

City Research Online

City, University of London Institutional Repository

Citation: Allefeld, C. ORCID: 0000-0002-1037-2735, Puetz, P., Kastner, K. and Wackermann, J. (2011). Flicker-light induced visual phenomena: Frequency dependence and specificity of whole percepts and percept features. Consciousness and Cognition, 20(4), pp. 1344-1362. doi: 10.1016/j.concog.2010.10.026

This is the accepted version of the paper.

This version of the publication may differ from the final published version.

Permanent repository link: http://openaccess.city.ac.uk/id/eprint/23080/

Link to published version: http://dx.doi.org/10.1016/j.concog.2010.10.026

Copyright and reuse: City Research Online aims to make research outputs of City, University of London available to a wider audience. Copyright and Moral Rights remain with the author(s) and/or copyright holders. URLs from City Research Online may be freely distributed and linked to.

City Research Online:	http://openaccess.city.ac.uk/	publications@city.ac.uk

Flicker-light induced visual percepts: Frequency dependence and specificity of whole percepts and percept features

Carsten Allefeld*, Peter Pütz, Kristina Kastner, Jiří Wackermann

Department of Empirical and Analytical Psychophysics, Institute for Frontier Areas of Psychology and Mental Health, Wilhelmstraße 3a, 79098 Freiburg, Germany

preprint, accepted for publication in *Consciousness and Cognition* doi:10.1016/j.concog.2010.10.026

Abstract

Homogeneous flickering light induces color and form hallucinations in human observers. Despite a long scientific history of the phenomenon, still little is known about the dependence of flicker-light induced impressions on the flicker frequency. We investigate this question using Ganzfeld (whole-field) stimulation and an experimental paradigm that combines a continuous frequency scan over the range 1–50 Hz with a focus on re-occurring, whole percepts. On the single-subject level, we find a high degree of frequency stability of re-occurring individual percepts across experimental passes. To generalize findings across subjects, we apply two rating systems, (1) a set of complex percept classes derived from subjects' verbal reports and sketches, and (2) a systematic enumeration of elementary percept features, and determine the distribution of percept occurrences over flicker frequency for each of the percept categories. For many categories, we find distributions that significantly deviate from a reference distribution. We observe a stronger frequency specificity for complex percept classes than elementary percept features, which points to a possible involvement of higher visual cortical areas in their generation. Comparing the similarity relations among percept categories to those among associated frequency profiles, we observe that though particular percepts are preferentially induced by particular frequencies, the flicker frequency does not unambiguously determine the induced percept. This ambiguity suggests that the underlying neurophysiological dynamical process exhibits multistability.

Key words: flicker light, Ganzfeld, visual hallucinations, frequency dependence, frequency specificity, phenomenology

1. Introduction

Stimulation with spatially uniform, colorless, flickering light induces in human observers hallucinatory perceptions of form and color. This phenomenon, which is known since the early 19th century, has been investigated by a number of researchers. However, until today relatively little is known about the relation between the subjective percepts and the most important property of the stimulation: the flicker frequency.

This relation was studied in detail only recently by Becker and Elliott (2006), who determined the frequency profiles associated with a set of elementary visual features. The present paper continues that line of investigation and expands on their work in the following way: we introduce a stimulation technique aimed at eliciting a strong and reliable response to the flicker light; we use an experimental paradigm focusing on re-occurring visual percepts; and we apply methods of data analysis tailored to assess the stability and specificity of the observed frequency dependence of flicker-induced phenomena.

The following section gives an overview of the history of investigations of flicker-induced and related phenomena. The aims and the design of our contribution are described in detail in Sec. 3 and the experimental protocol and data analysis procedures in Sec. 4. Following a report of our results in Sec. 5, their implications with respect to the underlying neural processes and the relation to previous findings are discussed in Sec. 6.

2. Flicker-induced and related phenomena

2.1. Observations

The first scientific report on flicker-light induced patterns was given by Purkinje (1819, Sec. I), in his study of various visual phenomena occurring under different

^{*}Corresponding author. Current affiliation: Bernstein Center for Computational Neuroscience and Charité, Berlin, Germany

Émail address: carsten.allefeld@bccn-berlin.de (Carsten Allefeld)

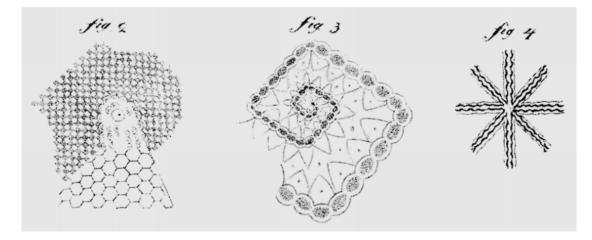


Figure 1: Sketches of flicker-light induced percepts drawn by Purkinje (1819, detail of figure plate), depicting "primary" patterns (left) and two instances of "secondary" patterns, "snail-rectangle" (center) and "eight-beam" (right).

conditions of non-physiological stimulation of the eyes. His stimulation technique was extremely simple: waving the spread fingers of his hand in front of his closed eyes with his face directed toward the sun. Under these conditions, Purkinje observed various patterns, among which he distinguished smaller, "primary" patterns from larger, "secondary" patterns, where the latter consist of an arrangement of the former (Fig. 1). Primary patterns are mainly rectangles in a raster or checkerboard arrangement, but may also include honeycomb patterns, semi-circles and plant-like structures; of secondary patterns Purkinje described two predominant ones which he called "snail-rectangle" (Schneckenrechteck) and "eightbeam" (Achtstrahl). About twenty years later, Fechner (1838) described subjective impressions of color as well as patterns observed on a spinning disk with alternating black and white segments. Both Purkinje's and Fechner's observations were briefly commented on in Helmholtz' monograph on physiological optics (1867, §23).

Although flicker stimulation was used in neurophysiology to study higher integrative functions of the brain (Sherrington, 1906), little attention was given to the subjective phenomena induced by flicker light. Their systematic study commenced with the work of Brown and Gebhard (1948). Using monocular stimulation, they reported for the "bright phase", corresponding to impressions obtained from the stimulated eye, the appearance of patterns described as "windmill vanes", "checkerboard", and "hexagons", but asserted that the patterns are much less stable than stated by Purkinje, and the general impression is rather kaleidoscopic.

The most extensive studies of flicker-light induced patterns to date are due to Smythies (1957, 1959a,b, 1960). In the second part of his series on the "stroboscopic patterns", Smythies examined the phenomena in the "bright phase" and gave detailed accounts of their numbers of occurrence under different conditions, summarized descriptions given by different subjects, provided illustrations of some of the patterns, and sorted them into seven groups:

"Class 1. Unformed elements such as odd blobs, spodges, dots, streaks, mottles. Class 2. Single lines, usually diagonals, may cross the field: there may be rainbow lines. Class 3. Patterns based on parallel straight lines. Class 4. Patterns based on radial arrangement of straight lines. Class 5. Patterns based on straight lines not simply parallel such as a honeycomb, herring-bone, maze, or zig-zags. Class 6. Patterns based on curved lines. Class 7. Designs and formed images." (Smythies, 1959b, p. 313)

Welpe examined in a series of studies in great detail phenomena induced by very specific forms of flickerlight stimulation; for instance (Welpe, 1970) the effects of pulse-shaped flicker at and above 33 Hz restricted to a circular part of the visual field of 23° diameter in a single subject.

As noted by several authors (Purkinje, 1819; Smythies, 1960; Freedman and Marks, 1965; Klüver, 1966), the visual hallucinations elicited by flicker light are similar to those induced by periodic electrical stimulation of the eyes, by hallucinogenic drugs, or those occurring in psycho- and neuropathological states, the hypnagogic state, and under sensory deprivation. For the case of mescaline, Klüver in his seminal book (1966, collecting publications of 1928 and 1942) described extensively its psychological effects including visual hallucinations. He came to the conclusion that the vast variety of mescalinduced impressions can be seen as variations, combinations, reduplications and elaborations of a limited number of basic forms which Klüver called "form constants":

"(a) grating, lattice, fretwork, filigree, honeycomb, or chessboard; (b) cobweb; (c) tunnel, funnel, alley, cone, or vessel; (d) spiral" (p. 66).

Similar hallucinations occur in epileptic visual auras, e.g. impressions of "flickering light", geometric forms such as "silver-white stars" or a "blinking square", and forms may be "partly coloured" and "stationary or moving" (Bien et al., 2000). Some of these hallucinations can also be elicited by electrical stimulation of the epileptogenic and adjacent cortical areas. Another group of related phenomena is constituted by hallucinatory percepts in migraine auras, namely scintillating and migrating scotomas and "fortification spectra", patterns characterized by pronounced zig-zag structures (Schott, 2007); a link between these phenomena and mescal-induced visual hallucinations was suggested by Lashley (1941). Spontaneous structuring and patterning of the visual field is also observed in the static Ganzfeld (non-flickering homogeneous visual field), in an initial phase before occurrence of more vivid hallucinatory percepts (Wackermann et al., 2008).

