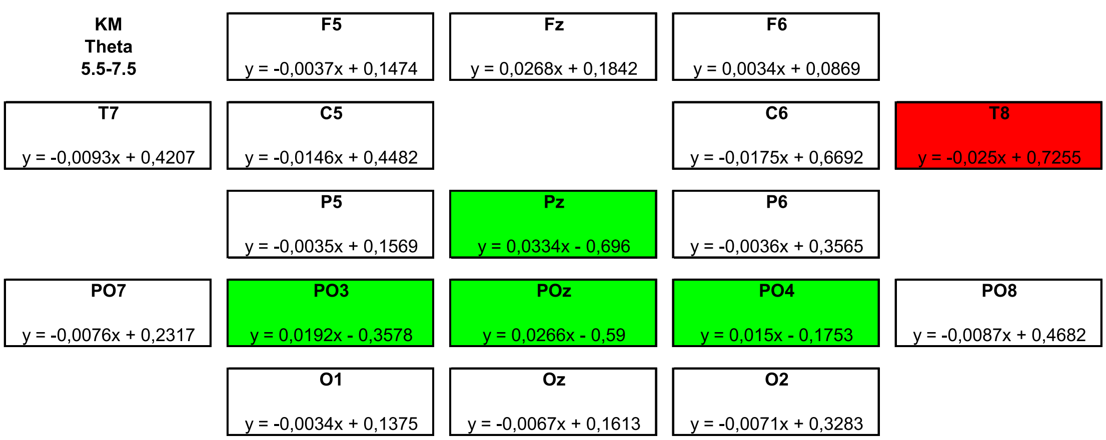


Figure I.14: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.13 and the text.

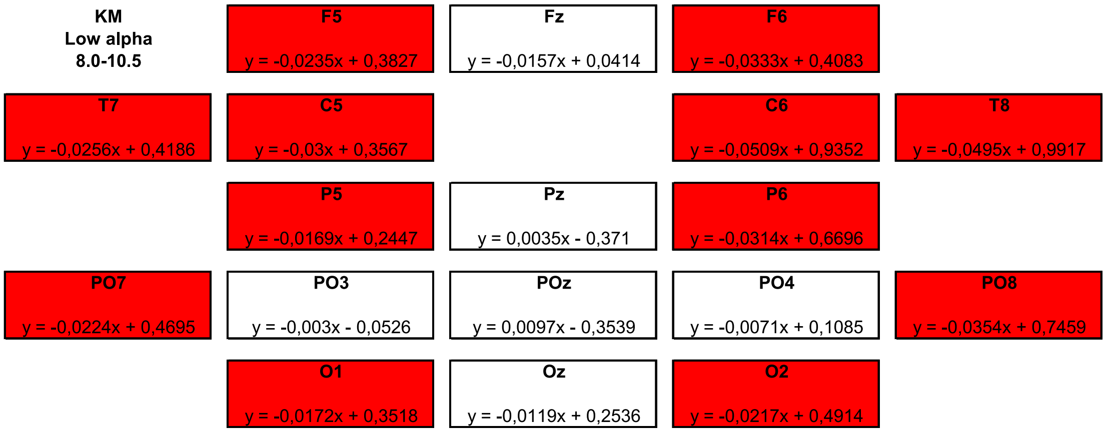


Figure I.15: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.13 and the text.

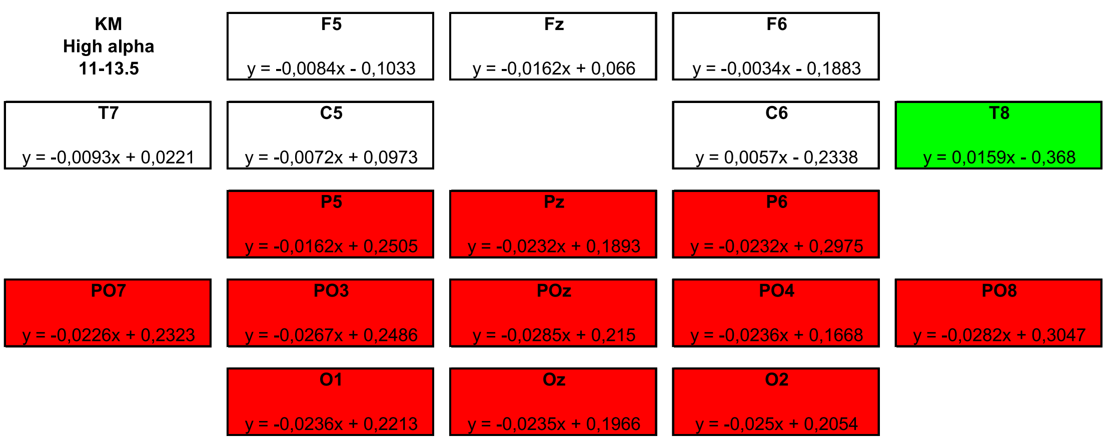


Figure I.16: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.13 and the text.

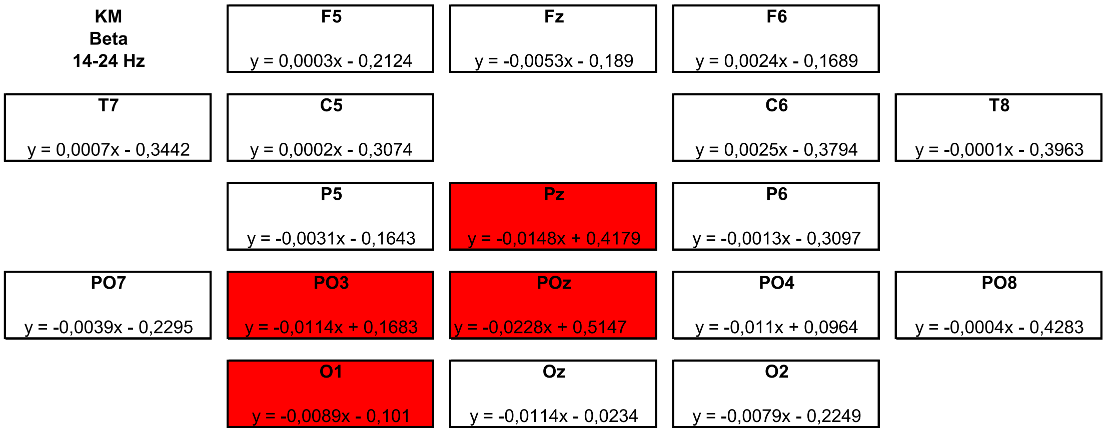


Figure I.17: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.13 and the text.

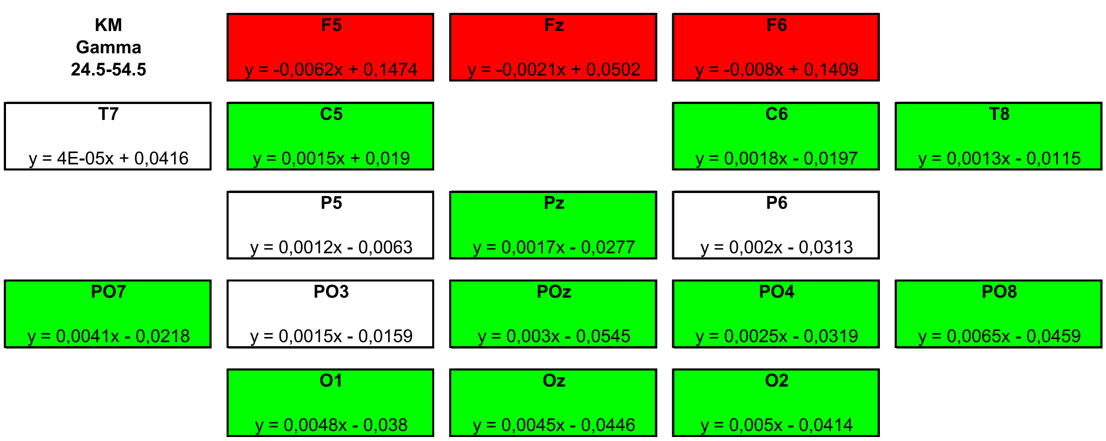


Figure I.18: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.13 and the text.

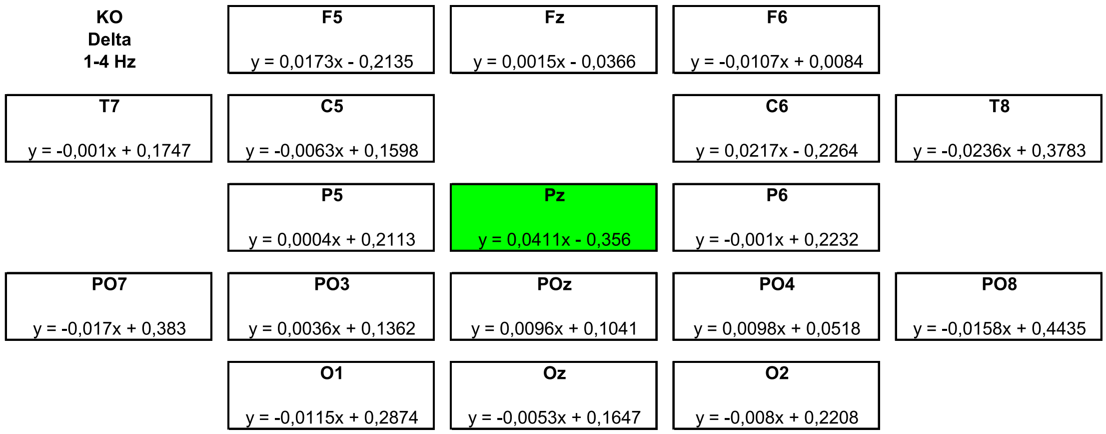


Figure I.19: Formulas of the regressions of corrected EEG power over time at different electrodes. The participant and its individual EEG bandwidth are given in the upper left of the figure. Significance of the regression slopes is indicated by colour: green colour represents electrodes at which a significant increase in EEG power over time was found, red colour represents a significant decrease of EEG power over time. Further information is given in the text.

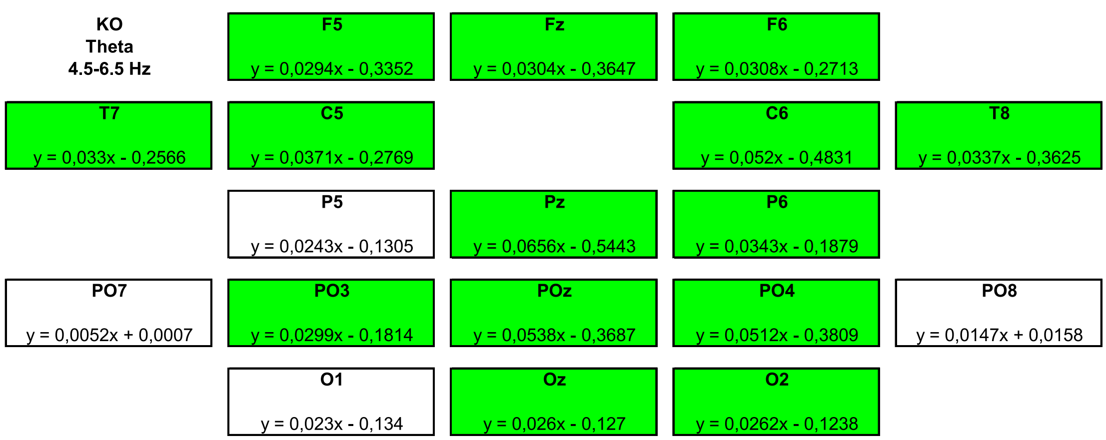


Figure I.20: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.19 and the text.

