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Flicker-induced color and form: Interdependencies and relation to stimulation frequency and phase

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Abstract

Our understanding of human visual perception generally rests on the assumption that conscious visual states represent the interaction of spatial structures in the environment and our nervous system. This assumption is questioned by circumstances where conscious visual states can be triggered by external stimulation which is not primarily spatially defined. Here, subjective colors and forms are evoked by flickering light while the precise nature of those experiences varies over flicker frequency and phase. What's more, the occurrence of one subjective experience appears to be associated with the occurrence of others. While these data indicate that conscious visual experience may be evoked directly by particular variations in the flow of spatially unstructured light over time, it must be assumed that the systems responsible are essentially temporal in character and capable of representing a variety of visual forms and colors, coded in different frequencies or at different phases of the same processing rhythm.

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Keywords: Flicker; Subjective color; Subjective form; Stroboscopic pattern; Frequency; Phase; Multidimensional scaling

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1. Introduction

Contemporary perspectives hold conscious experience as an emergent property arising from synchronous oscillations at widely dispersed brain areas (Tononi & Edelman, 2002). The precise role of neuronal synchronization for the conscious perceptual representation of visual space remains unknown, while evaluation of whether or not the mechanisms responsible for conscious content depend upon precise temporal coding remains a problem of considerable complexity. It has been shown, nevertheless, that light sensitive mechanisms may be triggered by appropriate periodic stimulation: for example, color opponent cells are capable of following high-frequency flicker well above heterochromatic fusion frequencies, and combine to generate color fusion (Gur & Snodderly, 1997). Further evidence for the role of temporal factors in the perception of colors has also been brought about by research on the subjective phenomena of color and form perception: in one very early description, Purkinje (1823) described the experience of color and form whilst waving his hand vigorously across his closed eyes while facing direct and bright sunlight. Phenomena of flicker-induced color and form experiences have attracted attention not only in scientific circles, but were also thoroughly investigated and discussed by artists (an example being the “Dream Machine” invented by Brion Gysin (Geiger, 2003)) and writers (e.g., Burroughs, 1987).

Subjective color has mostly been studied by using the Benham disk or similar stimuli (Benham, 1895; Campenhausen & Schramme, 1995; Cohen & Gordon, 1949; Fechner, 1838). The Benham disk is composed of a black sector on one half of the disk and white sectors, containing black arcs at different radii from the center of the disk, on the second half. When this disk is spun at frequencies of between 5 and 10 Hz, the different arcs appear with different colors. Counter-clockwise rotation of the disk causes a reversal of the colors on the disk. The role of spatial factors for the apperception of subjective colors in terms of lateral inhibitory effects induced by adjacent parts of the Benham disk is still under debate, and whereas Festinger, Allyn, and White (1971) report solely temporally induced subjective colors, Jarvis’ (1977) failure to replicate these findings suggests the necessity for spatial interactions as important determinant for the appearance of subjective colors.

Besides studies using Benham disks and related stimulations, there are a number of investigations studying not only subjective experiences of color but also subjective forms. Smythies (1959) describes in detail the subjective patterns and forms arising during intermittent stimulation in the visual field. He showed that even though subjective patterns differ in quite specific details from individual to individual, they are similar enough to allow classification. The patterns described in his study consisted of various radial patterns, patterns comprising straight lines on a square base, herringbone and honeycomb patterns, curvilinear patterns, and other complex mosaics. While binocular stimulation yields clearer subjective patterns, the patterns become more fine-grained with increasing stimulation frequency (Smythies compared stimulation frequencies of 6, 12, and 18 Hz). In a very similar vein, the work of Smythies corresponds with that of Knoll and Kugler (1959) who also showed subjective forms to be brought about through periodic electrical stimulation or by means of photic driving, i.e., as a function of exposure to high-frequency flicker. More recently, during an electroencephalographic (EEG) study of the cortical response to flickering light, Herrmann (2001) observed that most of his subjects reported forms (stars or stripes) and colors (blue, red, or purple). From a reexamination of Herrmann’s data, Herrmann

and Elliott (2001) described a range of color (red, blue, and purple) and form (lines, honeycombs, and tunnels) experiences which appear to be confined to certain ranges of flicker frequencies within approximately the lower 40% of 1–100 Hz stimulation frequencies examined by Herrmann.