Concerning the effects commonly referred to as Fechner–Benham colors, there seems to be an ambiguity as to whether they are induced solely by rhythmic changes in light intensity (i.e. flicker, cf. Herrmann and Elliott, 2001) or include the action of contrast contours in the visual field. While Fechner (1838) observed subjective colors using a rotating disk with black and white radial segments only, Benham's top (Anonymous, 1894, p. 113 f.) additionally features thin circular lines and the color effect depends on the orientation of these contrast edges. For more information on the latter phenomenon, more precisely called "pattern-induced flicker colors", see von Campenhausen and Schramme (1995).

Flicker-induced phenomena have been examined with respect to their correlation with personality traits. Freedman and Marks (1965) posited that the quantity of imagery experienced by a subject is correlated with certain personality factors which they summarized as a tendency toward suspension of the "generalized reality orientation" of a normal awake person, one of the included factors being an "artistic and imaginative self-concept". This observation is in line with the popularity of flickerlight stimulation in art and literary circles during the 1960s and 70s (cf. Geiger, 2003), used as a supplement or substitute for hallucinogenic drugs, especially LSD.

The effect of intermittent photic stimulation on the human electroencephalogram (EEG) was first studied by Adrian and Matthews (1934) during their examination of the alpha rhythm, which had just recently been discovered by Berger (1929). Later Walter (1950), who thought of the alpha rhythm as representing a scanning mechanism in the human visual system analogous to the one employed in television cameras, interpreted the stroboscopic patterns as resulting from an interference between that scanning process and the oscillatory stimulation—a theory unsupported by observations. Nowadays the EEG response to flicker stimulation, called "photic driving response" or "steady-state visual evoked potential", is routinely used for diagnostic purposes in neurology (cf. Regan, 1989). Herrmann (2001) seems to have re-discovered the color- and form-inducing property of flicker light when he systematically studied the photic driving response over the 1–100 Hz range. The electrophysiological correlates of flicker-induced subjective color were examined by Becker et al. (2009). ffytche (2008) measured EEG and blood oxygenation level dependent signal during visual hallucinations induced by flicker light and found activation in higher visual cortical areas as well as decreased connectivity between lateral geniculate nucleus and cortex.

2.2. Explanatory approaches and mathematical modeling

The most simple explanation for flicker-induced phenomena would be that they are of entoptic origin, i.e. that under the special conditions of flicker stimulation normally invisible structures of the visual system become visible. However, as Smythies (1960) pointed out, many flicker-induced patterns are too regular to reflect biological structures, and also observed rotation and other movements can not be explained this way.

In contrast, already Purkinje (1819) interpreted his findings as an effect of the "synthesizing activity of the sense" (*synthesirenden Thätigkeit des Sinnes*) which depends on previous experience of the subject as well as perceptual preferences spontaneously formed during the exposure to flicker light. In a similar vein, Brown and Gebhard (1948) postulated central physiological "biases" towards certain visual configurations, which are normally overridden by the articulation of the stimulus itself, but become effective under a homogeneous flicker stimulation. Smythies (1960) discussed the idea that flickerinduced patterns are the result of pattern-detecting mechanisms trying to cope with an irregular stimulus, or that they reflect the induction of standing wave patterns within the visual cortex by the oscillatory stimulus.

The two latter ideas are effectively combined in contemporary mathematical modeling approaches to simple visual hallucinations. Ermentrout and Cowan (1979) were the first to give a theoretical explanation for the occurrence of basic patterns of hallucinations in terms of a dynamical model of processes in primary visual cortex. The authors started from the observation that, under the action of the retino-cortical map, Klüver's "form constants" in visual space correspond to regular wave patterns of excitation within the cortex, and modeled the cortical area by a two-layer neural network. They examined its dynamics for parameter values at which the homogeneous ground state becomes unstable, and were able to demonstrate the existence of several types of spatially periodic solutions which correspond to the cortical patterns underlying the typical form constants: the global forms of funnel (radial pattern), tunnel (concentric pattern) and spiral, and the localized occurrence of hexagonal and square lattices.

Independently of this work, Stwertka (1993) proposed the similar idea to interpret the stroboscopic patterns as corresponding to dynamical patterns of excitation in the visual cortex driven by photic stimulation, in analogy to the spontaneous pattern formation occurring in certain dissipative physical systems (e.g. Bénard convection), however without constructing an explicit model.

Tass (1995) modified the model of Ermentrout and Cowan to reflect the conditions of hallucinatory pattern formation in the case of epilepsy. He derived different dynamical regimes leading to different types of stationary hallucinatory patterns, namely radial patterns, concentric circles, spirals, and cobweb-like structures. Tass (1997) extended the analysis to include oscillatory modes, giving rise to rotating spirals and stars, growing or shrinking sets of concentric circles, and blinking spirals, circles, or stars. Along similar lines, Dahlem et al. (2000) proposed a model for visual phenomena observed in migraine auras.

Bressloff et al. (2001, 2002) extended the model of Ermentrout and Cowan by taking into account the orientation tuning of neurons in the primary visual cortex and the anisotropy of their coupling. Utilizing the symmetries of the structure of V1, they derived possible excitation modes of this system, again corresponding to Klüver's "form constants". They concluded that the tendency towards hallucinatory pattern formation of the visual system is due to its pattern-detecting activity under normal stimulation conditions, thus substantiating the ideas of early researchers.

Though the case of hallucinatory percepts induced by flicker-light stimulation has not been explicitly theoretically treated up to now, the similarity of hallucinatory percepts across a wide range of different conditions suggests that there is a common mechanism at work (cf. Ermentrout and Cowan, 1979): A disturbance of the nervous system leads to a de-stabilization of the homogeneous ground state of primary visual cortical areas, activating dynamical states consisting of wave patterns of excitation that correspond to simple visual hallucinations. The destabilizing influence that induces this dynamical regime may be an increased excitability due to drugs or an exogenous excitation by a flicker-light stimulus; or in the case of epileptic auras one may hypothesize that it is the endogenous activity of epileptogenic cortical areas that takes on the role of an "external" stimulation of visual areas.

2.3. Frequency dependence

Since the basic physical characteristic of a flicker-light stimulus is its frequency, the question of a possible relation between the flicker frequency and flicker-induced visual phenomena naturally arises. Surprisingly, this problem has been relatively little investigated; most researchers used only one or a few single stimulus frequencies. For instance, Smythies (1959b) used 6 Hz-, 12 Hz-, and 18 Hz-flicker and reported merely that for higher frequencies patterns tend to become finer and composed of smaller elements. Knoll and Kugler (1959) reported on frequency dependence, but for patterns elicited by periodic electrical stimulation of the eye. They found that the occurrence of particular patterns in individual subjects was mainly limited to a bandwidth of less than 10% of the mean frequency, and that most patterns occurred in the range from 5 to 35 Hz.

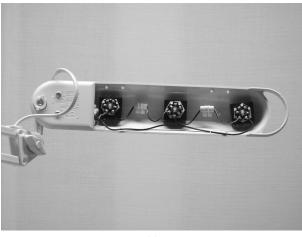
A continuous range of flicker-light frequencies from 2 to 50 Hz was used by Young et al. (1975) to investigate the visibility conditions, in terms of illuminance and flicker frequency, of two particular patterns which served as examples of the most fine-grained and coarse-grained forms occurring. For the first, a foveal honeycomb pattern consisting of small dots, they found that visibility is optimal around 20 Hz; while for the second, a square grid pattern, the optimal frequency lay around 9 Hz. Herrmann and Elliott (2001) investigated color and form illusions induced by flicker-light stimulation in the range from 1 to 40 Hz and reported that color occurs mainly around 12 Hz while subjective form is induced over the whole range of frequencies.

Becker and Elliott (2006) examined the frequency dependence of several categories of flicker-induced subjective colors and forms over the range of 1 to 60 Hz. Subjects were stimulated with each frequency in this range in 1 Hz-steps using 30 s-epochs of constant-frequency flicker in a randomized order. Freely verbalized reports of the subjects were recorded and later rated using a predefined set of elementary form properties and colors (adopted from Eichmeier and Höfer, 1974). The authors determined the ranges of flicker frequencies associated with the predefined categories as well as patterns of co-occurrence, obtaining for most of them unimodal but relatively broad distributions over the frequency scale. The frequency dependence of flicker-induced colors and forms observed by Becker and Elliott did not follow any apparent systematic pattern.