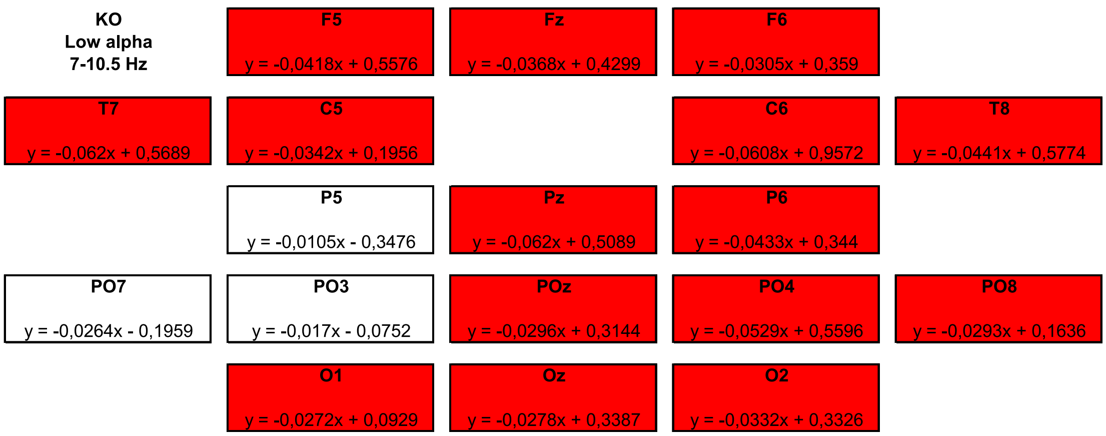


Figure I.21: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.19 and the text.

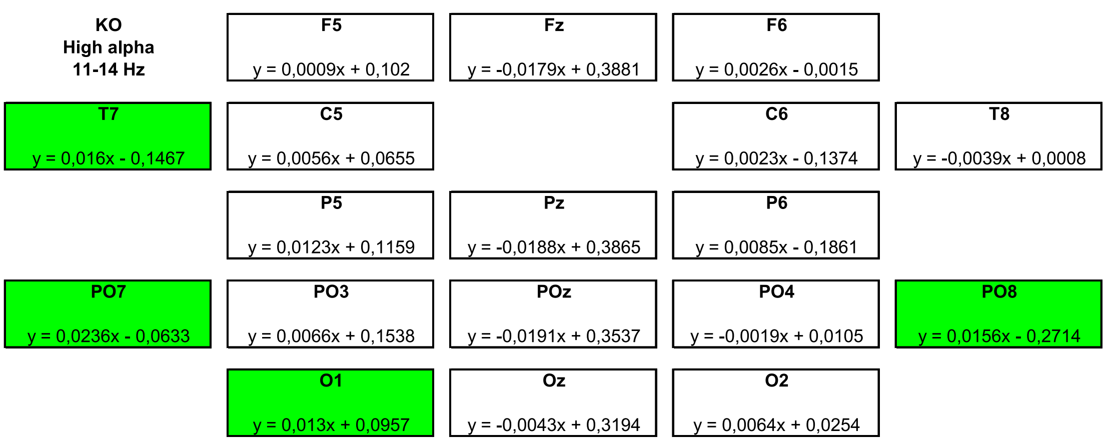


Figure I.22: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.19 and the text.

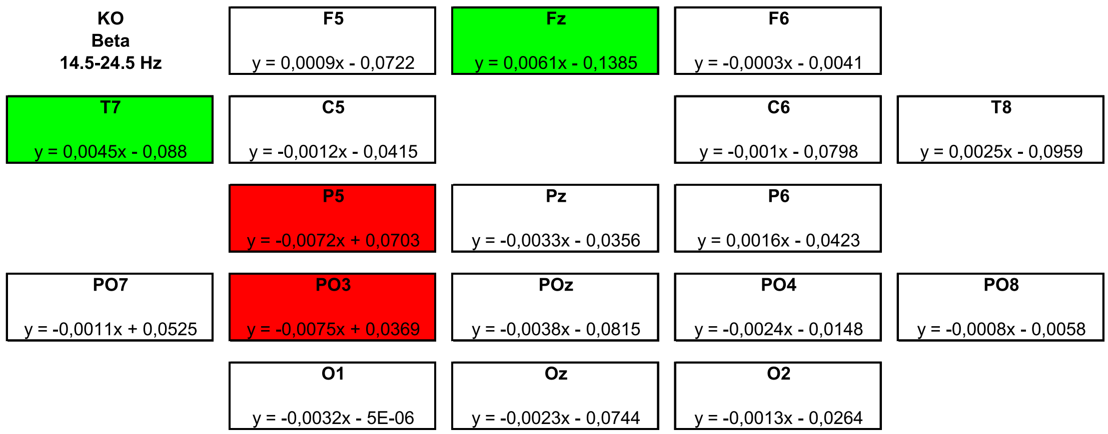


Figure I.23: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.19 and the text.

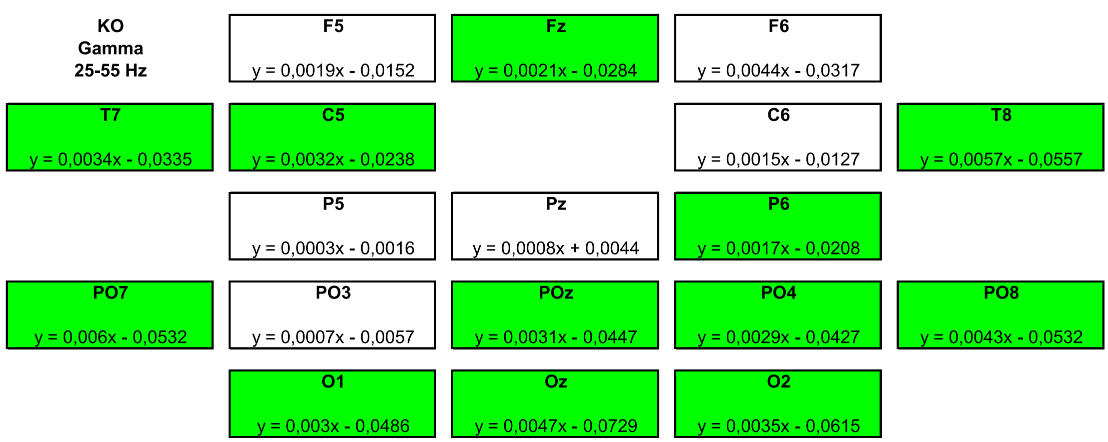


Figure I.24: Formulas of the regressions of corrected EEG power over time at different electrodes. For further information see Figure I.19 and the text.

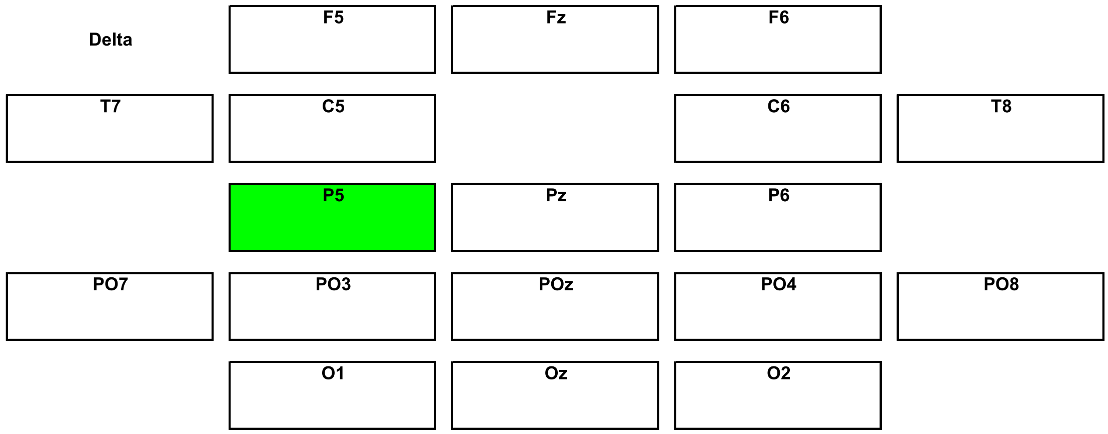


Figure I.25: Representation of significant regressions found in the majority of participants at different electrodes. The EEG bandwidth concerned is given in the upper left of the figure. Significance of the regression slopes is indicated by colour: green colour represents electrodes at which a significant increase in EEG power over time was found in at least 3 participants, red colour represents a significant decrease of EEG power over time in at least 3 participants. Further information is given in the text.

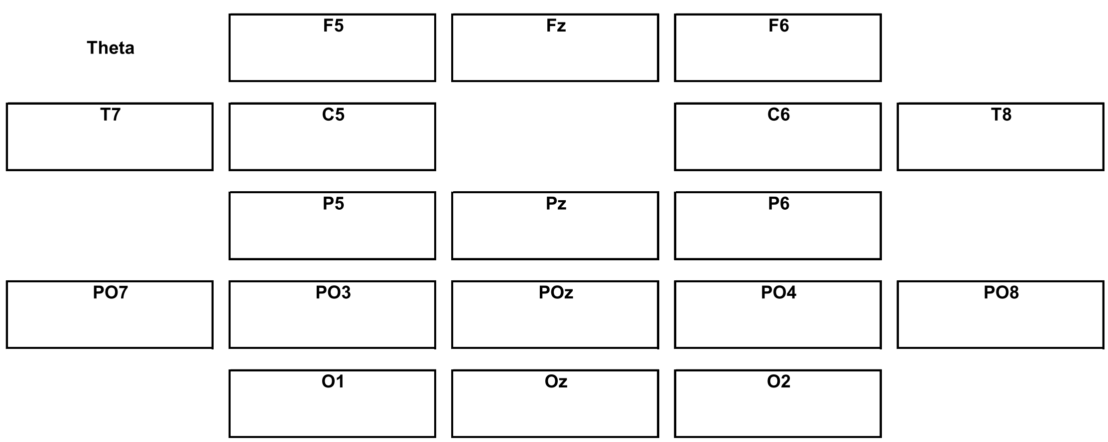


Figure I.26: Representation of significant regressions found in the majority of participants at different electrodes. No reliable regressions of power over time were found for the theta band. For further information see Figure I.25 and the text.