Recent attempts to model subjective colors were based on the temporal differences of processing between the different color pathways (Courtney & Buchsbaum, 1991; Grunfeld & Spitzer, 1995). Both models took into account the different temporal characteristics of the different cone types, as described by Schnapf, Nunn, Meister, and Baylor (1990) with 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 and 28 ms), and S-cones (61 and 34 ms). Courtney and Buchsbaum (1991) 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 the physiological data and took into account a nonlinearity of the $S + (L + M)-$ cells. Grunfeld and Spitzer (1995) developed a model which includes spatial as well as temporal parameters of the spatially- and cone-opponent ganglion cells ($L + M-$, $M + L-$, and $S - (L + M)$). Besides the temporal parameters, these authors suggest the relevance of a so-called rebound response, a common excitatory response to the turning-off of an inhibitory stimulus. In another approach, Stwertka (1993) suggests a dynamical account of self-organization in the brain as the underlying principle of the experience and transformation of subjective forms. Specifically, he states that the phasic synchronization of sets of spatial orientation tuning columns induced by the intermittent light stimulation might result in the conscious experience of features corresponding to the activity of those tuning columns and that the transformations observed in subjective forms correspond to the trajectory of the states of a dynamical system through its phase space.

The colors and forms reported during exposure to temporally modulated light may be called 'subjective' in the sense that they concern the experience of an external structure or quality in the absence of structure or quality-related information in the ambient optic array. Subjective experiences of color and form are thus conscious states that appear to occur solely as a function of the way our visual nervous systems respond to temporal modulation and with no obvious spatial references in the external world. If subjective color and form can arise solely as a function of intermittent stimulation, the possibility of describing conscious visual states exclusively in terms of variations in the temporal patterning of stimulation seems highly promising.

The aim of the studies presented here was to investigate the patterns of appearance of subjective colors and forms in more detail. The first experiment aimed to define: (i) the classes of subjective experience (for both color and form), and (ii) the exact frequency ranges over which subjective experiences are received. Of interest in addition were: (iii) what, if any, patterns of co-occurrence there were between these experiences. Two further experiments probed one transient characteristic of a subset of subjective experiences found to be generally reliably obtained in Experiment 1, aiming to measure the onset time of the subjective experience. Subsequent analyses examined the (iv) relationship of onset times with the phase of intermittent stimulation.

2. Experiment 1

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 expe-

riences 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 (2001) 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 dependence relations between subjective experiences alongside the existence of possible patterns of mutual inhibition.

2.1. Methods

2.1.1. 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 MS-DOS mode. The PC was connected to four LEDs (light emitting diodes; Type WU-2-310SWC-UR, luminous intensity 900 mcd, 3 mm diameter, emission color white, CIE 1931 Standard: $x = 0.29$, $y = 0.30$, Conrad Electronic GmbH, 92240 Hirschau, Germany, Order No. 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 10×20 cm) mounted within the box, some 12 cm from the viewing aperture. Aside from the viewing aperture, which was molded to fit a standard face, 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 four diodes. The applied level of illumination was chosen on the basis of reports by Eichmeier and Höfer (1974) that an illumination of less than 30 cd/m^2 is very efficient in generating subjective visual experiences of simple geometric forms. 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, $\text{FFF} < \sim 38 \text{ Hz}$) 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 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 epileptiform disorders.

2.1.2. Participants

Nine paid observers (three males, 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.

2.1.3. Design and procedure

Experiment 1 was conducted over two sessions, each of which consisted of 30 trials that were divided into a 60 s epoch of stimulation with flickering light followed by a 30 s 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 were 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.

2.2. Results and discussion

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 colors continually transformed into other forms or colors. Subjective experiences were thus and in general transitory phenomena, which could lead to the general experience of motion across the visual field. Forms might also be defined by colors, either in terms of 'filling in' or by virtue of their contour boundaries being of one or more colors.

Analysis of all reports produced by all observers proceeded in the following way: classes of subjective experiences were formed, which for colors comprise the achromatic colors black (11% of all trials), white (26%), and gray (21%) and the chromatic colors 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 and Höfer \(1974\)](#) that resulted from periodic electrical stimulation, although not all of the classes of subjective experiences described by Eichmeier and 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 three-dimensional space (14%), motion up and down (9%), motion towards the center (7%), motion sideways (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, combined with the fact that these motions were reported over almost the entire range of frequencies led to a decision to concentrate further analysis on variations in the distributions of forms and colors.

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, colors, and motion. Importantly, this entails the very strong possibility of patterns of interdependencies between subjective experiences.

2.2.1. 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 colors could be red or blue, for example) and the class of the subjective experience (which could include colors and/or forms) 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 colors.

For each class of subjective experience, histograms of the number of reports (i.e., the number of subjects reporting a given subjective experience) over stimulation frequency with bin widths of 1 Hz were calculated. 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 (1986). 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 (Chaudhuri & Marron, 1998). The SiZer technique allows the analysis of density estimates with the aim to derive significant peaks of the smooth as opposed to peaks in the distributions attributable to noise artifacts. 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 Figs. 1 (colors) and 2 (forms). These figures reveal either unimodal distributions or distributions with single prominent peaks for each class of subjective experience. Figs. 1 and 2 show that the report distribution for each class of subjective experiences is restricted to a particular range of stimulating frequencies (the lower colored panels in Figs. 1 and 2 show a range referred to as the ‘SiZer midrange,’ i.e., the frequency range over which the number of subjects reporting a particular class