3. Aims and design

The aim of the present study was to investigate systematically the relation between flicker-light induced color and form, and the flicker frequency, employing the whole continuum of frequencies up to the flicker-fusion threshold. To assess the reliability of assignment of visual phenomena to flicker frequencies, we asked our subjects to search for characteristic and recognizable perceptual configurations—in the following called "percepts" standing out from the stream of ever-changing visual experience induced by the flicker stimulation.

In contrast to the approach taken by Becker and Elliott (2006), we primarily focused on the complex, holistic quality of the percepts as described by the observers, while their elementary features were of secondary interest. Our strategy was to give the subjects a maximum of freedom to decide what constitutes an identifiable, recognizable, and reportable percept, and also leave it to the



(a)

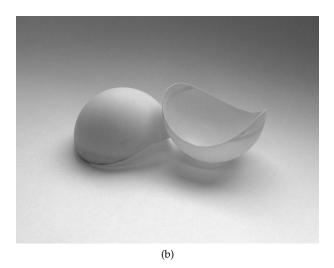


Figure 2: (a) The stimulation device, three high-power LEDs fixed to heat sinks mounted in a desk lamp housing. (b) Goggles made from ping-pong balls.

subject's discretion whether a percept occurring at a certain time during the experiment is "the same" as one observed and reported earlier. A primary rating system was developed based on this material of reliably identified, re-occurring percepts as revealed by the subjects's verbal reports and sketches. For the purpose of comparison, we additionally used a secondary rating system based on a systematic enumeration of possible percept properties rather than the inspection of the experimental material.

Another specific feature in our experimental design resulted from an observation made in pilot experiments, namely that the effect of flicker light depends not only on the current flicker frequency, but also on the "perceptual history", the sequence of flicker frequencies presented in the immediate past. To control for this factor, we decided to present different flicker frequencies always in the same order, in continuous scans over the chosen frequency range, in several repetitions, always starting from the lowest included frequency.

Thirdly, we explicitly addressed the question whether particular (categories of) percepts are specifically induced by particular flicker frequencies. Correspondingly, the guiding questions in our evaluation of the frequency data were:

— Does the same percept occur at similar flicker frequencies in different frequency scans of an individual subject? After identifying groups of similar percepts in different subjects:

— Do percepts of a particular category occur at similar frequencies in different subjects? And:

— Does the frequency profile for a percept category deviate from the general distribution of percept occurrences over flicker frequency?

4. Materials and methods

4.1. Apparatus and stimuli

In our experiment, subjects were exposed to a spatially uniform, colorless, flickering luminous field (Ganzfeld). The light source was a triplet of white highpower light-emitting diodes (LEDs), driven via an amplifier from the onboard audio system of a laboratory computer. The LEDs were mounted within a spring-balanced desk lamp for easy adjustment of the distance to the subject's eyes, which were covered by goggles made from anatomically shaped halves of ping-pong balls to achieve Ganzfeld illumination (Fig. 2). The lamp distance was individually adjusted to the maximum brightness still comfortable for the subject, resulting in distances from 38 to 53 cm. At the median distance of 50 cm, the timeaveraged illuminance of the flicker light under the goggles amounted to 10.5 lx. For further details of the apparatus, see App. A.

An experimental pass consisted of a continuous frequency scan at a speed of $0.1 \,\text{Hz/s}$, starting from a flicker frequency of $1 \,\text{Hz}$ up to a maximum of 50 Hz. If the subject did not give any more reports at high frequencies, the pass was stopped by the experimenter before the upper limit was reached. The subject was first familiarized with the effects of flicker-light stimulation in a warm-up pass, during which she was also asked to identify the flicker onset and flicker fusion frequencies.

Following the warm-up pass, four experimental passes were performed (in some cases extended to five or six, because there were only few reports). For these frequency scans, the subject was asked to look out for moments of relative stability and distinctness (*Prägnanz*), when a percept occurred that could be verbally characterized and recognized as "the same" when occurring again later; and also for such re-occurrences. The subject was instructed to signal these (re-)occurrences with a button

lines one or more lines or thin stripes, possibly moving around; straight or curved; solid, 48	(a)
dotted, dashed, or zigzag	
ripples formations of concentric circles that grow moving outwards, starting from a few 42.5	(b)
centers or covering the whole field	
tunnel an impression of spatial depth, possibly with movement into or out of this depth 39	(c)
honeycomb regular arrangements of hexagons, circles or similar forms, possibly filling the 33	(d)
whole field, possibly with smaller elements towards the center	
wheel a round structure with radial lines, rotating 32.5	(e)
spot a dark spot on a light background or vice versa 30.5	(f)
clouds very little structure, only slow movements, and no or very weak colors 30	(g)
cross an upright or diagonal cross 25.5	(h)
sun a glowing or dark sphere with a rim of spikes or flames 17.5	(i)
organic structures like those of plants, or of tissue or microorganisms under the microscope 17	(j)
bowls half-spheres or bowls, half-circles 15	(k)
raster two sets of regularly arranged parallel lines, superimposed at an angle 14.5	(1)
bars single wide stripes crossing the field, or several wide stripes in alternating colors 14.5	(m)
cracks an irregular network of crack-, vein-, or root-like structures, filling the whole field 11	(n)
star five or more straight lines from a central point; possibly thick, possibly asymmetric 11	(0)
drain a movement from the left and right sides towards the center and downwards 9	(p)
spiral curved lines around a common center 9	(f)
line segments a multitude of short line segments, distributed all over the field –	_

Table 1: The primary rating system of complex percept classes. Classes were defined by short descriptions, which formed the basis for the rating process. The class 'line segments' was removed from the final rating because of too few assignments, while the class 'bars' was newly introduced. The third column gives the number of reports n_r assigned to a class, computed as the sum of the individual reports' weights w. The fourth column refers to the panel of Fig. 9 where an example sketch for a percept assigned to the class can be found.

press. This signaled to the control software to pause the frequency scan, to allow the experimenter to write down the frequency and the subject's description of the percept, as well as her judgement whether it was identical to one reported before. After that, the frequency scan was continued. The typical duration of one experimental pass including the time for recording the subject's reports was about 15 minutes.¹

After the last experimental pass, the experimenter went with the observer through the written record, recapitulating the descriptions of re-occurring percepts and clarifying details wherever necessary. The subject was also asked to illustrate the description by a drawing, for those percepts where this seemed to be adequately possible.

4.2. Participants

Twenty subjects participated in the experiment (14 female), from 18 to 50 years old (median 24.5 years). During the recruitment phase we explicitly addressed students of art and graphic design, to benefit from their ability to analyze and graphically represent their visual impressions.

Subjects participated voluntarily after written consent, being informed about the background, purpose and possible hazards associated with flicker-light stimulation, and they were given monetary compensation depending on the time spent. The experimental procedure, subject information and data handling were approved by the ethics committee of the German Psychological Society (DGPs).

4.3. Data analysis

The material for the analysis consisted of the reoccurring individual percepts that were present in more than one pass of a single subject. For each individual percept, there was a number of occurrences, each associated with a flicker frequency and a brief report. For some percepts, there was additionally a sketch drawn by the subject after the experimental passes.

The association between a percept and a flicker frequency was in some cases uncertain, either because the subject forgot to press the button and the frequency scan was paused by the experimenter only after a delay, or because the subject was not completely confident about the identification of the percept. This was taken into account in further analyses by assigning reports a weight w = 1

¹The necessity to pause the frequency scan limits the control of the perceptual history we aimed for, giving different experimental passes a different stimulation structure. However, percepts reported at a given frequency correspond to approximately the same stimulation history, at least regarding the immediate past.

group feature	label	n _r	group feature	label	$ $ n_r
topography, general*			<i>light</i> , distribution*		
amorphous	Ta	83.5	bright on dark	Lbd	66
filling	Tf	190.5	dark on bright	Ldb	96
centered	Tc	319	bright on bright	Lbb	40.5
<i>topography</i> , specifications			dark on dark	Ldd	-
horizontal	Th	82	<i>light</i> , quality		
vertical	Tv	86.5	flickering	Lf	68
circular	Tz	177.5	pulsating	Lp	136
spiral	Ts	13.5	color	1	
other closed	То	219.5	red	Cr	105
radial	Tr	76.5	orange	Co	90
diagonal	Td	46.5	yellow		161
motion			green	~	279.5
horizontal	Mh	40.5	cyan	-	30
vertical	Mv	102.5	blue	Cb	263
into / out of depth	Mz	66	purple	Ср	139.5
rotational	Mr	183	brown	_	43
centrifugal / -petal	Mc	116.5	black		130
dynamic	My	34.5	white		201
pulsating	М́р	67	gray	Cgr	165.5
diagonal	Md	42	0 7	0	I
chaotic	Ma	39			

Table 2: The secondary rating system of elementary percept features, organized into six feature groups around the four basic dimensions of topography, motion, light, and color. Features within one of the two groups marked with a star (*) are mutually exclusive, other feature specifications can be freely combined. The last column gives the number of reports rated as exhibiting the feature, computed as the sum of the individual reports' weights w.

if the association was certain and w = 0.5 if it was uncertain.