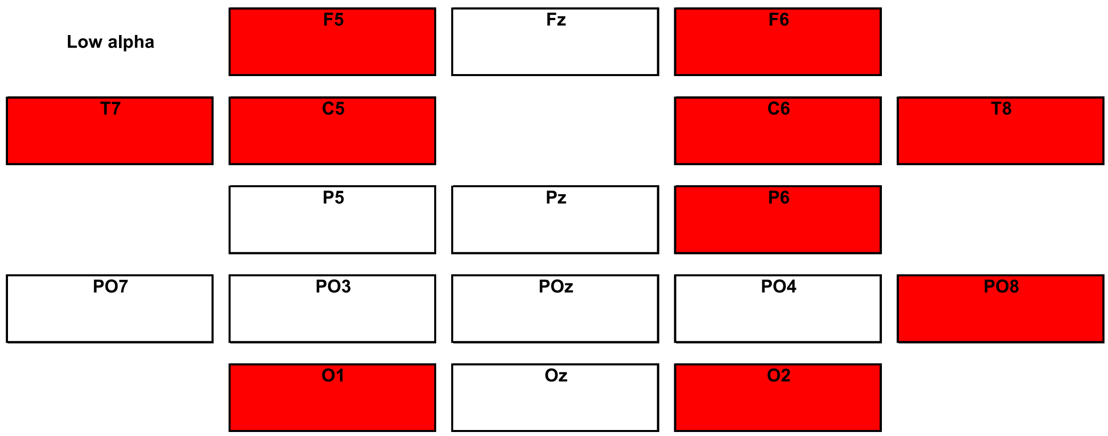


Figure I.27: Representation of significant regressions found in the majority of participants at different electrodes. For further information see Figure I.25 and the text.

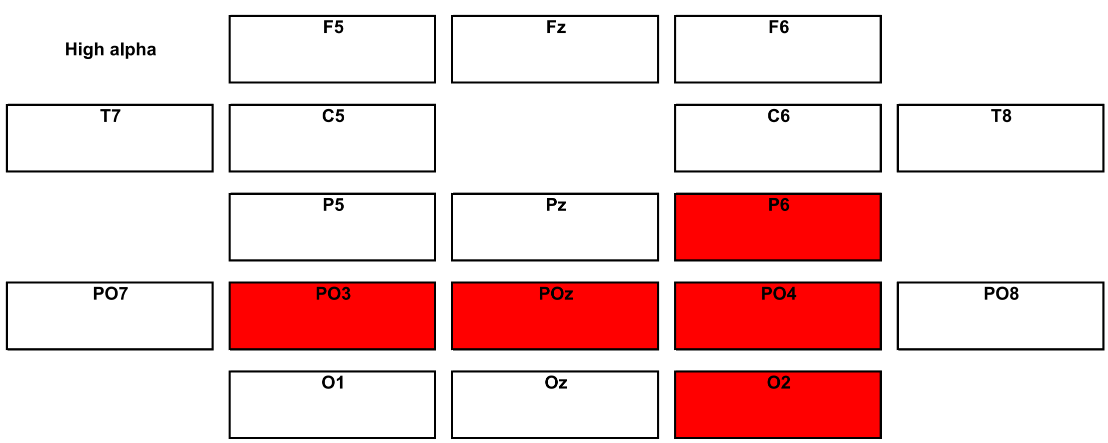


Figure I.28: Representation of significant regressions found in the majority of participants at different electrodes. For further information see Figure I.25 and the text.

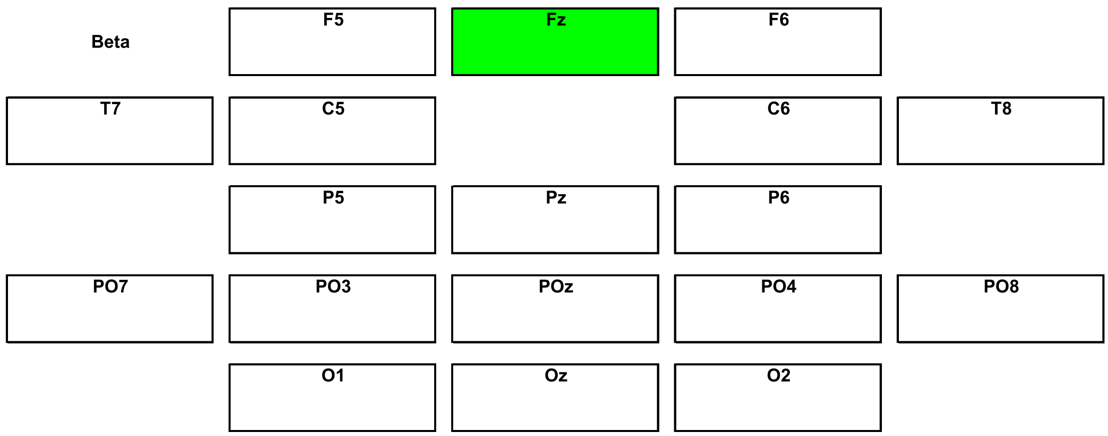


Figure I.29: Representation of significant regressions found in the majority of participants at different electrodes. For further information see Figure I.25 and the text.

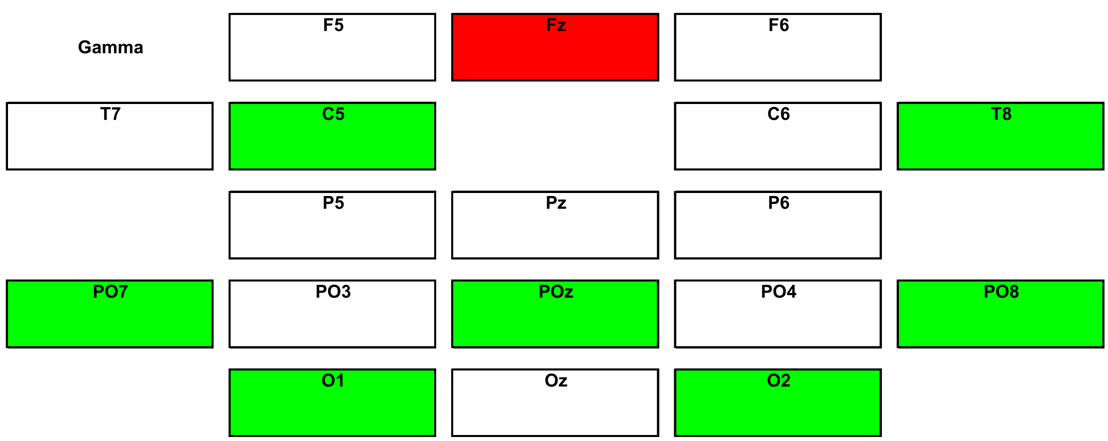


Figure I.30: Representation of significant regressions found in the majority of participants at different electrodes. For further information see Figure I.25 and the text.

Zusammenfassung

Diese Zusammenfassung gliedert sich in drei Teile: in der Einleitung wird zuerst ein Überblick über in der Literatur berichtete subjektive Erfahrungen verschiedenster Ursachen gegeben. Es folgen Befunde zu spezifisch durch visuelle Stimulation erzeugten subjektiven Farben und Formen, und anschließend Modellansätze zur Erklärung subjektiver Farben und Formen. Im zweiten Teil, der Ergebnisdarstellung, werden die experimentellen Befunde, die im Rahmen dieser Dissertation erhoben wurden, zusammengefasst. Der dritte Teil umfasst die Diskussion der Ergebnisse mit einer Erläuterung möglicher Entstehungsmechanismen subjektiver Farben und Formen, sowie einen Ausblick auf weitere Forschungsfragen.

Einleitung

Bewusste visuelle Wahrnehmung beruht auf der Interaktion unseres Nervensystemes mit Photonen, welche von räumlichen Strukturen der Umwelt reflektiert werden. Oft wird angenommen, dass visuelle Wahrnehmungen in direktem Bezug zum externen Reiz stehen, so dass zum Beispiel die räumlichen Eigenschaften des externen Reizes direkt auf die räumlichen Eigenschaften der inneren Wahrnehmung abgebildet werden. Dieser Ansatz scheitert bereits, wenn man sich mit der Farbwahrnehmung beschäftigt. Hier kann die innere visuelle Wahrnehmung nicht direkt auf die physikalischen Eigenschaften des Reizes im Sinne der Lichtreflexion und Lichtabsorption von Objekten abgebildet werden. Farbmetamere zum Beispiel sind Paare von perzeptuell nicht unterscheidbaren Farben, welche auf der Interaktion des visuellen Systems mit Licht unterschiedlicher physikalischer Eigenschaften (d.h. Spektralverteilungen) beruhen [2]. Einige jüngere philosophisch-psychologische Diskussionen zur Subjektivität von Farbwahrnehmungen (siehe [3] und [4] und die anschließenden Diskussionen) zeigen das kontroverse Potential dieses Abbildungsproblemes.

Die vorliegende Arbeit beschäftigt sich mit flackerinduzierten subjektiven Wahrnehmungen von Farbe und Formen. Obwohl diese visuellen Erfahrungen keine direkten Abbildungen der physikalischen Eigenschaften (d.h. der Wellenlänge und der räumlichen Zusammensetzung) der externen Stimulation sind, werde ich zeigen, dass sie in der Tat in physiologisch erklärbarem Bezug zu bestimmten Charakteristika der Stimulation stehen.

Visuelle Wahrnehmungen werden im Folgenden als 'subjektiv' bezeichnet, wenn sie die Wahrnehmung einer Struktur oder Eigenschaft bei gleichzeitiger Abwesenheit dieser Struktur oder Eigenschaft im externen visuellen Feld betreffen. Subjektive visuelle Wahrnehmungen wurden in einer Vielzahl von Kontexten berichtet, wovon einige hier kurz aufgezeigt werden.

Es ist bekannt, dass während der Ausführung schamanistischer Praktiken subjektive Wahrnehmungen auftreten können [14]. Aus diesen Befunden wurde die Hypothese abgeleitet [17], dass einfache geometrische Felsmalereien im Paläolithikum Repräsentationen subjektiver visueller Erfahrungen darstellen. Es wurde desweiteren vorgeschlagen [13], dass eine Vielzahl religiöser Berichte auf subjektive Wahrnehmungen, ausgelöst zum Beispiel durch meditative Zustände, zurückzuführen sind.

Subjektive visuelle Wahrnehmungen können auch durch eine Reihe halluzinogener Substanzen, wie zum Beispiel LSD [25] und Meskalin [26] hervorgerufen werden. Klüver [29, 30] stellte fest, dass sich diese und eine Reihe anderer subjektiver Wahrnehmungen (z.B. in Entspannungszuständen, oder bei Fieber) auf wenige geometrische Grundmuster zurückführen lassen, die in Anzahl, Größe und Form variieren.

Epileptische Episoden werden häufig durch eine sogenannte Aura eingeleitet, einen Zustand, in welchem der Epileptiker eine Reihe subjektiver Wahrnehmungen haben kann. Diese reichen von unspezifischen Erscheinungen (z.B. Lichtern [35]), über Formen (z.B. Kreise [36]), bis zu komplexen Gestalten (z.B. Gesichtern [37]). Ein ähnliches Phänomen ist das Flackerskotom, eine subjektive visuelle Wahrnehmung, welche einem Migräne-Anfall vorangehen kann [38]. Es wird oft als sich entwickelnder Halbkreis aus Zickzackmustern beschrieben [39, 40], welcher einen zentral im Gesichtsfeld liegenden Gesichtsfeldausfall umgibt.

Subjektive Wahrnehmungen können nachweislich auch durch sensorische Deprivation ausgelöst werden [50, 51]. Dabei scheint jedoch ein minimaler sensorischer Reiz förderlich für die Entstehung subjektiver Wahrnehmungen [53].