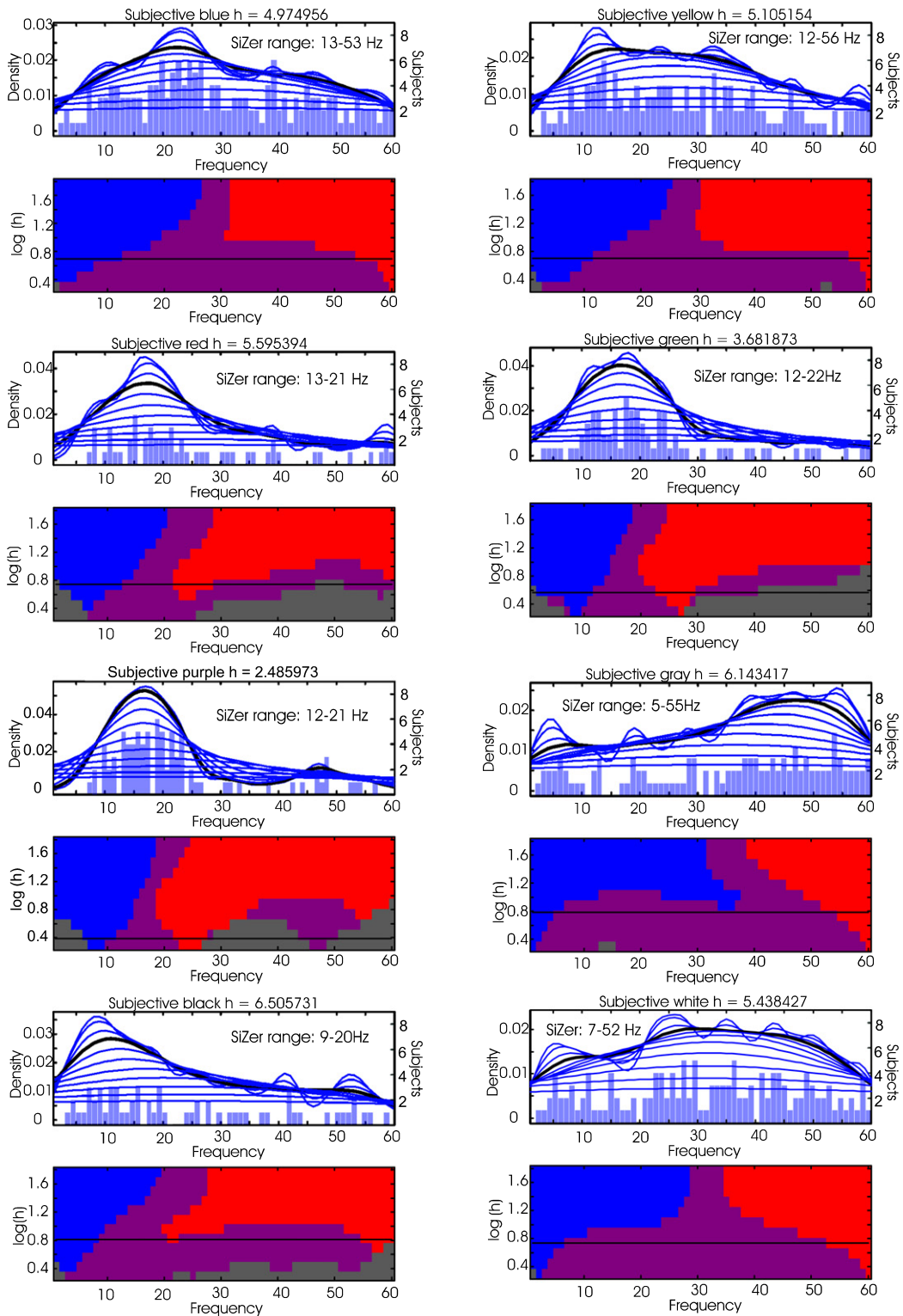


Fig. 1. Graphical representation of the SiZer analysis for subjective colors reported in Experiment 1. The upper part of each graph shows histograms denoting the number of subjects reporting a given subjective color at a specific frequency and a family of density estimations with different smoothing parameters h , where the black line marks the smoothing with bandwidth h calculated by the Silverman algorithm (the numerical value of h being given in the title of the graph). The lower part of the 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 color, respectively, while regions of no significant changes of the density curve are plotted in purple. Gray regions mark regions with few observation which cannot be included in the SiZer analysis. Again, the critical Silverman bandwidth is marked in black and 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 color of the plot. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

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.

Taken as a whole, forms were reported across the 8–40 Hz range (range spanned by the SiZer ranges of all forms), while colors were reported across the range 5–56 Hz (SiZer ranges of all colors). Reports of forms were given at a median frequency of 25 Hz while colors were reported at a median frequency of 30 Hz. Although on a first inspection subjective colors seem to follow a bimodal distribution over frequency (see Fig. 3A), this cannot be confirmed by a SiZer analysis of the overall color and form distributions showing unimodal density distributions with a SiZer midrange from 9 to 54 Hz for subjective colors (see Fig. 4) and from 9 to 36 Hz for subjective forms.