Frequency stability of individual percepts across experimental passes was quantified using the standard deviation s_f of the per-pass mean frequencies of all occurrences. The distribution of $s_f(f)$ under the hypothesis that there is no specific relation between the flicker frequencies of occurrences in different passes was estimated using a bootstrap approach. A bootstrap sample of four per-pass mean frequencies under this hypothesis was generated by randomly drawing, with replacement, from the set of all per-pass mean frequencies of all individual percepts. The overall mean frequency and standard deviation of per-pass mean frequencies were computed for 10⁷ bootstrap samples. The results were binned according to the mean frequency (1 Hz width), and the 0.05-quantile of s_f was determined for each frequency bin containing at least 100 replications.

To investigate the relation between percepts and flicker frequency across subjects, two rating systems were defined: (i) A set of complex percept classes resulting from a review and clustering of the collected report and sketch material (Tab. 1), representing the appearance of percepts in their entirety. (ii) A system of elementary percept features, based on an a priori enumeration along four dimensions: topology, motion, light characteristic, and color (Tab. 2).

For the primary rating system, which involves an interpretation of reports and class definitions, we separated among us the tasks of class definition and rating of individual percepts (two raters) and assessed the degree of inter-rater reliability using the proportion of overall agreement

$$p_0=\frac{n_0}{N},$$

where n_0 is the number of individual percepts for which both raters agreed whether the class applies or not, and N is the number of all individual percepts, as well as by Cohen's (1960) coefficient,

$$\kappa=\frac{p_0-p_e}{1-p_e},$$

where

$$p_e = \frac{n_+^{\rm A} n_+^{\rm B} + (N - n_+^{\rm A})(N - n_+^{\rm B})}{N^2}$$

is the value of p_0 expected by chance from the base rates; n_+^{A} and n_+^{B} are the numbers of individual percepts assigned to the class by each rater separately.

The density of the distribution of percept category occurrences over flicker frequency was estimated using a Gaussian kernel on a logarithmic frequency scale, ℓ = log *f*. That is, for associated flicker frequencies f_i of reports assigned to the percept category and weights w_i (*i* = 1...*n*), the density $p(\ell)$ was estimated according to

$$p(\ell) = \frac{1}{\sum w_i} \sum_{i=1}^n w_i \frac{1}{\sigma} \phi\left(\frac{\ell - \ell_i}{\sigma}\right)$$

where $\ell_i = \log f_i$ and ϕ is the probability density function of the standard normal distribution. The optimal kernel bandwidth σ was estimated for each of the complex percept classes using Botev's (2006) method, and the median of the resulting values was used for every density estimation in order to obtain results that can be meaningfully compared. The ℓ -scale was sampled at 201 equidistant points covering the range corresponding to f = 0.3...100 Hz, making the estimated density $p(\ell)$ a vector p with components p_{ℓ} .

A distribution density r_{ℓ} was estimated in the same way from the set of all reported frequencies to serve as a common reference. The percept category distributions were tested for a statistically significant deviation from the reference distribution by generating 1 000 replications via resampling from that set, using as the test statistic the measure of divergence of distributions introduced by Kullback and Leibler (1951),

$$D_{\mathrm{KL}}(\boldsymbol{p},\boldsymbol{r}) = \sum_{\ell} p_{\ell} \log \frac{p_{\ell}}{r_{\ell}}.$$

We defined a space of distributions by assigning to each density p a position vector $p' = (p'_{\ell})$ with

$$p'_\ell = rac{p_\ell - r_\ell}{\sqrt{2r_\ell}}.$$

In this space the origin represents the reference distribution and squared Euclidean distances approximate the Kullback–Leibler divergence (see App. B). For a comprehensive visual representation of the (dis-)similarity relations between distributions of different percept categories, the space was reduced to two dimensions using principal component analysis of the cloud of data points.

5. Results

Subjects made between 15 and 67 reports (median 37), 828 over all subjects. Of these, from 6 to 48 reports per subject (median 30.5) were associated with a percept occurring in more than one experimental pass, overall 585 (70.7%). From 0 to 16 of these associations were uncertain (median 4), overall 92. The number of different percepts occurring in more than one pass ranged from from 2 to 19 per subject (median 8), 168 over all subjects. These percepts form the basis of the following analysis.

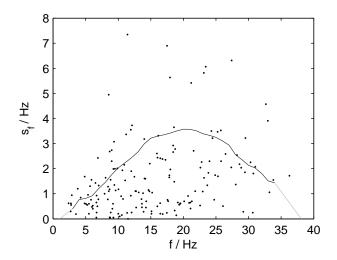


Figure 4: Stability of per-pass mean frequencies of the occurrence of individual percepts. The plot shows the standard deviation of per-pass mean frequencies s_f versus the overall mean frequency f for each of the 168 individual percepts (dots). The black line indicates the 0.05-quantile of $s_f(f)$ under the null hypothesis, i.e. no specific relation between percept occurrences and flicker frequency. Gray lines extrapolate this estimated curve by connecting to $s_f = 0$ at the points of minimum and maximum perpass mean frequency.

5.1. Frequency stability of individual percepts

Figure 3 gives an overview of the flicker frequencies and experimental passes at which the occurrence of a percept was reported, for all 20 subjects. While there are percepts occurring over a larger range of frequencies, it is apparent that many percepts are reported at almost exactly the same flicker frequency over several subsequent experimental passes, in some cases with a precision better than 1 Hz. Even with larger deviations, often at least the order of occurrence of different percepts over the frequency axis is preserved. On the other hand, there is a large intersubject variability of the number of reports and percepts as well as concerning the borders of the frequency range where the stimulation was experienced as flicker.

The visual impression of a high degree of frequency stability over passes is substantiated by the statistical analysis summarized in Fig. 4, comparing the standard deviation s_f of the per-pass mean frequencies of individual percepts to the 0.05-quantile to be expected under the hypothesis of no specific relation between the flicker frequencies of occurrences in different passes. For 122 out of 168 percepts (72.6 %), s_f lies below this quantile, i.e. the report frequencies of individual percepts are much more stable across passes than to be expected by chance.

5.2. Complex percept classes

In a second step, the descriptions and sketches made by the subjects associated with their individual percepts

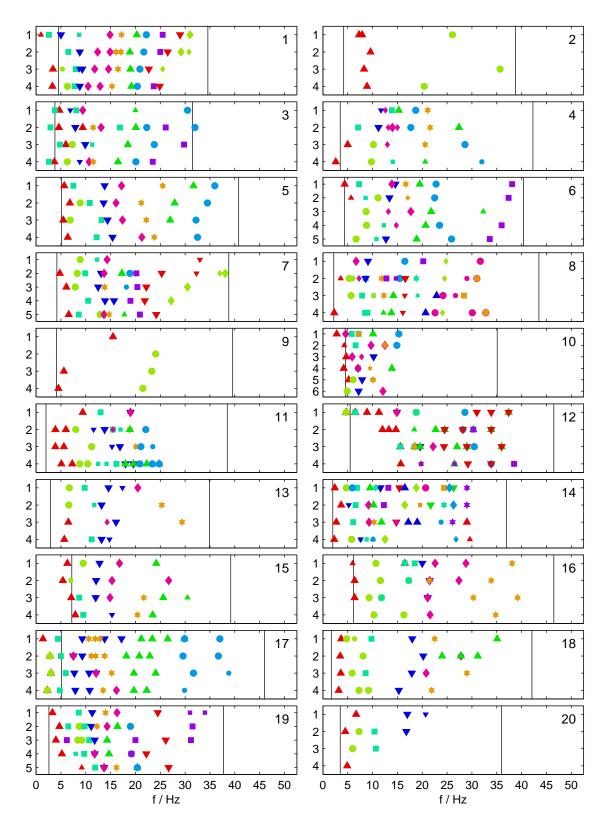


Figure 3: Occurrences of individual percepts. Each plot shows the data for one of the subjects (its number given in the upper right corner). The horizontal scale gives the frequency at which the occurrence of a percept was reported, the vertical scale the number of the experimental pass. Within each plot, one type of symbol (form & color) marks occurrences of the same percept at different frequencies and/or passes. Note that the same symbol in plots for different subjects indicates different individual percepts. Smaller symbols denote uncertain assignments. Vertical black lines mark the flicker onset and flicker fusion frequencies.