Eine Reihe von Studien hat die Möglichkeit aufgezeigt, subjektive visuelle Wahrnehmungen durch transkraniale magnetische Stimulation (TMS) auszulösen. Eine systematische Studie magnetisch induzierter Wahrnehmungen wurde von Seidel et al. [62, 63] vorgelegt. Die durch magnetische Rechteckwellen induzierten Wahrnehmungen von Formen konnten in verschiedene distinkte Formklassen eingeteilt werden. Dabei konnte allerdings kein Zusammenhang zwischen der Frequenz der Reizung und den beobachteten Formen festgestellt werden.

Knoll und Kollegen [66, 67] präsentierten eine Vielzahl von Befunden zu elektrisch induzierten geometrischen Wahrnehmungen. Auch hier konnten verschiedene Formklassen unterschieden werden, die Frequenz der Stimulation hatte jedoch keinen differentiellen Einfluss auf die wahrgenommenen Formen.

Subjektive visuelle Wahrnehmungen lassen sich auch durch geeignete Stimulation mit rhythmischem Licht erzeugen. Im Folgenden werde ich mich auf drei Hauptmöglichkeiten einer solchen Reizung beschränken: (i) die sogenannte Benham-Scheibe, (ii) Paradigmen, welche die Reizparameter der Benham-Scheibe imitieren, und (iii) periodische Stimulationen des gesamten visuellen Feldes.

(i) Vor mehr als hundert Jahren, 1894, präsentierte Benham in der Zeitschrift *Nature* [69] eine Methode zur Erzeugung eines ‘künstlichen Spektrums’. Wenn die sogenannte Benham-Scheibe, welche halb schwarz und halb weiß ist, und zusätzliche schwarze Linien auf der weißen Hälfte aufweist, mit einer bestimmten Geschwindigkeit gedreht wird, erscheinen die Linien an den unterschiedlichen Stellen der Scheibe in unterschiedlichen Farben. Die optimale Drehfrequenz zur Erzeugung lebendiger Farben liegt dabei zwischen 5 und 10 Hz [71].

(ii) Subjektive Farben wurden auch beobachtet, wenn die einzelnen Teile der

Benham-Scheibe als stationäre Muster mit geeigneter zeitlicher Modulation dargeboten wurden [77, 78]. Dabei betonten Festinger et al. [77] besonders die Rolle zeitlicher Faktoren für die Entstehung subjektiver Farben.

(iii) In einer Reihe von Publikationen beschreibt Smythies [79, 80, 81] subjektive Wahrnehmungen bei stroboskopischer Stimulation des gesamten visuellen Feldes. Die Probanden wurden mit stroboskopischem Licht mit den Frequenzen 6, 12 oder 18 Hz stimuliert, wobei ein Einfluss der Stimulationsfrequenz beobachtet werden konnte: bei höheren Frequenzen traten mehr Wahrnehmungen auf, und diese waren feiner gegliedert als bei niedrigeren Reizfrequenzen. Die beobachteten visuellen Muster wurden in folgende Gruppen eingeteilt: ungeformte Elemente (z.B. Flecken), einzelne Linien, Muster aus parallelen geraden Linien, Muster aus radial angeordneten geraden Linien, komplexe Muster aus geraden Linien (z.B. Wabenmuster), Muster aus gebogenen Linien, komplexe Bilder. Die beschriebenen Farben variierten stark zwischen den Probanden.

Knoll und Welpe ([83], zitiert in [13]) haben gezeigt, dass lichtinduzierte subjektive Wahrnehmungen jenen unter elektrischer Stimulation ähneln. Die optimale Anregungsfrequenz für lichtinduzierte Wahrnehmungen lag dabei zwischen 5 und 30 Hz. Bei diesen Stimulationsfrequenzen und einer Reizhelligkeit von etwa 30 cd/m^2 konnten eine Vielzahl verschiedener subjektiver Formwahrnehmungen erzeugt werden.

Die Ergebnisse der vorgestellten Studien lassen sich wie folgt zusammenfassen: (1) subjektive Farb- und Formwahrnehmungen lassen sich durch periodische visuelle Reizung erzeugen. (2) Die Effekte beschränken sich auf bestimmte Frequenzbereiche der Stimulation. (3) Subjektive Wahrnehmungen sind abhängig von Änderungen der Reizstärke über die Zeit: die Form oder Phase eines Reizes ist kritisch für die erzeugten Wahrnehmungen. (4) Die genauen Eigenschaften der subjektiven Wahrnehmungen hängen von einer Reihe von Reizparametern, wie der Helligkeit oder der räumlichen Ausdehnung der Stimulation, ab.

Es folgt eine Reihe von Erklärungsansätzen, insbesondere zur Wahrnehmung subjektiver Farben, welche in der Literatur dargestellt werden.

Von Campenhausen et al. (siehe [71] für einen Überblick) schlugen vor, dass subjektive Farben der Benham-Scheibe auf phasen-sensiblen lateralen Interaktionen neuronaler Aktivität in der Retina, gefolgt von zusätzlichen räumlichen Interaktionen im visuellen Kortex basieren. Experimente unter Nutzung binokularer Fusion zeigten [129], dass die Erzeugung subjektiver Farben wahrscheinlich in Hirnarealen stattfindet, welche funktional vor dem Ort der binokularen Fusion liegen.

Die neuartigen Reize mit einer Amplitudenvariation über die Zeit, welche von Festinger et al. [77] eingeführt wurden, waren später die Basis für ein physiologisch motiviertes Model subjektiver Farben [130]. Die Grundlage des Modelles von Courtney und Buchsbaum [130] sind zeitliche Verarbeitungsdifferenzen zwischen den Verarbeitungpfaden verschiedener Farben. Schnapf et al. [131] hatten in einer Studie gezeigt, dass die verschiedenen Zapfentypen der Retina unterschiedliche zeitliche Eigenschaften haben. Die Zapfen, welche besonders sensitiv auf kurzwelliges Licht reagieren, hatten eine Antwortlatenz von 61 ms. Mittelwellig-sensitive Zapfen wiesen eine Antwortlatenz von 51 ms auf, und langwellig-sensitive Zapfen von 55 ms. Das Model von Courtney und Buchsbaum war in der Lage, ein Ungleichgewicht in den Antworten der verschiedenen Farbpfade zu generieren, wenn das Modell mit Festinger-Reizen stimuliert wurde. Dieses Ungleichgewicht führt in Abhängigkeit vom präsentierten Reiz dann zur deutlichen Aktivierung bestimmter farbkodierender Ganglionzellen.

Die Festinger-Reize stellen bereits das hypothetische Ergebnis einer Interaktion der Benham-Reize mit den ersten Stufen des visuellen Systemes dar [77]. Grunfeld und Spitzer [132] entwickelten ein Modell, welches die direkte Stimulation mit einer Benham-Scheibe simuliert. Zu diesem Zweck bezogen die Autoren sowohl räumliche als auch zeitliche Parameter der Ganglionzellen ein, welche sowohl räumlich opponent, als auch gegenfarbkodierend sind. Neben den oben ausgeführten zeitlichen Parametern der verschiedenen Zapfentypen wurden weitere physiologische Parameter, wie inhibitorische und exzitatorische neuronale Antworten, in das Modell integriert. Das Modell erlaubte die korrekte Modellierung der Aktivität verschiedener Ganglion-Zellen bei der Stimulation mit Benham-Reizen.

Ein Modellansatz zur Erklärung subjektiver Formen wurde von Stwertka entwickelt [134]. Er schlug vor, dass die Formen, welche bei stroboskopischer Reizung des gesamten Gesichtsfeldes beobachtet werden (z.B. [79]), sogenannte dissipative Muster sind, d.h. selbst-organisierende Makrozustände räumlich-zeitlicher Kohärenz im Kortex. Die Annahme ist, dass die subjektiven Formen die bevorzugten Muster kortikaler Organisation, welche auf den dynamischen Eigenschaften des Nervensystemes beruhen, widerspiegeln. Genauer scheinen die beobachteten Formen ein Ausdruck der sogenannten Orientierungssäulen, in den visuellen kortikalen Arealen zu sein. Eckhorn [135] schlug vor, dass die Aktivität der räumlich verteilten Orientierungs-Säulen im Kortex gebunden wird, indem die lokalen Oszillationen der kortikalen Säulen synchronisiert werden. Stwertkas Modell nimmt nun einen ähnlichen Mechanismus für die Entstehung subjektiver Formen an, nämlich die Synchronisation von Gruppen von Orientierungs-Säulen, welche den perzeptuellen Eigenschaften der wahrgenommenen Muster entsprechen.

Experimentelle Befunde

Das Phänomen subjektiver Erfahrungen, welche durch zeitlich modulierte visuelle Stimulation ausgelöst werden, ist so fasziniend wie umstritten. Die Existenz visuell induzierter subjektiver Wahrnehmungen wurde in vielen Studien berichtet (siehe oben); jedoch sind einige der berichteten Ergebnisse recht widersprüchlich. Es ist zum Beispiel nicht abschließend geklärt, ob subjektive Wahrnehmungen zuverlässig durch die rhythmische Stimulation des gesamten visuellen Feldes ausgelöst werden können [71, 78, 132]. Wenn dies möglich ist, wird die Frage aufgeworfen, welche Faktoren neben räumlicher Information, wie sie bei der Benham-

Scheibe vorhanden ist, die subjektiven Wahrnehmungen determinieren. Desweiteren wurde der Zusammenhang zwischen subjektiven Farben und subjektiven Formen nie explizit untersucht, sondern war immer eher ein Nebenprodukt der Untersuchung eines der beiden Effekte (siehe z.B. [79]). Das Ziel dieser Dissertation ist es, diese und eine Reihe weiterer Fragen zu untersuchen. Die Ergebnisse dieser Studien werden im Folgenden vorgestellt.

In einer ersten Studie wurde den Teilnehmern flackerndes Licht über das gesamte Gesichtsfeld im Frequenzbereich von 1 bis 60 Hz dargeboten. Die Probanden wurden gebeten, ihre subjektiven Wahrnehmungen von Farbe und Form frei zu berichten. Kapitel 2 stellt die deskriptive Analyse der Ergebnisse dieses ersten Experimentes vor. Die berichteten Farben und Formen wurden in distinkte Kategorien eingeteilt. Folgende Farben wurden berichtet: weiß, schwarz, grau, blau, gelb, rot, grün, violett. Es traten folgende Formkategorien auf: Linie, Kreis, radiales Muster, Spirale, Viereck, Gitter, Welle, Zickzack-Muster und Punkt. Es konnte gezeigt werden, dass diese Wahrnehmungen zuverlässig von der Mehrzahl der Teilnehmer berichtet wurden. Dabei war das Auftreten der Wahrnehmungen an bestimmte Frequenzbereiche gebunden: Formen wurden am zuverlässigsten zwischen 8 und 40 Hz, Farben zwischen 5 und 56 Hz berichtet. Zusätzlich differenzierten die effektiven Frequenzbereiche zwischen den verschiedenen Wahrnehmungskategorien.