2.2.2. Analysis of interdependencies between subjective experiences

Consistent with our expectations subjective experiences were particular to quite specific ranges of stimulation frequency. A second question concerned 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 subjective experiences may be considered related or whether there is a distinct pattern of interdependencies.

To examine the reports for potential interdependencies the data of Experiment 1 were subjected to a multidimensional scaling (MDS). The analysis was conducted in two steps: first, individual patterns of co-occurrences were assessed using Kruskal's non-metric 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 of the resulting representation of the reports over a set of input distances (Kruskal, 1964). The stress as a measure of the badness of fit is calculated with the formula

$$S = \sqrt{\frac{\sum_{i=1}^n (\text{diss}_{\text{input}} - \text{dist}_{\text{model}})^2}{(\sum_{i=1}^n \text{dist}_{\text{model}})^2}},$$

where S is the stress, $\text{diss}_{\text{input}}$ is the measured dissimilarity between experiences, $\text{dist}_{\text{model}}$ are the distances of the model configuration, and n is the number of distances between the data points.

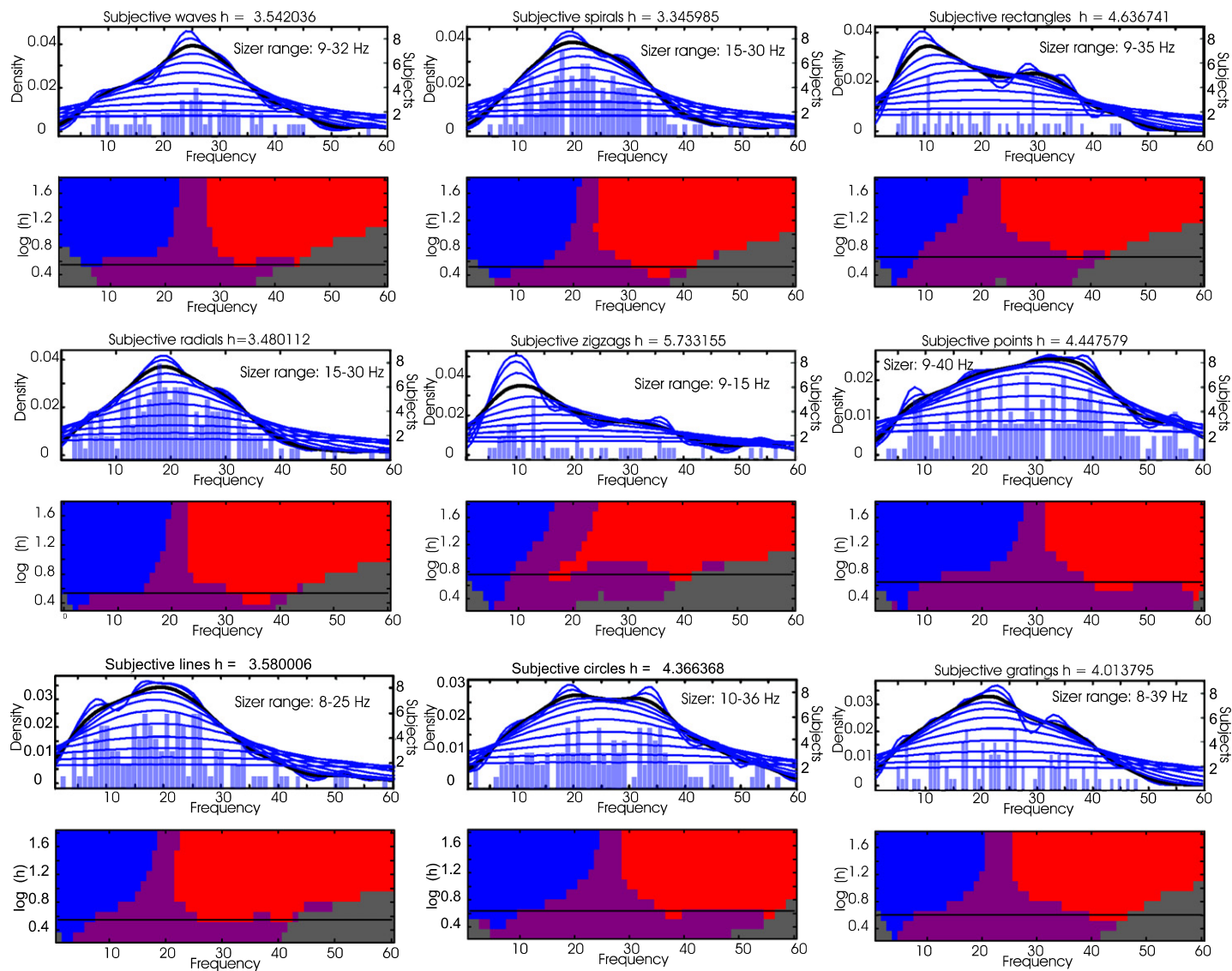


Fig. 2. Graphical representation of the SiZer analysis for subjective forms reported in Experiment 1. For more information, see the caption of Fig. 1 and the text.