class	n_0	p_0	n_{+}^{A}	n^B_+	n_+	κ
lines	147	0.875	11	30	10	0.434
ripples	160	0.952	7	15	7	0.614
tunnel	159	0.946	5	14	5	0.505
honeycomb	153	0.911	6	19	5	0.366
wheel	164	0.976	8	12	8	0.788
spot	167	0.994	7	8	7	0.930
clouds	160	0.952	4	10	3	0.408
cross	167	0.994	7	8	7	0.930
sun	160	0.952	5	11	4	0.479
organic	162	0.964	4	8	3	0.484
bowls	164	0.976	4	8	4	0.656
raster	165	0.982	3	6	3	0.659
cracks	167	0.994	4	3	3	0.854
star	167	0.994	3	4	3	0.854
drain	165	0.982	3	6	3	0.659
spiral	164	0.976	3	7	3	0.590
line segments	167	0.994	1	2	1	0.664

Table 3: Inter-rater reliability data for complex percept classes. n_0 : Number of percepts for which both raters agreed whether the class applies or not. p_0 : Proportion of overall agreement, $p_0 = n_0/N$, where N = 168. n_+^A , n_+^B : Number of percepts assigned to this class by rater A or B, respectively. n_+ : Number of percepts assigned by both raters (positive agreement). κ : Cohen's coefficient.

were analyzed. The material was searched for characteristic patterns and motifs occurring in more than one subject, in order to define inter-subjectively valid classes of percepts and to investigate whether there are frequency ranges specific to each of them.

Based on the subjects' reports and sketches, a set of percept classes was defined by one of us using brief descriptions (Tab. 1), each identified by a short label: 'ripples', 'tunnel', 'sun', 'raster', 'honeycomb', 'cracks', 'drain', 'organic', 'bowls', 'lines', 'line segments', 'clouds', 'spot', 'cross', 'star', 'spiral', and 'wheel'. The individual percepts of all subjects were then rated whether they belonged to one or more of these classes by two of us independently.

Of the 168 individual percepts, 80 (47.6 %) received the exact same rating from both raters. More detailed data characterizing the inter-rater reliability are given in Tab. 3. On a per-class basis, the proportion of overall agreement between the two raters lies between 87.5 and 99.4 % (column p_0). Even though the assessment via the coefficient κ introduced by Cohen (1960) indicates only moderate levels of rating reliability for several of the classes, an examination of the numbers of percepts assigned to the classes by the two raters separately and by both of them (columns n_+^A , n_+^B , and n_+) reveals that the difference between the two raters mainly consists in a different willingness to assign a percept to a class at all, but does not concern the question which class to assign to: Almost ev-

ery assignment made by rater A is confirmed by rater B.

To establish a unified basis for further evaluation, cases of disagreement were discussed by the two raters and a consensus rating agreed upon. In this process, the necessity to introduce a new percept class 'bars' in distinction from 'lines' arose. On the other hand, the class 'line segments' had to be dropped since there were too few percepts assigned to it to allow for a statistical evaluation.

From the sketches made by the subjects, a representative subset was selected to serve as illustrations of the final set of percept classes; they are shown in Fig. 9 and briefly commented on in App. C. The numbers of reports assigned to each of the percept classes are given in Tab. 1, along with references to the respective panels of Fig. 9.

We determined the frequency ranges over which percepts of a given class preferentially occurred in the form of a distribution density, using a logarithmic frequency scale since reports occurred more closely to each other at lower frequencies. For comparison, a reference distribution density was estimated from the set of all reported frequencies.

The results are shown in Fig. 5. For most percept classes, the estimated density exhibits a clearly defined maximum, a result that is supported by the scatter plots of report frequencies. This indicates that the definition of complex percept classes did not pick up arbitrary similarities between different subjects' reports, but is related to characteristics of the underlying neurophysiological process. The frequency profiles become less clear and pronounced for percept classes for which there are only few reports.

5.3. Elementary percept features

In order to assess whether the relation between the flicker frequency and the particular percept induced by the flicker light is specifically captured by the set of percept classes derived from the reports, or ultimately rests on more primitive features, we applied a second set of percept categories aiming to systematically cover the space of elementary percept features. This secondary rating system was organized along the four basic dimensions of topography (overall structure of the percept), motion occurring within it, the distribution of light between figure and ground and the light quality, and the colors involved. The complete set of features is laid out in Tab. 2, along with the numbers of reports assigned to each of the categories.

The results of the distribution density estimation for these categories are shown in Fig. 6. The light distribution category 'Ldd' had to be excluded from this analysis because there were too few reports.

5.4. Frequency specificity of percept categories

Visual inspection of the distribution densities of occurrences over flicker frequency (Figs. 5 & 6), especially

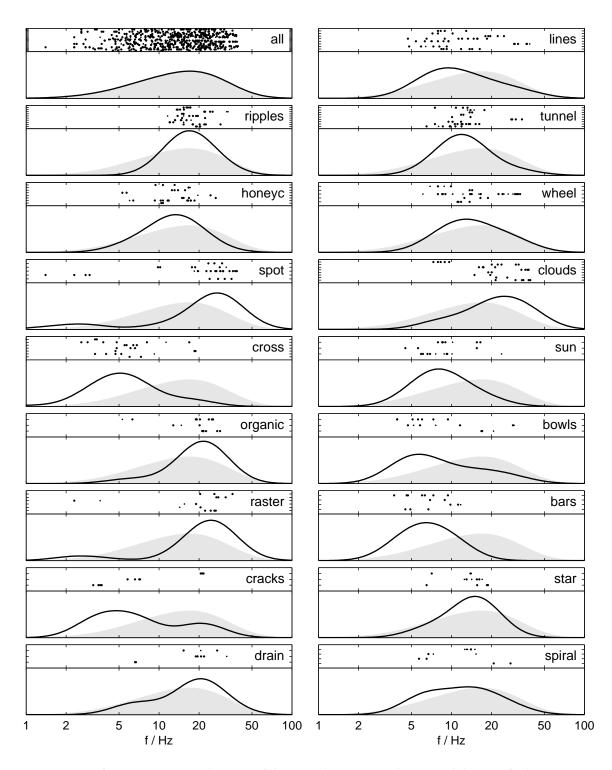


Figure 5: Occurrences of percepts assigned to one of the complex percept classes and the set of all re-occurring percepts ('all'). Within each plot the result for one of the classes is displayed, on a logarithmic frequency scale. The upper panels display the flicker frequencies of all reports associated with a class, where contributions from different subjects are separated by different positions along the vertical axis. The lower panels show the density of percept occurrences over log *f*, estimated using a Gaussian kernel (bandwidth $\sigma = 0.403$). The reference density estimated from the set of all reported frequencies is shown for comparison as a gray background shape in each of the plots.

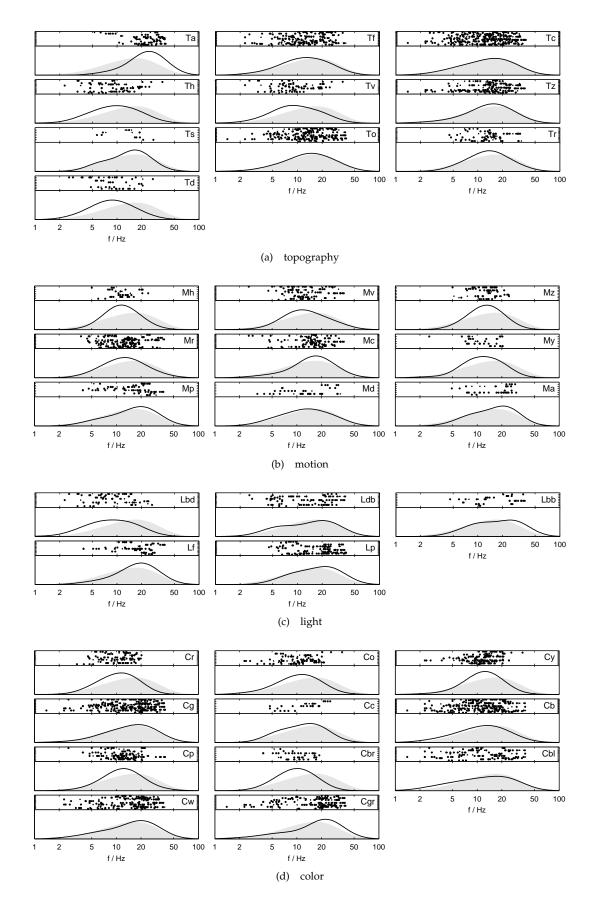


Figure 6: Occurrences of percepts assigned to one of the categories defined by elementary percept features. Upper panels: flicker frequencies of reports, lower panels: estimated density, background: reference density; cf. Fig. 5. See Tab. 2 for an explanation of the category labels.