In Kapitel 3 wurden Abhängigkeiten im Auftreten der verschiedenen subjektiven Wahrnehmungen untersucht. Die Daten des ersten Experimentes wurden mit folgenden Zielen untersucht: (i) festzustellen, welche Wahrnehmungen gemeinsam innerhalb einer Stimulation auftreten, bzw. welche ihr gemeinsames Auftreten gegenseitig ausschließen. (ii) Die Reihenfolge, mit der die Wahrnehmungen innerhalb eines Durchganges berichtet wurden, sollte auf Regelmäßigkeiten hin untersucht werden. Die Analyse (i) zeigte ein komplexes Muster von Abhängigkeiten in der Wahrnehmung subjektiver Farben und Formen auf. Mögliche Beziehungen dieser Abhängigkeiten zu Gegenfarbmechanismen und topographischen Prinzipien der Formwahrnehmung wurden diskutiert. In der Analyse (ii) fanden sich keinerlei Hinweise auf spezifische Muster in der Abfolge berichteter subjektiver Wahrnehmungen über die Zeit. Dies gibt einen Hinweis darauf, dass bestimmte Wahrnehmungen zwar gemeinsam auftreten können, ihre Abfolge jedoch nicht auf präzisen internalen Sequenzen von Farb- oder Formentwicklung beruht.

Die Experimente 2 und 3, welche im Kapitel 4 vorgestellt werden, untersuchten den Einfluss weiterer zeitlicher Charakteristika der Stimulation neben der Stimulationsfrequenz auf die Wahrnehmung subjektiver Farben und Formen. In einer Reihe von Studien mit elektrischer [68] oder Benham-artiger [71] Stimulation zur Erzeugung subjektiver Farben wurde die Rolle phasen-sensitiver Mechanismen für die Wahrnehmung subjektiver Farben unterstrichen. In dem experimentellen Paradigma, welches im Rahmen dieser Dissertation zur Anwendung kommt, kann die Phase als Beziehung zwischen der zyklischen Eigenschaft der Stimulation und dem Zeitpunkt des Auftretens einer subjektiven Wahrnehmung ausgedrückt werden. Daher wurde in den Experimenten 2 und 3 ein Paradigma mit manueller Antwort verwendet. Den Teilnehmern wurde vorab eine bestimmte Wahrnehmung genannt, welche im aktuellen Durchgang zu beachten sei. Dann wurde ihnen rhythmisch flackerndes Licht dargeboten, und sie wurden gebeten, sofort bei Auftreten einer subjektiven Wahrnehmung einen Tastendruck auszuführen. Die Antwortzeiten wurden in Bezug auf die Phase der ryhthmischen Stimulation ausgewertet. Die Ergebnisse der Experimente 2 und 3 zeigen deutlich, dass subjektive Farben und Formen in einer phasenspezifischen Art und Weise kodiert werden. Dabei lässt sich annehmen, dass die Phasenspezifität einen effizienten Mechanismus für die Kodierung von Gegenfarben darstellt.

Subjektive visuelle Wahrnehmungen wurden in der Literatur auch bei Abwesenheit zeitlich modulierter Stimulation beschrieben, zum Beispiel in Zuständen sensorischer Deprivation [50, 52]. Die Experimente 4 und 5 (siehe Kapitel 5) wurden entworfen, um subjektive Wahrnehmungen, welche bei der Stimulation mit konstantem Licht über das gesamte Gesichtsfeld hinweg auftreten, zu messen.

Zusätzlich wurden diese Berichte unter konstanter Stimulation dazu genutzt, die Ergebnisse der Experimente 1 bis 3 auf Artefakte hin zu korrigieren. Bei konstanter Stimulation berichteten die Teilnehmer eine Reihe von subjektiven Wahrnehmungen. Die Ergebnisse von Experiment 1 wurden daher in Bezug auf die effektiven Frequenzbereiche der Wahrnehmungserzeugung und in Bezug auf die Abhängigkeiten zwischen den Wahrnehmungen hin angepasst. In gleicher Art und Weise wurden die Frequenzbereiche der Experimente 2 und 3 modifiziert. Die Korrekturen betonten die Frequenzspezifität der subjektiven Wahrnehmungen, da sie im Allgemeinen die effektiven Frequenzbereiche verkleinerten. Außerdem konnte das Muster der Abhängigkeiten zwischen den Wahrnehmungen verfeinert werden. Die Ergebnisse der Experimente 4 und 5 lieferten weiterhin klare Befunde für die statistische Validität der Phasenspezifität subjektiver Erfahrungen.

Das Kapitel 6 erforscht im Detail die Phänomenologie der subjektiven Farben und Formen, welche bei der Stimulation mit flackerndem Licht berichtet werden. In Experiment 6 erzeugten die Teilnehmer am Computerbildschirm mit Hilfe von Rot-Grün-Blau-Werten (RGB-Werten) Farben, die denen ihrer subjektiven Wahrnehmungen entsprachen. Als ein Kontrollexperiment wurde die Fähigkeit der Probanden gemessen, reale Zielfarben auf dem Computerbildschirm einzustellen. Es konnte gezeigt werden, dass die Probanden sehr gut in der Lage waren, diese Kontrollaufgabe auszuführen. Anschließend wurden die RGB-Farben, welche die subjektiven Farben repräsentierten, mit Hilfe ihrer dominanten Wellenlänge dargestellt. Die berichteten Farbkategorien ließen sich eindeutig auf der Basis der dominanten Wellenlängen unterscheiden. Während einige Farbschätzungen nur kleine interindividuelle Unterschiede in der dominanten Wellenlänge aufwiesen (zum Beispiel, gelb oder violett), zeigten andere eine höhere interindividuelle Variabilität (zum Beispiel blau, grün oder rot). In Kapitel 6 wird erläutert, wie dieser Effekt auf physiologischen Eigenschaften des farbkodierenden Systemes beruhen kann. Desweiteren korreliert die dominante Wellenlänge der subjektiven Farben signifikant mit der Stimulationsfrequenz. Weitergehende

Analysen zeigten, dass dieser Effekt sich eher auf Farbkategorien, denn auf ein Farbkontinuum bezieht. Dies gibt Hinweise darauf, dass mit einer Veränderung der Stimulationsfrequenz Übergänge von einer Farbkategorie zu einer anderen stattfinden. In Experiment 7 wurden die Probanden gebeten, die bei flackernder Stimulation wahrgenommenen Formen zu zeichnen. Eine detaillierte Beschreibung dieser Zeichnungen wird in Kapitel 6 gegeben, die Zeichnungen selbst finden sich im Anhang H. Die berichteten Formen zeigten klare Übereinstimmungen zwischen den Probanden. Die Zeichnungen zeigen auch eine deutliche Ähnlichkeit zu Berichten in der Literatur (siehe z.B. [80]). Die Ähnlichkeit der gezeichneten Formen zu Mustern, welche in computationalen Modellen erzeugt wurden (z.B. [136]) gibt außerdem Hinweise auf ihre Entstehungsmechanismen.

Während es schon einige elektroenzephalographische (EEG) Studien zur Wahrnehmung subjektiver Formen gab, finden sich keine Berichte über ähnliche Versuche hinsichtlich der Wahrnehmung subjektiver Farben. Unter Nutzung electroenzephalographischer Aufzeichnungen hatte das Experiment 8 das Ziel, elektrophysiologische Antworten während der Wahrnehmung subjektiver Farben zu messen. Die in Kapitel 7 dargestellten Befunde lassen sich wie folgt zusammenfassen: Berichten einer subjektiven Farbe geht ein spezifisches Muster von Aktivitätsanstiegen und -abfällen in verschiedenen EEG-Frequenzbändern voraus. Ein Abfall der Aktivität in Alpha-Frequenzbändern weist auf einen Anstieg aufgabenbezogener Informationsverarbeitung während des Zeitintervalls von 2000 ms, welches der Antwort vorausgeht, hin. Zusätzlich könnte die abfallende Alpha-Aktivität Prozesse reflektieren, welche den Wechsel zwischen verschiedenen Wahrnehmungen (d.h. hier Farben) oder die Reizentdeckung begleiten. Der beobachtete Anstieg in der Gamma-Aktivierung kann zum Einen ebenfalls mit einem perzeptuellen Wechsel korreliert sein, könnte aber auch die Bildung eines kohärenten Wahrnehmungsinhaltes im Intervall vor der Antwort bedeuten.

Diskussion

Ein theoretisches Modell subjektiver Farbwahrnehmung

Im Folgenden wird auf der Basis der Ergebnisse dieser Dissertation und Befunden der Literatur ein theoretisches Modell der Mechanismen subjektiver Farbwahrnehmung entwickelt.

Wenn das flackernde Licht auf die Retina trifft, werden die retinalen Rezeptoren wiederholt stimuliert. Dabei hängt die Periode dieser Wiederholungen von der Stimulationsfrequenz ab und liegt bei den hier vorgestellten Experimenten zwischen 100 ms (1 Hz) und 17 ms (60 Hz). Diese Intervalle interferieren deutlich mit den Antwortlatenzen der retinalen Zapfentypen. In Experiment 1 konnte gezeigt werden, dass die Differenzen zwischen den effektivsten Stimulationsfrequenzen für die subjektiven Farben blau, grün und rot in etwa den Latenzen der Zapfentypen [131] entsprechen (siehe Abschnitt 2.4). Dieser Befund und vorhandene Modelle subjektiver Farbwahrnehmung [130, 132] geben deutliche Hinweise darauf, dass die der Retina folgenden Verarbeitungstufen in Abhängigkeit von der Interaktion der Zapfenlatenzen und der Stimulationsfrequenz unterschiedlich stimuliert werden.

Ein wesentlicher Befund dieser Dissertation ist der Nachweis der Phasenspezifität subjektiver Wahrnehmungen. Dabei wurde insbesondere gezeigt, dass die Gegenfarbenpaare rot-grün und blau-gelb sich klar nach der Phase unterscheiden lassen. Daraus wurde geschlossen, dass die Phase eine effiziente Möglichkeit der Kodierung von Gegenfarben darstellen könnte. Das wiederholte Feuern retinaler Zellen während anhaltender Stimulation kann als oszillatorisch angesehen werden. Die Befunde der Phasenspezifität und jene von Young [68] berichteten Ergebnisse weisen darauf hin, dass die oszillatorischen Aktivitäten gegenfarbkodierender Zellen jeweils unterschiedliche Phasen aufweisen könnten. Die Aktivierung von Zellen, welche Gegenfarben (z.B. blau und gelb) kodieren, könnte in mehr oder weniger entgegengesetzter Phase erfolgen, wohingegen z.B. blau und rot durch ähnliche Phasen gekennzeichnet wären.

Diese Phaseneigenschaften könnten im Auftreten subjektiver Farben deswegen sichtbar sein, weil ein physiologischer Tormechanismus existiert, welcher normalerweise die Aktivität aus niedrigeren Verarbeitungsstufen am Zutritt in kortikale Verarbeitungsstufen hindert. Wenn sich dieses Tor jedoch öffnet, würde die Wahrnehmung einer subjektiven Farbe davon abhängen, welche der oszillatorischen Gegenfarben-Aktivationen sich in dem Moment gerade auf ihrem Maximum befindet.