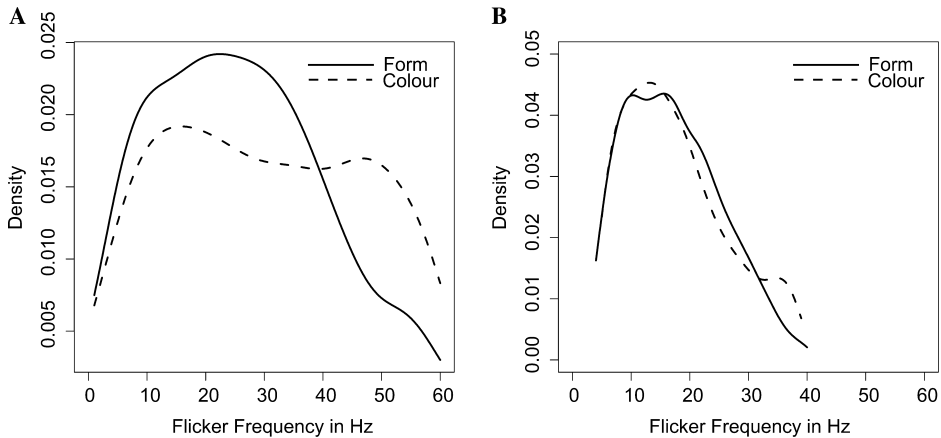


Fig. 3. Density estimates for the overall distributions of subjective colors and forms in Experiment 1 (A) and in Experiments 2 and 3 (B). Given that the area under each curve equals 1, the height of the curve at a specific flicker frequency represents the probability for color or form to be seen at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

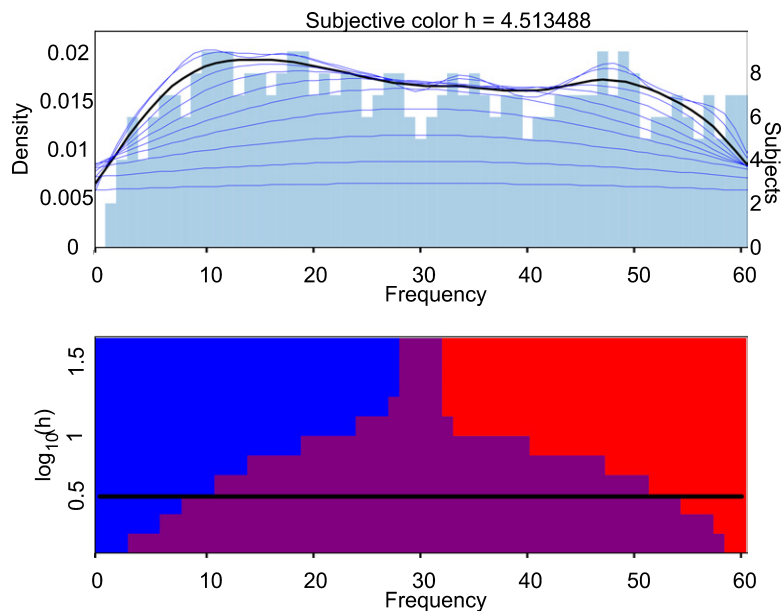


Fig. 4. Graphical representation of the overall SiZer analysis for subjective colors reported in Experiment 1 showing unimodality of the response distribution. For more information, see the caption of Fig. 1 and the text.

The measured dissimilarity represented the degree to which two different subjective experiences (from the eight colors and nine forms described earlier) were experienced in the same stimulation epoch (i.e., trial). This dissimilarity for two subjective experiences was 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 dissimilarity 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 dissimilarity 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 dissimilarity between the two experiences). For trials in which none of the experiences was reported, the dissimilarity value did not change. A dissimilarity 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 dissimilarity 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 of the stimulation frequency of this stimulation epoch. In contrast, the results presented above showed experiences to co-occur over frequency (as expressed by the different, but overlapping response distributions over frequency).

Four participants only reported subjective experiences of some classes: the dissimilarity matrix of participant 1 extended only 15×15 data points as the participant did not report green and yellow; the dissimilarity matrix of participant 4 was 14×14 (green, grating, and rectangle not seen); participant 5 had a 15×15 dissimilarity matrix (zigzag and rectangle not seen); and the dissimilarity matrix of participant 6 was 14×14 (black, gray, and zigzag not seen).