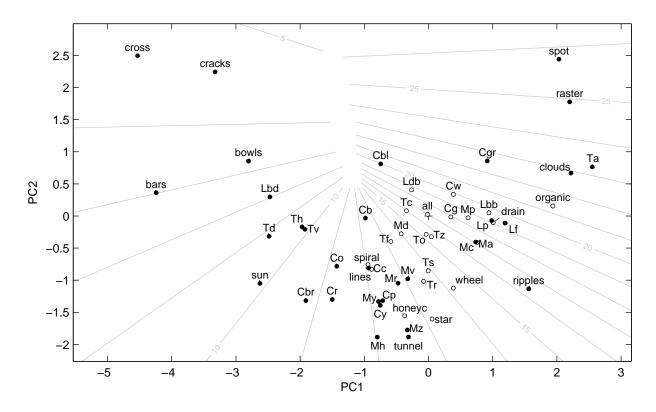


Figure 7: The space of distributions of percept occurrences over frequency, visualized using the first two principal components of the point cloud. The origin (+) represents the reference distribution, squared distances approximate the Kullback–Leibler divergence of distributions. Closed markers (•) indicate those categories for which the divergence from the reference distribution is significantly different from zero at a level of $\alpha = 0.01$. Gray contour lines refer to the location of the maximum (f/Hz) of a distribution reconstructed from the first two principal components. The area where contour lines converge (extending from the center upwards) represents densities with two equally pronounced peaks.

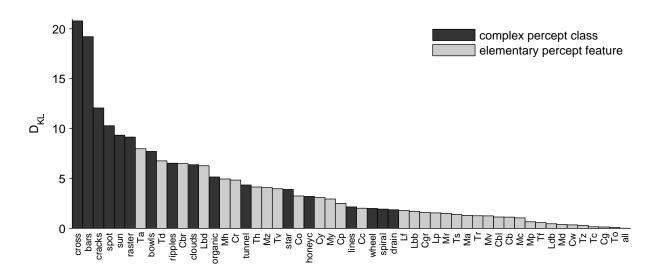


Figure 8: Kullback–Leibler divergence of percept categories' distributions from the reference distribution, sorted in descending order. Categories of the primary rating system (dark gray) tend to exhibit larger divergences than those of the secondary rating system (light gray).

those belonging to elementary percept features, reveals that some of them deviate only weakly from the reference distribution of all reports of re-occurring percepts, and others are very similar among each other. Though these distribution densities exhibit a clearly defined peak which shows that there is a preferred flicker frequency to evoke percepts of the respective category, this frequency preference is not category-specific.

To obtain an overview over the similarity relations between distribution densities, we assigned to them positions within an abstract space whose structure approximately reflects their dissimilarities as measured using the Kullback–Leibler divergence, and which is centered onto the reference distribution. This space is displayed in Fig. 7 using the first two principal components of the data cloud (accounting for 92% of the total variance), combined with information on the approximate location of the peak of distribution densities and on the statistical significance of a distribution's deviation from the reference. The distribution densities' locations disclose a tendency towards stronger deviations from the reference distribution for complex percept classes than for elementary percept features. This is confirmed by the ranking of Kullback–Leibler divergences of categories' distributions from the reference distribution shown in Fig. 8.

In Fig. 7, groupings of distributions belonging to complex percept classes do not follow any apparent similarity relation between class definitions. The closeness of elementary percept categories 'Th', 'Tv', and 'Td' seems to reveal a region of stimulation frequencies inducing percepts characterized by strongly oriented structures regardless of orientation. The pairing of 'Lf' and 'Lp' might reflect the lack of a clear-cut distinction between these categories. In the group of motion categories a weak clustering around 12–14 Hz can be observed. For some of the complex percept classes whose definition features prominently one of the features included in the systematic rating system—'clouds' and 'Ta', 'wheel' and 'Tr', 'tunnel' and 'Mz'—a similarity of frequency profiles results.

6. Discussion

The experimental strategy of the present study was to focus on re-occurring percepts and on classes of percepts characterized by particular combinations of properties. This approach enabled us to observe a high degree of frequency stability for individual percepts and a pronounced profile of the distribution over flicker frequency for many of the percept classes. This result is further confirmed by the observation that frequency profiles resulting from an alternative rating of percepts using a predefined systematic scheme of elementary features tend to be less pronounced.

The space of frequency distributions associated with percept categories (Fig. 7) reveals that related classes do not necessarily exhibit a similar frequency preference (for example the pairs 'cross'-'star', 'star'-'sun', 'sun'-'wheel'; or the sequence of chromatic colors). Also, the observed similarities between frequency profiles of different complex percept classes have no apparent interpretation in terms of percept similarity (e.g. 'cross'-'cracks', 'spot'-'raster', 'spiral'-'lines'), which shows that even though particular percepts occur preferentially at certain flicker frequencies, the latter does not unambiguously determine the percept. Rather, a particular flicker frequency seems to induce a dynamical regime that allows for relative stability of several different modes (multistability), leading to different possible but not co-occurring percepts. This interpretation may also account for the dependency on the stimulation history (hysteresis) we observed in pilot experiments.

Unlike Becker and Elliott (2006), we did not explicitly investigate patterns of co-occurrence of different visual features, since our experimental paradigm and analysis strategy focused on whole percepts. However, our observation that a large proportion of these individual percepts can be assigned to a small number of complex percept classes implicitly reflects patterns of co-occurrence of more elementary features. Co-occurrences of complex percepts were rare; one exception is documented in Fig. 9f, where a subject sketched an impression belonging to both of the percept classes 'spot' and 'spiral'.

Our finding of a high degree of frequency stability of percepts is consistent with the observations of Knoll and Kugler (1959) for the case of hallucinations induced by intermittent electrical stimulation of the eyes. Smythies' (1959b) claim that higher frequencies generally lead to smaller structures of the induced percepts could not be confirmed by us.² Also, the frequencies for optimal visibility given by Young et al. (1975) for two particular percepts do not agree with our findings for the two percept classes most closely resembling their observations ('honeycomb' & 'raster'). Flicker-induced chromatic color occurred in our experiment preferentially over the frequency range of 11–18 Hz ('Co'–'Cg') and form over the range 5-26 Hz ('cross'-'spot'), a finding that is consistent with the observations of Herrmann and Elliott (2001). Specific peak flicker frequencies associated with colors found by us (Fig. 6d) do not agree with those appearing in the results of Becker and Elliott (2006).

It should be noted that the frequencies at which individual percepts occur in different experimental passes (Fig. 3) exhibit a very high degree of stability for some percepts in some of the subjects. Though it was possi-

²This might be due to stimulation with a continuously changing frequency instead of the large, abrupt frequency changes used by Smythies. Stated in terms of dynamical systems theory, stimulation using a slow frequency scan allows to observe a quasi-stationary response of the system, while abrupt changes induce transients; both stimulation methods may provide evidence regarding the underlying dynamical processes. Further research should examine explicitly the effects of different stimulation protocols, while still controlling not only the current flicker frequency, but also the stimulation history.

ble to define classes of percepts valid across subjects that retain a specific relation to the flicker frequency, still in this process of generalization part of an even stronger specificity on the level of individual subjects has been lost. This observation leads to the interesting question of how intra-individual regularities are related to commonalities across subjects ("idioversal" vs "universal laws"; cf. Wackermann, 2006). To address this question in further research, repeated experimental sessions and subjectcentered data analysis would be required.

Many of the percept classes that we derived from the report and sketch material are characterized by structural elements strongly reminiscent of the geometric patterns called "form constants" by Klüver (1966) and resulting from modeling of the dynamic processes in early visual cortical areas (Ermentrout and Cowan, 1979; Tass, 1995, 1997; Dahlem et al., 2000; Bressloff et al., 2001, 2002). However, as Klüver already pointed out, these forms provide only the building blocks of hallucinatory percepts, which are more complex themselves: Often several instances of a basic form are combined (see Fig. 9b and 9e), or the basic form provides a structural skeleton that is fleshed out by further interpretation (Fig. 9c). Occasionally even more vivid impressions arise; for example one of the subjects reported that she felt situated within a hallucinated scene.