In der Tat wurde in der EEG-Untersuchung ein solcher möglicher Tormechanismus beschrieben. Die Synchronisation großer Teile des Kortex mit einem Alpha-Rhythmus wird normalerweise von einem Zustand der Entspannung begleitet, in dem die Person keine kognitiven oder Wahrnehmungsinhalte hat. Daher verhindert eine hohe Alpha-Aktivität unter Umständen die Repräsentation perzeptueller Inhalte im Kortex. Strüber und Herrmann [156] schlugen vor, dass in Situationen ohne äußere Veränderungen der Stimulation ein spontaner und endogener Abfall der Alpha-Aktivität auftreten könne. Wenn diese abfallende Alpha-Aktivität eine bestimmte Schwelle erreicht, wird die Synchronisation in anderen Frequenzbändern möglich und ein neues Perzept kann sich manifestieren. Die in den hier beschriebenen Experimenten beobachtete abfallende Alpha-Aktivität könnte also bei Erreichen einer kritischen Schwelle die Öffnung des oben beschriebenen Tores darstellen. Diese Öffnung erlaubt den Informationen aus frühen Verarbeitungsarealen in den Kortex vorzudringen und dort perzeptuelle Repräsentationen in anderen Frequenzbändern zu bilden. Wahrscheinlich stellt der beobachtete Anstieg der Gamma-Aktivität einen möglichen Mechanismus der Repräsentation subjektiver Farbe auf kortikaler Ebene dar.

Mechanismen subjektiver Formwahrnehmung und die Beziehung zwischen subjektiver Farbe und Form

Die erstaunlichste Eigenschaft der durch flackerndes Licht ausgelösten subjektiven Formen ist ihre Ähnlichkeit zu resonanten Systemen, wie z.B. vibrierenden Wasser- oder Sandoberflächen (siehe z.B. [133]). In der Retina finden sich nicht nur vorwärtsgerichtete neuronale Verbindungen, sondern auch eine grosse Anzahl lateraler inhibitorischer Verbindungen. Diese lateralen Verbindungen haben bestimmte zeitliche Eigenschaften, d.h. Weiterleitungslatenzen. Wenn die Retina mit flackerndem Licht gereizt wird, könnte die Stimulation ähnlich wie für die subjektive Farbwahrnehmung beschrieben mit den Latenzen der lateralen Verbindungen interagieren. Es ist möglich, dass die wiederholte Stimulation in Interaktion mit dem kontinuierlich ablaufendem lateralen Informationsfluss die Gesamtheit der neuronalen Zellen auf retinalem Niveau in einen Zustand der Resonanz versetzt. Dieser Resonanzzustand könnte Muster differenzieller Zellaktivation auslösen, welche Resonanzmustern in physikalischen Systemen [133] ähneln. Die durch Resonanzphänomene generierte Aktivität würde weitere Stufen im visuellen Verarbeitungssystem durchlaufen und schließlich die entsprechenden Orientierungssäulen im Kortex stimulieren und damit bestimmte, klar umrissene Formen repräsentieren [135]. Dabei muss die neuronale Aktivität wahrscheinlich dieselben Tormechanismen passieren, wie für subjektive Farben beschrieben.

Eine weiteres Problem betrifft das gemeinsame Auftreten von subjektiven Farben und Formen. Dies ist mutmaßlich darauf zurückzuführen, dass farbkodierende Zellen ebenfalls für die Repräsentation räumlicher Eigenschaften von Reizen zuständig sind. Die Abhängigkeiten in den Berichten subjektiver Wahrnehmungen zeigten, dass insbesondere Zellen, welche rot und grün kodieren, in die Entstehung resonanter Muster involviert sind. Vermutlich beruht dieser Effekt auf den spezifischen zeitlichen Charakteristika dieser rot/grün-Zellen, welche sie besonders geeignet für die Erzeugung resonanter Strukturen bei rhythmischer Stimulation mit bestimmten Frequenzen machen.

Ausblick

Es scheint zum Einen von Interesse, die in dieser Arbeit zur Wahrnehmung subjektiver Farben und Formen gewonnenen Befunde im Bereich der Wahrnehmung realer Farben und Formen zu überprüfen.

Aber auch in Bezug auf das Phänomen subjektiver Wahrnehmungen gibt es eine Reihe von offenen Fragen, welche in zukünftigen Forschungsprojekten beantwortet werden könnten. Häufig berichteten Probanden von deutlichen Bewegungswahrnehmungen bei der Stimulation mit rhythmischem Licht, ein Effekt, welcher in dieser Arbeit nicht im Detail untersucht wurde. Es wäre interessant zu überprüfen, ob eine spezifische Beziehung zwischen der Wahrnehmung von Farben, Formen und Bewegung besteht, und welche physiologischen Prozesse dem zugrundeliegen.

Desweiteren könnte die physiologische Untersuchung der Phasenspezifität auf dem Einzelzellniveau interessante Einblicke in die zeitlichen Charakteristika der physiologischen Mechanismen visueller Verarbeitung liefern.

Letztendlich wäre der weitere Einsatz elektroenzephalographischer oder anderer bildgebender Verfahren eine gute Möglichkeit, die Prozesse und Orte, welche der Wahrnehmung subjektiver und realer Farben und Formen zugrundeliegen, zu verstehen.

Bibliography

[1] D. Kuhn & W. von Engelhardt (Eds.) (1965). *Goethe. Die Schriften zur Naturwissenschaft (Leopoldina). Erste Abteilung: Texte. Band 10: Aufsätze, Fragmente, Studien zur Morphologie.* Hermann Böhlaus, Weimar.

[2] Palmer, S. E. (1999). *Vision Science. Photons to Phenomenology.* MIT Press, Cambridge, MA.

[3] Ross, P. W. (2001). The location problem for color subjectivism. *Consciousness and Cognition*, 10:42–58.

[4] Byrne, A. & Hilbert, D. R. (2003). Color realism and color science. *Behavioral and Brain Sciences*, 26:3–64.

[5] Hardin, C. L. (1993). *Color for philosophers: Unweaving the rainbow.* Hackett, Indianapolis, IN.

[6] Ross, P. W. (2001). Locating color: Further thoughts. *Consciousness and Cognition*, 10:146–156.

[7] Revonsuo, A. (2001). Putting color back where it belongs. *Consciousness and Cognition*, 10:78–84.

[8] Cornelissen, F. W., Brenner, E., & Smeets, J. (2003). True color only exists in the eye of the observer. *Behavioral and Brain Sciences*, 26(1):26–27.

[9] Chalmers, D. J. (1996). *The Conscious Mind. In Search of a Fundamental Theory.* Oxford University Press, Oxford.

[10] Crick, F. & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6(2):119–126.

[11] Dennett, D. C. (1991). *Consciousness Explained*. Penguin Books, London.

[12] Koch, C. (2004). *The Quest for Consciousness. A Neurobiological Approach*. Roberts and Company Publishers, Englewood, Colorado.

[13] Eichmeier, J. & Höfer, O. (1974). *Endogene Bildmuster*. Urban & Schwarzenberg, München.

[14] Eliade, M. (1956). *Schamanismus und archaische Ekstasetechnik*. Rascher, Zürich.

[15] Knoll-Greiling, U. (1959). Rauschinduzierende Mittel bei Naturvölkern und ihre individuelle und soziale Wirkung. *Sociologus*, 9:47–60.

[16] Shonle, R. (1925). Peyote, the giver of visions. *American Anthropologist*, 27:53–75.

[17] Bednarik, R. G. (1990). On neuropsychology and shamanism in rock art. *Current Anthropology*, 31:77–80.

[18] Bradley, R. (1989). Deaths and entrances: contextual analysis of megalithic art. *Current Anthropology*, 30:68–75.

[19] Lewis-Williams, J. D. & Dowson, T. A. (1993). On vision and power in the Neolithic: Evidence from the decorated monuments. *Current Anthropology*, 34:55–65.

[20] Kellog, R., Knoll, M., & Kugler, J. (1965). Form similarity between phosphenes of adults and pre-school children's scribblings. *Nature*, 208:1129–1130.

[21] Bahn, P. G. & Vertut, J. (1997). *Journey through the Ice Age*. Weidenfeld and Nicolson, London.

[22] Hodgson, D. (2000). Shamanism, phosphenes, and early art: An alternative synthesis. *Current Anthropology*, 41(5):866–873.

[23] Rosenberg, A. (1955). *Die christliche Bildmeditation*. O.W. Barth, Planegg.

[24] Zimmer, H. (1951). *Mythen und Symbole in indischer Kunst und Kultur*. Rascher, Zürich.

[25] Abraham, H. D. (1983). Visual phenomenology of the LSD flashback. *Archives of General Psychiatry*, 40:884–889.

[26] Knauer, A. & Maloney, W. J. M. A. (1913). A preliminary note on the psychic action of mescaline, with special reference to the mechanism of visual hallucinations. *Journal of Nervous and Mental Disease*, 40:425–436.

[27] Huxley, A. (1954). *Doors of perception*. Harper, New York.

[28] Knoll, M., Kugler, J., Höfer, O., & Lawder, S. D. (1963). Effects of chemical stimulation of electrically-induced phosphenes on their bandwidth, shape, number and intensity. *Confinia neurologica*, 23:201–226.

[29] Klüver, H. (1942). Mechanisms of hallucinations. In *Studies in Personality*.

[30] Klüver, H. (1966). *Mescal and mechanisms of hallucinations*. University of Chicago Press, Chicago.

[31] Purkinje, J. E. (1819). *Beiträge zur Kenntnis des Sehens in subjektiver Hinsicht*. J. G. Calve, Prag.

[32] Oster, G. (1970). Phosphenes. *Scientific American*, 222:83–87.

[33] ffytche, D. H. & Howard, R. J. (1999). The perceptual consequences of visual loss: 'positive' pathologies of vision. *Brain*, 122:1247–1260.

[34] Kolmel, H. W. (1984). Coloured patterns in hemianopic fields. *Brain*, 107(1):155–167.

[35] Remy, M. (1958). Über einen Fall von visueller Aura. *Ciba Symposium*, 6:206–210.

[36] Penfield, W. & Jasper, H. (1954). *Epilepsy and the functional anatomy of the human brain*. London.

[37] Marchand, L. & de Ajuliaguerra, I. (1948). *Epilepsies*. D. de Brouwer, Paris.

[38] Dahlem, M. A. & Chronicle, E. P. (2004). A computational perspective on migraine aura. *Progress in Neurobiology*, 74:351–361.

[39] Ahlenstiel, H. (1958). Der Zackenbogen des Flimmerskotoms. *Archiv für Psychiatrie*, 196:577–579.

[40] Lashley, K. S. (1941). Patterns of cerebral integration indicated by the scotomas in migraine. *Archives of Neurology and Psychiatry*, 46:331–339.

[41] Vignoli, T. (1880). *Mythus und Wissenschaft*. Brockhaus, Leipzig.

[42] Sachs, O. (1995). *Migraine*. Picador, London.

[43] Gagel, O. (1953). *Migräne. Handbuch der inneren Medizin V/2*. Springer, Berlin.

[44] Crotogino, J., Feindel, A., & Wilkinson, F. (2001). Perceived scintillation rate of migraine aura. *Headache*, 41:40–48.

[45] Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, 29:169–295.

[46] Bowman, K. M. & Raymond, A. F. (1931). A statistical study of hallucinations in the manic-depressive psychoses. *American Journal of Psychiatry*, 88:299–309.