Applying MDS with different dimensionality, three-dimensional models were shown to be suitable for the representation of the input distances in all participants. The stress of the three-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): 0.07, 0.09, 0.11, 0.05, 0.07, 0.13, 0.10, 0.08, and 0.11 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, which 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.

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 five participants) are graphically represented in Figs. 5–7. For reasons of clarity, the color–color, form–form, and color–form pairs are depicted in different graphs.

The interindividual analysis of the three-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 colors (i.e., white and blue) tend to be seen independently from the occurrence of other colors (see Fig. 5). While the experience of purple excludes the experience of blue and gray, the experience of white shows inhibitory relations (i.e., significantly large model distances) to all chromatic colors, and gray. Despite this independence of white and

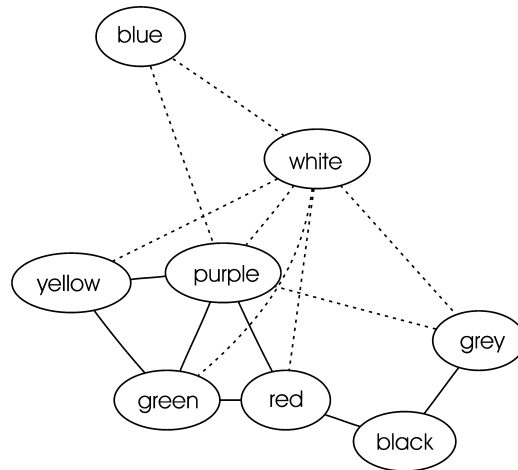


Fig. 5. Graphical representation of the co-occurrence of subjective colors. Pairs of subjective colors which have significantly small or significantly large model distances in more than 50% of the participants are connected by black and dotted lines, respectively. Further information is given in the text.

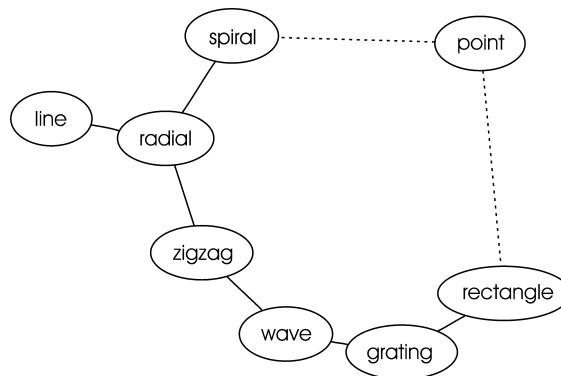


Fig. 6. Graphical representation of the co-occurrence of subjective forms. Pairs of subjective forms which have significantly small or significantly large model distances in more than 50% of the participants are connected by black and dotted lines, respectively. Further information is given in the text.

blue (and partly gray), there are a number of reliable relations between color reports in a given stimulation epoch (Fig. 5). When black is reported, gray 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 suggestive in terms of color-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 colors co-occur in time, or they develop out of each other, or the same phenomenological colors are named differentially (i.e., either green or yellow) due to a changing response criterion during a stimulation epoch.

Regarding form–form co-occurrences (Fig. 6), one finds that the apperception of points and circles is not reliably related to the experience of other subjective forms. In the multidimensional

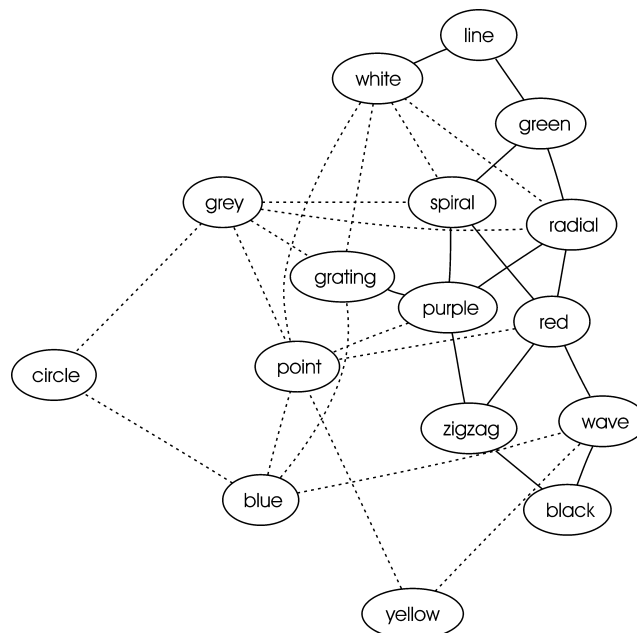


Fig. 7. Graphical representation of the co-occurrence of subjective colors and forms. Pairs of subjective experiences which have significantly small or significantly large model distances in more than 50% of the participants are connected by black and dotted lines, respectively. Further information is given in the text.

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 experience of radial patterns and spirals. 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.