None of these cases are covered by current modeling approaches restricted to processes in early visual cortical areas, but seem to involve interpretive top-down influences from higher visual regions (cf. Rao and Ballard, 1999). Apparently the processes of spontaneous pattern formation underlying flicker-induced percepts include not only those arising from the structure of e.g. contoursensitive visual areas (Bressloff et al., 2001), but involve processes of pattern detection on higher levels of abstraction, possibly including object recognition. This conjecture is supported by recent findings of hallucinationspecific activations in higher visual cortical areas in fMRI (ffytche, 2008). These higher-level effects may also account for the adequacy of distinct classes of complex percepts constituted by a characteristic combination of elementary features to represent a large part of the variety of flicker-induced percepts.

Moreover, none of the existing modeling approaches was formulated specifically for flicker-light induced visual hallucinations, so that there are no predictions concerning frequency dependence that might be validated or challenged by experimental studies. On the other hand, the detailed findings provided by Becker and Elliott (2006) as well as by the present study now provide rich material to serve as a basis for new modeling efforts on the part of theoretical neuroscience.

To our knowledge, the present study of flickerinduced hallucinations is the first one to combine a detailed investigation of frequency dependence with a focus on the phenomenal wholeness of induced percepts. The higher frequency specificity obtained in this manner indicates that our approach is a meaningful and promising way to link the phenomenology of hallucinatory subjective experience with brain function.

Acknowledgments

The authors would like to thank Mark Elliott for inspiring discussions, Andreas Fischer, Gerhard Mayer, and Karin Moos for participating in the experiment, and María Herrojo Ruiz, Ida Momennejad, and Martin Hebart, as well as two anonymous referees for helpful comments on drafts of the present paper.

Appendix

A. Apparatus

We used three high-power light-emitting diodes of type Philips Lumileds "Luxeon III Star" color "neutral white" (LXHL-LW3C, max. 1 A, \sim 3.4 V, 80 lm, Lambertian radiation pattern, correlated color temperature 8 000 K) in series, connected in parallel to a series of three general purpose rectifiers (CE 1N4007) with opposite polarity, and combined with a series resistor of 8 Ω for 10 W operation. The LEDs were fixed to heat sinks mounted into the housing of a desk lamp.

This circuit was driven using one channel of the speaker output of a Sony integrated stereo amplifier (TA-FE310R) connected to the onboard audio of a standard personal computer. The control program was implemented in C using the Allegro game programming library running under a GNU/Linux operating system. To avoid high-amplitude nonlinearities of the devices, the amplifier volume and onboard audio mixer settings were fixed at intermediate values. The output voltage of the amplifier was regulated via the digital signal amplitude generated by the control program, to a maximum of 16.5 V.

The sound card operated at a sampling frequency of 48 kHz and 16 bit resolution. Since the low-frequency rectangular signal needed for flicker-light stimulation would be severely distorted by the amplifier, we used a low-frequency rectangular modulation of a high-frequency carrier signal (using a waveform of 6 samples length, optimized for maximum mean luminous flux), i.e. the carrier was regularly switched on and off for an integer number *n* of subsequent elementary waveforms. Since the carrier frequency of 8 kHz is far beyond the flicker fusion frequency, the perceptual effect is identical to switching on and off a continually shining light source. In this way, flicker-light frequencies $f_n = 4 \text{ kHz} / n$ can be realized, leading to a frequency resolution from $2.5 \cdot 10^{-4}$ Hz (at 1 Hz) to 0.625 Hz (at 50 Hz).

B. Distribution density space

For two discrete probability distributions p_i and q_i , the Kullback–Leibler divergence of p from q is defined as

$$D_{\mathrm{KL}}(\boldsymbol{p},\boldsymbol{q}) = \sum_{i} p_i \log \frac{p_i}{q_i}.$$

Applied to a distribution over flicker frequency associated with a percept category p and the reference distribution of all reported frequencies r, $D_{\text{KL}}(p, r)$ can be interpreted as the amount of information about the flicker frequency that is gained by learning that a report belongs to the category (cf. Rényi, 1961). Applied to two different percept categories' distributions p and q, $D_{\text{KL}}(p,q)$ is a measure of how well the two categories can be discriminated based on the flicker frequency (cf. Kullback and Leibler, 1951).

This measure is not a metric of the space of distributions because it is asymmetric. However, if p and q are close to each other, such that $q_i = p_i + \Delta_i$ with small Δ_i , the expression for the divergence,

$$D_{\mathrm{KL}}(\boldsymbol{p}, \boldsymbol{q}) = -\sum_{i} p_{i} \log \left(1 + \frac{\Delta_{i}}{p_{i}}\right),$$

can be simplified using the approximation $\log(1+\epsilon) \approx \epsilon - \frac{1}{2} \epsilon^2$ for small ϵ to

$$D_{\mathrm{KL}}(\boldsymbol{p},\boldsymbol{q}) \approx \sum_{i} \frac{(q_i - p_i)^2}{2p_i}.$$

If all the pairs of distributions p and q that are considered are close to a common reference distribution r, by further approximating p_i in the denominator by r_i , the divergence can be given the form of a squared Euclidean distance,

$$D_{\mathrm{KL}}(\boldsymbol{p},\boldsymbol{q}) \approx \sum_{i} \left(\frac{q_{i}}{\sqrt{2r_{i}}} - \frac{p_{i}}{\sqrt{2r_{i}}} \right)^{2},$$

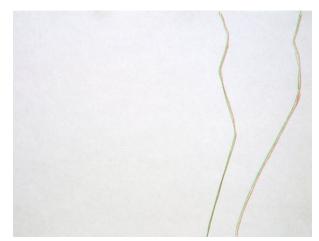
in a space where each distribution p is assigned a position vector p' with

$$p_i' = \frac{p_i}{\sqrt{2r_i}}.$$

C. Illustrations of percepts

To give a visual impression of the phenomena induced by flicker light, sketches drawn by the subjects are reproduced in Fig. 9. They additionally serve as illustrations of the classes of the primary rating system to which the corresponding percepts were assigned. For some of the sketches comments are in order:

(a) 'lines': The color combination of (neon-) red and green often occurred in percepts featuring lines or other thin structures; see also (o).



(a) 'lines'



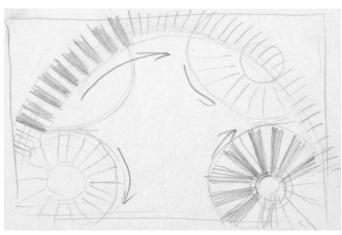
(b) 'ripples'



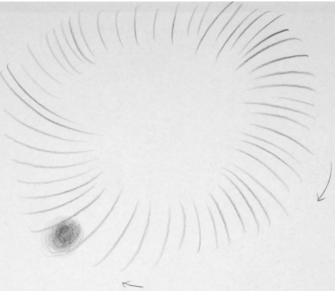
Figure 9: Illustrations of percepts



(d) 'honeycomb'



(e) 'wheel'

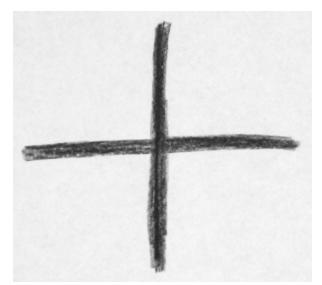


(f) 'spot' and 'spiral'

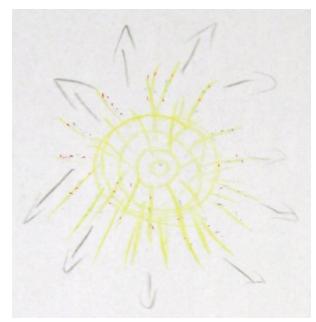
Figure 9: (cont.)



(g) 'clouds'

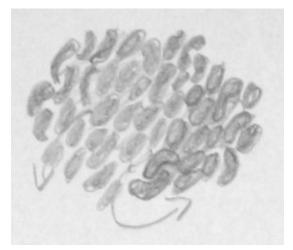


(h) 'cross'

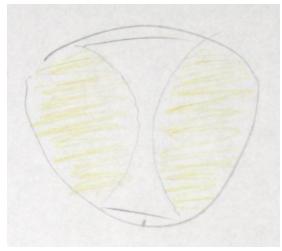


(i) 'sun'

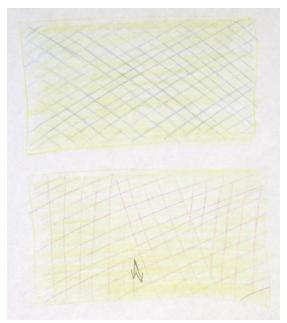
Figure 9: (cont.)



(j) 'organic'

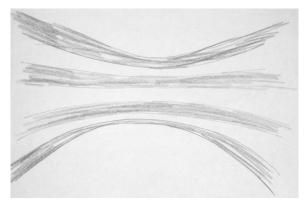


(k) 'bowls'



(l) 'raster'

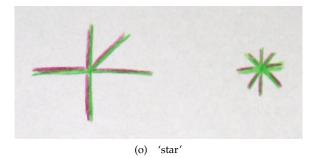
Figure 9: (cont.)