[47] Gelder, M., Mayou, R., & Geddes, J. (1999). *Psychiatry*. Oxford University Press, Oxford.

[48] Feinberg, I. (1962). A comparison of the visual hallucinations in schizophrenia with those induced by mescalin and LSD-25. In L. I. West (Ed.), *Hallucinations*. Gruner and Stratton, New York.

[49] Müller, J. (1826). *Über die fantastischen Gesichtserscheinungen*. Coblenz.

[50] Solomon, P. (1961). *Sensory deprivation*. Harvard University Press, Cambridge, MA.

[51] Heron, W., Doane, B. K., & Scott, T. H. (1956). Visual disturbances after prolonged perceptual isolation. *Canadian Journal of Psychology*, 10:13–18.

[52] Vernon, J., Marton, T., & Peterson, E. (1961). Sensory deprivation and hallucinations. *Science*, 133:1808–1812.

[53] Vernon, J. (1963). *In the dark room*. New York.

[54] S. Baron-Cohen & J. Harrison (Eds.) (1997). *Synaesthesia: Classic and Contemporary Essays*. Blackwell Publishers, Oxford.

[55] H. Hildebrandt (Ed.) (1998). *Pschyrembel. Klinisches Wörterbuch*. Walter de Gruyter, Berlin.

[56] Kammer, T., Puls, K., Erb, M., & Grodd, W. (2005). Transcranial magnetic stimulation in the visual system. II. Characterization of induced phosphenes and scotomas. *Experimental Brain Research*, 160:129–140.

[57] Ray, P. G., Meador, K. J., Epstein, C. M., Loring, D. W., & Day, L. J. (1998). Magnetic stimulation of the visual cortex: factors influencing the perception of phosphenes. *Journal of Clinical Neurophysiology*, 15:351–357.

[58] Dunlap, K. (1911). Visual sensations from an alternating magnetic field. *Science*, 33:68–71.

[59] Barlow, H. B., Kohn, H. J., & Walsh, E. G. (1947). Visual sensation aroused by magnetic fields. *American Journal of Physiology*, 148:372–375.

[60] Thompson, S. P. (1910). The effects of magnetic fields. *Proceedings of the Royal Society*, B 82:996.

[61] Magnusson, C. E. & Stevens, H. C. (1911). Visual sensations caused by changes in the strength of a magnetic field. *American Journal of Physiology*, 29:124–136.

[62] Seidel, D. (1968). Der Existenzbereich elektrisch und magnetisch-induktiv angeregter subjektiver Lichterscheinungen (Phosphene) in Abhängigkeit von äußeren Reizparametern. *Elektromedizin*, 13:194–206, 208–211.

[63] Seidel, D., Knoll, M., & Eichmeier, J. (1968). Anregung von subjektiven Lichterscheinungen (Phosphenen) beim Menschen durch magnetische Sinusfelder. *Pflügers Archiv für die gesamte Physiologie des Menschen und der Tiere*, 299:11–18.

[64] Müller, G. E. (1897). Über die galvanischen Gesichtsempfindungen. *Zeitschrift fr die Psychologie und Physiologie der Sinnesorgane*, 14:329–374.

[65] Barnett, A. & Posner, M. (1941). Effects produced by impressing alternating electric fields of low frequency and intensity on the human skull. *Journal of Psychology*, 11:271–278.

[66] Knoll, M. (1958). Anregung geometrischer Figuren und anderer subjektiver Lichtmuster in elektrischen Feldern. *Schweizer Zeitschrift für Psychologie*, 17:110–126.

[67] Knoll, M. & Kugler, J. (1959). Subjective light-pattern spectroscopy in the electroencephalographic frequency range. *Nature*, 184:1823.

[68] Young, R. A. (1977). Some observations on temporal coding of color vision: psychophysical results. *Vision Research*, 17:957–965.

[69] Benham, C. E. (1894). The artificial spectrum. *Nature*, 51(113):200.

[70] Fechner, G. T. (1838). Ueber eine Scheibe zur Erzeugung subjectiver Farben. In J. C. Poggendorf (Ed.), *Annalen der Physik und Chemie*, pp. 227–232. Verlag von Johann Ambrosius Barth, Leipzig.

[71] Campenhausen, C. v. & Schramme, J. (1995). 100 years of Benham's top in colour science. *Perception*, 24:695–717.

[72] Cohen, J. & Gordon, D. A. (1949). The Prevost-Fechner-Benham subjective colors. *Psychological Bulletin*, 46:97–136.

[73] Roelofs, C. O. & Zeeman, W. P. C. (1957). Colour phenomena associated with increases and decreases in physical brightness. *Acta Psychologica*, 13:173–196.

[74] Roelofs, C. O. & Zeeman, W. P. C. (1958). Benham's top and the colour phenomena resulting from interaction with intermittent light stimuli. *Acta Psychologica*, 13:334–356.

[75] Vienot, F. & Rohellec, J. L. (1992). Reversal in the sequence of the Benham colours with a change in the wavelength of illumination. *Vision Research*, 32(12):2369–2374.

[76] Kozak, W. M., Reitboeck, H. J., & Meno, F. (1989). Subjective color sensations elicited by moving patterns: effect of luminance. In J. J. Kulikowski, C. M. Dickinson, & I. J. Murray (Eds.), *Seeing Contour and Color*. Pergamon Press, Oxford.

[77] Festinger, L., Allyn, M. R., & White, C. W. (1971). The perception of color with achromatic stimulation. *Vision Research*, 11:591–612.

[78] Jarvis, J. R. (1977). On Fechner-Benham subjective colour. *Vision Research*, 17:445–451.

[79] Smythies, J. R. (1959). The stroboscopic patterns. I. The dark phase. *British Journal of Psychology*, 50:106–116.

[80] Smythies, J. R. (1959). The stroboscopic patterns. II. The phenomenology of the bright phase and after images. *British Journal of Psychology*, 50:305–324.

[81] Smythies, J. R. (1960). The stroboscopic patterns: III. Further experiments and discussion. *British Journal of Psychology*, 51(3):247–255.

[82] Piggins, D. J., Kingham, J. R., & Holmes, S. M. (1972). Colour, colour saturation, and pattern induced by intermittent illumination: an initial study. *British Journal of Physiological Optics*, 27(2):120–125.

[83] Knoll, M. & Welpe, E. (1968). Vergleich von Anregungsbedingungen, Formklassen und Bewegungsarten optischer und elektrischer Phosphene. *Elektromedizin*, 13:128–134.

[84] Herrmann, C. S. (2001). Human EEG responses to 1-100 Hz flicker: resonance phenomena in visual cortex and their potential correlation to cognitive phenomena. *Experimental Brain Research*, 137:346–353.

[85] Herrmann, C. S. & Elliott, M. A. (2001). Fechner's colors are induced by flickering monochromatic light. In E. Sommerfeld, T. Lachmann, R. Kompass, & H.-G. Geissler (Eds.), *Proceedings of the Seventeenth Annual Meeting of the International Society of Psychophysics*, pp. 427–431. Pabst Science Publishers, Lengerich.

[86] Shevelev, I. A., Kamenkovich, V. M., Bark, E. D., Verkhlutov, V. M., Sharaev, G. A., & Mikhailova, E. S. (2000). Visual illusions and travelling alpha waves produced by flicker at alpha frequency. *International Journal of Psychophysiology*, 39:9–20.

[87] Shevelev, I. A., Kamenkovich, V. M., & Sharaev, G. A. (1996). Visual illusions and EEG alpha-rhythm. *Zhurnal vysshei nervnoi deiatelnosti*, 46:34–39.

[88] Goldstein, E. B. (2002). *Sensation and Perception*. Wadsworth.

[89] Dacey, D. M. (2000). Parallel pathways for spectral coding in primate retina. *Annual Review of Neurosciences*, 23:743–775.

[90] Gegenfurtner, K. R. & Kiper, D. C. (2003). Color vision. *Annual Review of Neurosciences*, 26:181–206.

[91] Ungerleider, L. G. & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfeld (Eds.), *Analysis of Visual Behavior*, pp. 549–586. MIT Press, Cambridge, MA.

[92] Young, T. (1802). On the theory of light and colours. *Transactions of the Royal Society of London*, 92:12–48.

[93] von Helmholtz, H. (1852). On the theory of compound colors. *Philosophical Magazine*, 4:519–534.

[94] Dartnall, H. J. A., Bowmaker, J. K., & Mollon, J. D. (1983). Human visual pigments: Microspectrophotometric results from the eyes of seven persons. *Proceedings of the Rocal Society of London*, 220B:115–130.

[95] Schnapf, J. L., Kraft, T. W., & Baylor, D. A. (1987). Spectral sensitivity of human cone receptors. *Nature*, 325:439–441.

[96] Lennie, P. (2000). Color vision: Putting it together. *Current Biology*, 10(16):589–591.

[97] Hering, E. (1878). *Zur Lehre vom Lichtsinn*. Gerold, Wien.

[98] De Valois, R. L., Abramov, I., & Jacobs, G. H. (1966). Analysis of response patterns in LGN cells. *Journal of the Optical Society of America*, 56:966–977.

[99] De Valois, R. L. & Jacobs, G. H. (1968). Primate color vision. *Science*, 162:533–540.

[100] Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, 22:1123–1131.

[101] Chatterjee, S. & Callaway, E. M. (2003). Parallel colour-opponent pathways to primary visual cortex. *Nature*, 426:668–671.

[102] Gegenfurtner, K. R. (2003). Cortical mechanisms of colour vision. *Nature Reviews Neuroscience*, 4:563–572.

[103] Levine, M. W. (2000). *Fundamentals of Sensation and Perception*. Oxford University Press, Oxford.

[104] Michael, C. R. (1978). Color vision mechanisms in monkey striate cortex: Dual-opponent cells with concentric receptive fields. *Journal of Neurophysiology*, 41:572–588.

[105] Kiper, D. C., Fenstemaker, S. B., & Gegenfurtner, K. R. (1997). Chromatic properties of neurons in macaque area V2. *Visual Neuroscience*, 14:1061–1072.

[106] Livingstone, M. S. & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 240:740–749.

[107] Zeki, S. M. (1983). Colour coding in the cerebral cortex: The reaction of cells in monkey visual cortex to wavelengths and colours. *Neuroscience*, 9(4):741–765.

[108] Conway, B. R. (2003). Colour vision: A clue to hue in V2. *Current Biology*, 13:R308–R310.

[109] Zeki, S. M. (1980). The representation of colours in the cerebral cortex. *Nature*, 284:412–418.

[110] Gegenfurtner, K. R., Kiper, D. C., & Levitt, J. B. (1997). Functional properties of neurons in macaque area V3. *Journal of Neurophysiology*, 77:1906–1023.

[111] Thiele, A., Dobkins, K. R., & Albright, T. D. (1999). The contribution of color to motion processing in macaque middle temporal area. *Journal of Neuroscience*, 19(15):6571–6587.

[112] Derrington, A. M., Krauskopf, J., & Heeley, D. W. (1984). Chromatic mechanisms in the lateral geniculate nucleus of macaque. *Journal of Physiology*, 357:241–265.

[113] Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience*, 10:649–669.