Fig. 7 represents quite clearly one hitherto undescribed aspect of the observer's verbal reports: in many instances experience of color relates to experience of distinct forms (e.g., black, red, green, and purple), while other colors 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, gray, yellow, and blue. Also, some forms (circle, point, and rectangle) are not reliably experienced together with specific colors, but rather tend to be reported in relation to different colors by different participants. In addition, circles and points show specific patterns of inhibition with a number of colors. Large model distances can be found for the pairs circle–blue, and circle–gray, as well as for point–white, point–purple,

point–red, point–yellow, and point–blue. This means, for example, that the report of a point or points is very unlikely to be accompanied by a report of gray, white, purple, red, yellow, or blue. At the same time it is not related to the experience of any other specific color. 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 experience 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, gray, or blue. The co-occurrences between colors and forms match very well with the co-occurrences of either color–color 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 colors 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 colors (red, green, and purple) or black, while the experience of blue, yellow, white, and gray is either independent from any form experience or even negatively (i.e., in terms of mutual inhibitions) related to the experience of form.

2.2.3. Discussion of Experiment 1

Experiment 1 shows that it is possible to induce the experience of subjective colors and forms on the strength of temporal information alone. In the case of subjective color, this seems to contradict the descriptions of outcomes achieved in some previous research using Benham and Benham-like stimuli (Campenhausen & Schramme, 1995; Grunfeld & Spitzer, 1995; Jarvis, 1977) in which the authors conclude a necessary role for external spatial stimulation in order to bring about the experience of subjective colors. It is also the case that no specific distribution of the stimulus magnitude in relative phase was necessary in our study for the experience of subjective color as was claimed by Festinger et al. (1971) who used a specific distribution of stimulation magnitude, which was said to mimic in form 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, 1959) 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 rather small sized stimuli. Stimulating the visual ganzfeld 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. These differences in post-retinal coding of temporal information might result in later asynchronies which mimic the latency differences induced by an external spatially differentiated stimulation. In interaction with the stimulation frequency, the latency differences of the different cone types (Schnapf et al., 1990) and/or the latency differences between the two color coding channels (L/M and S/(L + M)) shown by Cottaris and De Valois (1998) may possibly explain for the subjective color experiences. The most astonishing characteristic of the subjective forms investigated here is their similarity to resonant systems, such as vibrating surfaces of water or sand (e.g., Christiansen, Alstrom, & Levinsen, 1992). As it happens, this similarity may be more than just analogy: the lateral retinal connections provided by horizontal and bipolar cells have specific transfer latencies. Thus,

when the retina is stimulated with flickering light, the period of stimulation (i.e., the stimulation frequency) may interfere with the latencies of the lateral connections in the neuronal tissue and may drive the population of cells in the neuronal tissue at retinal level (and later) into a state of resonance. This state of resonance may generate patterns of differential cell activation that not only resemble resonance patterns in physical systems (e.g., Christiansen et al., 1992), but possibly also patterns of activation that would result from the stimulation with real forms. As under standard viewing conditions, 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 (Eckhorn, 1991; Stwertka, 1993).

The distinct co-occurrence of subjective color and form may rely on the fact that the color-coding cells are as well responsible for the representation of spatial properties of the stimulus. The interdependencies in the reports suggest that it is especially the cells coding the colors 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 L/M coding cells and therefore the specific temporal resolution with which information is transferred into the lateral connections.

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 (Eichmeier & Höfer, 1974), but also to the patterns described by Smythies (1959). 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 (1959) by showing a direct frequency dependence of the probability of subjective form (and color) experience. Additionally, a complex pattern of mutual dependencies was found in the report probabilities for the different subjective experiences, be it color or form.

3. Experiments 2 and 3

The tendency for subjective experiences of form and color to be non-uniformly distributed over flicker frequency indicates the existence of a critical bandwidth within which 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 (but not of other frequencies, see Herrmann, 2001). On this basis it might reasonably be assumed that the responses in occipital cortex is periodic and follows the frequency of stimulation in the paradigm employed here.

The role of phase-sensitive mechanisms has been emphasized in studies investigating the experience of subjective colors following electrical stimulation (Young, 1977), the viewing of Benham disks (Roelofs & Zeeman, 1957) or Benham-like stimulations (Campenhausen & Schramme, 1995). However, although stimulus features presented at specific phases during stimulus presentation were found to determine the experience of particular colors, these effects were either attrib-

uted to a clear role for spatial information (i.e., the presentation of phase shifted flicker at adjacent regions of the stimulation field; Campenhausen & Schramme, 1995; Roelofs & Zeeman, 1957) or patterns of temporally modulated stimulus magnitude (Festinger et al., 1971; Young, 1977). In the studies presented here, neither spatial variations nor variations in stimulus magnitude were necessary to induce subjective colors and forms. However, should the phase of stimulation play a critical role in establishing subjective colors and forms, it might be observable in the time of onset of the experiences. These considerations were addressed in Experiments 2 and 3, which examined the time of onset of subjective experiences relative to the phase of the flicker frequency.