(m) 'bars'



(n) 'cracks'





(p) 'drain'

Figure 9: (cont.)

(b) 'ripples': For this subject, concentric waves seemed to emerge from the current point of fixation. When the eyes moved after a time (indicated by the arrow to the left labeled 't') a new set of circles emerged from the new fixation point, being superimposed onto the persistent earlier pattern.

(c) 'tunnel': Here an especially vivid form of the percept class is illustrated; the subject had the impression of driving in a car through a tunnel or on a street during the night. The light area on the left was interpreted as the headlights of cars approaching on the other lane, and even a faint impression of a windshield was present.

(d) 'honeycomb': The pattern of hexagons is supposed to fill the whole field but was sketched only partially by the subject. In this case, the lines making up the honeycomb pattern are spotted with blue and red dots.

(e) 'wheel': Several wheels seem to rotate together, forming something reminiscent of a clockwork mechanism.

(f) 'spot' and 'spiral': In this percept, two classes are combined: A small dark spot is located close to a large spiral structure.

(g) 'clouds': Gray clouds move slowly out of the lower right area over the whole field, covering a uniformly gray background (movement indicated by the arrow).

(i) 'sun': The arrows indicate a pulsating movement of growing and shrinking.

(j) 'organic': The subject had the impression of a grainy structure as if it were seen through a microscope. The arrows indicate a constant movement of the single grains around each other.

(k) 'bowls': The outer line indicates the border of the visual field, within which two large yellow spherical shapes are opposed to each other.

(l) 'raster': Two forms of the percept seen by the same subject.

(n) 'cracks': A network of thin blue lines; the arrows indicate that it extends over the whole field.

(o) 'star': Two forms of the percept, the left one with a structure tending towards 'cross'.

References

- Adrian, E. D., Matthews, B. H. C., 1934. The Berger rhythm: Potential changes from the occipital lobes in man. Brain 57 (4), 355–385. Anonymous, 1894. Notes. Nature 51 (1309), 110–114.
- Becker, C., Elliott, M. A., 2006. Flicker-induced color and form: Interdependencies and relation to stimulation frequency and phase. Consciousness and Cognition 15, 175–196.
- Becker, C., Gramann, K., Müller, H. J., Elliott, M. A., 2009. Electrophysiological correlates of flicker-induced color hallucinations. Consciousness and Cognition 18, 266–276.
- Berger, H., 1929. Über das Elektrenkephalogramm des Menschen. Archiv für Psychiatrie 87 (1), 527–570.
- Bien, C. G., Benninger, F. O., Urbach, H., Schramm, J., Kurthen, M., Elger, C. E., 2000. Localizing value of epileptic visual auras. Brain 123 (2), 244–253.
- Botev, Z. I., 2006. A novel nonparametric density estimator. Tech. rep., The University of Queensland, School of Physical Sciences. URL http://espace.library.uq.edu.au/view.php?pid=UQ:12535

- Bressloff, P. C., Cowan, J. D., Golubitsky, M., Thomas, P. J., Wiener, M., 2001. Geometric visual hallucinations, Euclidean symmetry and the functional architecture of striate cortex. Philosophical Transactions of The Royal Society B 356 (1407), 299–330.
- Bressloff, P. C., Cowan, J. D., Golubitsky, M., Thomas, P. J., Wiener, M., 2002. What geometric visual hallucinations tell us about the visual cortex. Neural Computation 14, 473–491.
- Brown, C. R., Gebhard, J. W., 1948. Visual field articulation in the absence of spatial stimulus gradients. Journal of Experimental Psychology 38 (2), 188–200.
- Cohen, J., 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement 20 (1), 37–46.
- Dahlem, M. A., Engelmann, R., Löwel, S., Müller, S. C., 2000. Does the migraine aura reflect cortical organization? European Journal of Neuroscience 12 (2), 767–770.
- Eichmeier, J., Höfer, O., 1974. Endogene Bildmuster. Urban & Schwarzenberg, München.
- Ermentrout, G. B., Cowan, J. D., 1979. A mathematical theory of visual hallucination patterns. Biological Cybernetics 34, 137–150.
- Fechner, G. T., 1838. Ueber eine Scheibe zur Erzeugung subjectiver Farben. Annalen der Physik 121 (10), 227–232.
- ffytche, D. H., 2008. The hodology of hallucinations. Cortex 44 (8), 1067– 1083.
- Freedman, S. J., Marks, P. A., 1965. Visual imagery produced by rhythmic photic stimulation: Personality correlates and phenomenology. British Journal of Psychology 56 (1), 95–112.

Geiger, J., 2003. Chapel of Extreme Experience. A Short History of Stroboscopic Light and the Dream Machine. Soft Skull Press, New York.

Helmholtz, H., 1867. Handbuch der physiologischen Optik. Leopold Voss, Leipzig.

- 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.
- Herrmann, C. S., Elliott, M. A., 2001. Fechner's colors are induced by flickering monochromatic light. In: Sommerfeld, E., et al. (Eds.), Fechner Day 2001. Pabst Science Publishers, Lengerich, pp. 427–431.
- Klüver, H., 1966. Mescal and Mechanisms of Hallucinations. University of Chicago Press, Chicago.
- Knoll, M., Kugler, J., 1959. Subjective light pattern spectroscopy in the encephalographic frequency range. Nature 184 (4701), 1823–1824.
- Kullback, S., Leibler, R. A., 1951. On information and sufficiency. Annals of Mathematical Statistics 22 (1), 79–86.
- Lashley, K. S., 1941. Patterns of cerebral integration indicated by the scotomas of migraine. Archives of Neurology and Psychiatry 46 (9), 331– 339.
- Purkinje, J., 1819. Beiträge zur Kenntniss des Sehens in subjectiver Hinsicht. Calve, Prague.
- Rao, R. P. N., Ballard, D. H., 1999. Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nature Neuroscience 2 (1), 79–87.
- Regan, D., 1989. Human Brain Electrophysiology. Evoked Potentials and Evoked Magnetic Fields in Science and Medicine. Elsevier, New York.
- Rényi, A., 1961. On measures of entropy and information. In: Neyman, J. (Ed.), Fourth Berkeley Symposium on Mathematical Statistics and Probability. University of California Press, Berkeley, pp. 547–561.
- Schott, G. D., 2007. Exploring the visual hallucinations of migraine aura: the tacit contribution of illustration. Brain 130 (6), 1690–1703.
- Sherrington, C. S., 1906. The Integrative Action of the Nervous System. Yale University Press, New Haven.
- Smythies, J. R., 1957. A preliminary analysis of the stroboscopic patterns. Nature 179 (4558), 523–524.
- Smythies, J. R., 1959a. The stroboscopic patterns. I. The dark phase. British Journal of Psychology 50 (2), 106–116.
- Smythies, J. R., 1959b. The stroboscopic patterns. II. The phenomenology of the bright phase and after-images. British Journal of Psychology 50 (4), 305–324.
- Smythies, J. R., 1960. The stroboscopic patterns. III. Further experiments and discussion. British Journal of Psychology 51 (3), 247–255.
- Stwertka, S. A., 1993. The stroboscopic patterns as dissipative structures. Neuroscience and Biobehavioral Reviews 17, 69–78.
- Tass, P., 1995. Cortical pattern formation during visual hallucinations.

Journal of Biological Physics 21, 177-210.

- Tass, P., 1997. Oscillatory cortical activity during visual hallucinations. Journal of Biological Physics 23, 21–66. von Campenhausen, C., Schramme, J., 1995. 100 years of Benham's top
- in colour science. Perception 24, 695–717.
- Wackermann, J., 2006. Rationality, universality, and individuality in a functional conception of theory. International Journal of Psychophysiology 62 (3), 411–426.
- Wackermann, J., Pütz, P., Allefeld, C., 2008. Ganzfeld-induced hallucinatory experience, its phenomenology and cerebral electrophysiology. Cortex 44 (10), 1364–1378.
- Walter, W. G., 1950. Features in the electro-physiology of mental mechanisms. In: Richter, D. (Ed.), Perspectives in Neuropsychiatry. H. K. Lewis, London, pp. 67–78.
- Welpe, E., 1970. Über die Strukturierung des Gesichtsfeldes bei intermittierender Belichtung des Auges im Frequenzbereich zwischen 33 Hz und der Flimmerverschmelzungsfrequenz. Vision Research 10, 1457-1469.
- Young, R. S. L., Cole, R. E., Gamble, M., Rayner, M. D., 1975. Subjective patterns elicited by light flicker. Vision Research 15, 1291–1293.