[114] Leventhal, A. G., Thompson, K. G., Liu, D., Zhou, Y., & Ault, S. J. (1995). Concomitant sensitivity to orientation, direction, and color of cells in layers 2, 3, and 4 of monkey striate cortex. *Journal of Neuroscience*, 15:1808–1818.

[115] Gegenfurtner, K. R., Kiper, D. C., & Fenstemaker, S. B. (1996). Processing of color, form, and motion in macaque area V2. *Visual Neuroscience*, 13:161–172.

[116] Fiorentini, A., Burr, D. C., & Morrone, C. M. (1991). Temporal characteristics of colour vision: VEP and psychophysical measurements. In A. Valberg & B. Lee (Eds.), *From Pigments to Perception*, pp. 139–149. Plenum Press, New York.

[117] Cottaris, N. P. & De Valois, R. L. (1998). Temporal dynamics of chromatic tuning in macaque primary visual cortex. *Nature*, 395:896–900.

[118] Smithson, H. E. & Mollon, J. D. (2004). Is the S-opponent chromatic subsystem sluggish? *Vision Research*, 44:2919–2929.

[119] McKeefry, D. J., Parry, N. R. A., & Murray, I. J. (2003). Simple reaction times in color space: The influence of chromaticity, contrast, and cone opponency. *Investigative Ophtalmology & Visual Science*, 44(5):2267–2276.

[120] Hubel, D. H. (1982). Exploration of the primary visual cortex, 1955-1978. *Nature*, 299:515–524.

[121] Campbell, F. W., Kulikowski, J. J., & Levinson, J. (1966). The effect of orientation on the visual resolution of gratings. *Journal of Physiology*, 187:427–436.

[122] De Valois, R. L., Yund, E. W., & Hepler, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research*, 22:531–544.

[123] Maffei, L. & Fiorentini, A. (1973). The visual cortex as a spatial frequency analyzer. *Vision Research*, 13:1255–1267.

[124] Campbell, F. W. & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology*, 197:551–566.

[125] Merigan, W. H. & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, 16:369–402.

[126] Tanaka, K. (1993). Neuronal mechanisms of object recognition. *Science*, 262:684–688.

[127] Fujita, I., Tanaka, K., Ito, M., & Cheng, K. (1992). Columns for visual features of objects in monkey inferotemporal cortex. *Nature*, 360:343–346.

[128] Tanaka, K., Siato, H.-A., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology*, 66:170–189.

[129] Campenhausen, C. v. (1973). Detection of short time delays between photic stimuli by means of pattern induced flicker colors PIFCs. *Vision Research*, 13:2261–2272.

[130] Courtney, S. M. & Buchsbaum, G. (1991). Temporal differences between color pathways within the retina as a possible origin of subjective colors. *Vision Research*, 31:1541–1548.

[131] Schnapf, J. L., Nunn, B. J., Meister, M., & Baylor, D. A. (1990). Visual transduction in cones of the monkey Macaca fascicularis. *Journal of Physiology*, 427:681–713.

[132] Grunfeld, E. D. & Spitzer, H. (1995). Spatio-temporal model for subjective colours based on colour coded ganglion cells. *Vision Research*, 35(2):275–283.

[133] Christiansen, B., Alstrom, P., & Levinsen, M. T. (1992). Ordered capillary-wave states: Quasicrystals, hexagons, and radial waves. *Physical Review Letters*, 68(14):2157–2160.

[134] Stwertka, S. A. (1993). The stroboscopic patterns as dissipative structures. *Neuroscience and Biobehavioral Reviews*, 17:69–78.

[135] Eckhorn, R. (1991). Stimulus-specific synchronizations in the visual cortex: Linking of local features into global features? In J. Kruger (Ed.), *Neuronal cooperativity*, pp. 184–224. Springer-Verlag, Berlin.

[136] Tass, P. (1995). Cortical pattern formation during visual hallucinations. *Journal of Biological Physics*, 21:177–210.

[137] Silverman, B. W. (1986). *Density estimation*. Chapman and Hall, London.

[138] Chaudhuri, P. & Marron, J. S. (1997). Sizer for exploration of structures in curves. *Journal of the American Statistical Association*, 94(447):807–823.

[139] Kruskal, J. B. (1964). Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, 29(1):1–27.

[140] Jammalamadaka, S. R. SenGupta, A. (2001). *Topics in Circular Statistics*. World Scientific Press, Singapore.

[141] Mardia, K. V. (2000). *Directional Statistics*. John Wiley & Sons Ltd.

[142] Brainard, D. H., Roorda, A., Yamauchi, Y., Calderone, J. B., Metha, A. B., Neitz, M., Neitz, J., Williams, D. R., & Jacobs, G. H. (2000). Functional consequences of the relative numbers of L and M cones. *Journal of the Optical Society of America A*, 17:607–614.

[143] Neitz, J. & Jacobs, G. H. (1986). Polymorphism of the long-wavelength cone in normal human colour vision. *Nature*, 323:623625.

[144] Neitz, J. & Jacobs, G. H. (1990). Polymorphism in normal human color vision and its mechanism. *Vision Research*, 30(4):621–636.

[145] Tass, P. (1997). Oscillatory cortical activity during visual hallucinations. *Journal of Biological Physics*, 23:21–66.

[146] Lutzenberger, W., Elbert, T., Rockstroh, B., & Birbaumer, N. (1985). *Das EEG*. Springer-Verlag, Berlin.

[147] Zschocke, S. (1995). *Klinische Elektroenzephalographie*. Springer, Berlin.

[148] Mecklinger, A., Kramer, A., & Strayer, D. (1992). Event-related potentials and EEG components in a semantic memory search task. *Psychophysiology*, 29:104–119.

[149] Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*, 26:319–340.

[150] Basar, E., Basar-Eroglu, C., Karakas, S., & Schrmann, M. (1999). Are cognitive processes manifested in event-related gamma, alpha, theta and delta oscillations in the EEG? *Neuroscience Letters*, (259):165–168.

[151] Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, 20:376–383.

[152] Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., & Pecherstorfer, T. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neuroscience Letters*, 375:64–68.

[153] Müller, T. J., Federspiel, A., Horn, H., Lövblad, K., Lehmann, C., Dierks, T., & Strik, W. K. (2005). The neurophysiological time pattern of illu-

sionary visual perceptual transitions: a simultaneous EEG and fMRI study. *International Journal of Psychophysiology*, 55:299–312.

[154] Müller, T. J., Federspiel, A., Fallgatter, A. J., & Strik, W. K. (1999). EEG signs of vigilance fluctuations preceding perceptual flips in multistable illusionary motion. *Neuroreport*, 10:3423–3427.

[155] Isoglu-Alkac, U., Basar-Eroglu, C., Ademoglu, A., Demiralp, T., Miener, M., & Stadler, M. (2000). Alpha activity decreases during the perception of Necker cube reversals: an application of wavelet transform. *Biological Cybernetics*, 82:313–320.

[156] Strüber, D. & Herrmann, C. S. (2002). MEG alpha activity decrease reflects destabilization of multistable percepts. *Cognitive Brain Research*, 14:370–382.

[157] Basar-Eroglu, C., Strüber, D., Kruse, P., Basar, E., & Stadler, M. (1996). Frontal gamma-band enhancement during multistable visual perception. *International Journal of Psychophysiology*, 24:113–125.

[158] Basar-Eroglu, C., Strüber, D., Schürmann, M., Stadler, M., & Basar, E. (1996). Gamma-band responses in the brain: a short review of psychophysiological correlates and functional significance. *International Journal of Psychophysiology*, 24:101–112.

[159] Tiitinen, H., Sinkkonen, J., Reinikainen, K., Alho, K., Lavikainen, J., & Naatanen, R. (1993). Selective attention enhances the auditory 40 Hz transient response in humans. *Nature*, 364:59–60.

[160] Tallon, C., Bertrand, O., Bouchet, P., & Pernier, J. (1995). Gamma-range activity evoked by coherent visual stimuli in humans. *European Journal of Neuroscience*, 7:1285–1291.

[161] Tallon-Baudry, C. & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences*, 3(4):151–162.

[162] Stein, A. v. & Sarnthein, J. (2000). EEG frequency and the size of cognitive neuronal assemblies. *Behavioral and Brain Sciences*, 23(3):413–414.

[163] Stein, A. v. & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology*, 38:301–313.

[164] Harmony, T., Fernandez, T., Silva, J., Bernal, J., Diaz-Comas, L., Reyes, A., Marosi, E., Rodriguez, M., & Rodriguez, M. (1996). EEG delta activity: an indicator of attention to internal processing during performance of mental tasks. *International Journal of Psychophysiology*, 24:161–171.

Curriculum Vitae

Name	Cordula Becker
Date of Birth	15.06.1976
Citizenship	German
Address	In der Rönnepöhle 27, D-39126 Magdeburg

2001 - 2005	Researcher (Wissenschaftlicher Mitarbeiter, DFG) General and Experimental Psychology (Prof. H. J. Müller) Ludwig-Maximilians-University München
2001 - 2005	PhD in Experimental Psychology *Subjective visual experiences of colour and form induced by temporally modulated light* Subsidiary subjects: Philosophy, Computer Science
2001 - 2004	PhD Scholarship awarded by the "German National Academic Foundation"(Studienstiftung des deutschen Volkes)
1998 - 1999	Maitrise de Psychologie Cognitive et Experimentale (M. Ps.) University Louis Pasteur, Strasbourg, France Thesis: *Effets d'une prise des benzodiazepines diazepam ou lorazepam sur une tache d'amorçage a 40 Hz (Effects of the benzodiazepines diazepam and lorazepam on a 40-Hz priming task)*
1998 - 1999	Scholarship awarded by the "German Academic Exchange Service"(Deutscher Akademischer Austauschdienst, DAAD)
2000 - 2001	Scholarship awarded by the "German National Academic Foundation"(Studienstiftung des deutschen Volkes)
1997 - 2001	Research Assistant (Studentische Hilfskraft) General and Experimental Psychology (Prof. H. J. Müller) University Leipzig
1995 - 2001	Diploma in Psychology (Dipl. Psych.), Grade: 1.1 University Leipzig, Germany Diploma thesis: *Reading as a binding process: Evidence for impaired integration-segmentation processes and effects of oscillatory synchrony on stimulus coding in dyslexics*
1995	Abitur (A levels), Grade: 1.0 Johannes-Kepler-Gymnasium, Magdeburg, Germany

Publications

Becker, C., & Elliott, M.A. (In press). Flicker induced colours and shapes: Interdependencies and relation to stimulation frequency and phase. *Consciousness & Cognition*

Becker, C., Lachmann, T., & Elliott, M.A. (2005). Evidence for impaired visuo-perceptual organization in developmental dyslexics and its relation to temporal processes. *Cognitive Neuropsychology.*, 22 (5), 499-522.

Conci, M., Elliott, M. A., Müller, H. J., Wendt, J., & Becker, C. (2004). The dynamics of operations in visual memory: A review and new evidence for oscillatory priming. *Experimental Psychology*, 51 (4), 300-310.

Elliott, M. A., Becker, C., Boucart, M., & Müller, H. J. (2000). Enhanced GABAA inhibition enhances synchrony coding in human perception. *Neuroreport*, 11 (15), 3403-3407.