3.1. *Methods*

The methods employed in Experiment 2 and 3 were as given for Experiment 1 with the following exceptions or specifications.

3.1.1. *Participants*

Twelve practiced observers (four males, mean age 24.4 years, vision normal or corrected to normal) participated in Experiment 2 while 12 practiced observers (five 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.

3.1.2. *Design and procedure*

Experiments 2 and 3 used a simple response-time paradigm in that observers were asked to depress 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 one PC running in MS-DOS mode and programmed in C.

Each trial consisted of a 30 s epoch of flickering stimulation followed by a 15 s dark or resting period. The ranges of frequencies concerned were narrower than those used in Experiment 1. In Experiments 2 and 3, subjective colors 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 colors) and 296 trials (37 frequencies \times 8 target forms), divided into three and four 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 class 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.

3.2. Results and discussion

Analyses of report frequency distributions in Experiments 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 colors and forms are given in Table 1.

3.2.1. 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 colors were reported across the range 9–26 Hz (SiZer range of all colors, median frequency: 16 Hz).

3.2.2. Response time analysis

Analysis of response times (in milliseconds) to the apperception of an subjective experience revealed no significant differences between the response latencies to different subjective colors or to different subjective forms ($F(4, 425) = 0.46$ ns and $F(7, 924) = 2.23$ ns, respectively). That is, responses to different subjective experiences were given at approximately equivalent times during an epoch of flicker irrespective to the class of experience concerned. The mean response time to subjective colors was 7530 ms, the minimum and maximum response times were 742 and 29,470 ms, respectively, whereas 50% (median) and 75% (3rd quartile) of all responses were given no later than 5218 and 10,370 ms after flicker onset, respectively. For subjective forms, the mean response time was 8842 ms, the minimum and maximum response times were 778 and 29,550 ms, respectively. For subjective forms 50 and 75% of all responses were given no later than 7028 and 12,840 ms following flicker onset, respectively.

3.2.3. Analysis of response times over phase

The role of phase-sensitive mechanisms for the experience of subjective colors and forms was investigated by the analysis of the relation between the times of onset of the subjective experience

Table 1

Subjective colors and forms reported in Experiments 2 and 3 with SiZer midranges, i.e., frequency ranges in which a significant number of subjects reported seeing the color or form, and the frequency of the report distribution peak in hertz

Color	SiZer midrange (Hz)	Peak frequency (Hz)	Form	SiZer midrange (Hz)	Peak frequency (Hz)
Purple	9–18	14	Lines	10–24	12
Blue	9–18	10	Circles	9–26	21
Green	11–19	14	Radials	9–22	12
Yellow	10–26	13	Spirals	11–24	17
Red	10–16	11	Gratings	10–19	14
			Points	10–26	13
			Rectangles	8–21	9
			Zigzag	10–19	14

(i.e., the response times) relative to the phase of the flicker. For each trial, the phase angle of the flicker frequency cycle at which the manual response was given, was calculated by

$$\phi = \frac{\text{RT mod}(1000/F) * 360^\circ}{1000/F},$$

where ϕ is the phase angle, RT is the reaction time, and F is the flicker frequency in the respective trial. Although the measure ϕ 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 subjects and trials (i.e., all different frequencies) should result in an uniform distribution of response times over all phase angles due to 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 revealed all responses to be distributed normally (with $p > .01$, Watson's goodness-of-fit test) following a von Mises distribution (i.e., the circular analogue of the normal distribution on a line (Jammalamadaka & SenGupta, 2001; Mardia, 2000), see Fig. 8B). This indicates that, irrespective of the absolute time at which a subjective experience starts to be perceived, the onset time of the subjective experience relates quite specifically to a particular phase of the evoking flicker. Fig. 8A illustrates circular distributions related to the onset times of subjective rectangles and subjective blue. Interestingly, the onset of different subjective experiences may be distributed around different phases. Fig. 8C 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 colors (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).

3.2.4. Discussion of Experiments 2 and 3

What has been indicated by our study and the study of others (i.e., Roelofs & Zeeman, 1957) is the relevance of stimulus phase for the experience of subjective colors. In our study, a relation of the phase specificity to the opponent color system is suggestive: the opponent color pairs red–green and blue–yellow are clearly separated in their time of appearance relative to the flicker cycle. The question arises whether color opponency might not only be coded spatially (as by color-opponent ganglion cells), but also temporally. Colors might be coded in the temporal frequency domain, expressed by neuronal oscillations in specific frequency ranges. As shown by Cottaris and De Valois (1998) the two color opponent system exhibit different processing delays from the retina to V1 (the L/M cells in V1 responding faster than the S/(L + M) cells). It might be that these latency differences rather than being a fixed time, are an expression of oscillatory processes modulating color coding, where red–green opponency is coded with a latency different from the yellow–blue opponency, while the intra-opponent colors (i.e., red and green) might be coded in

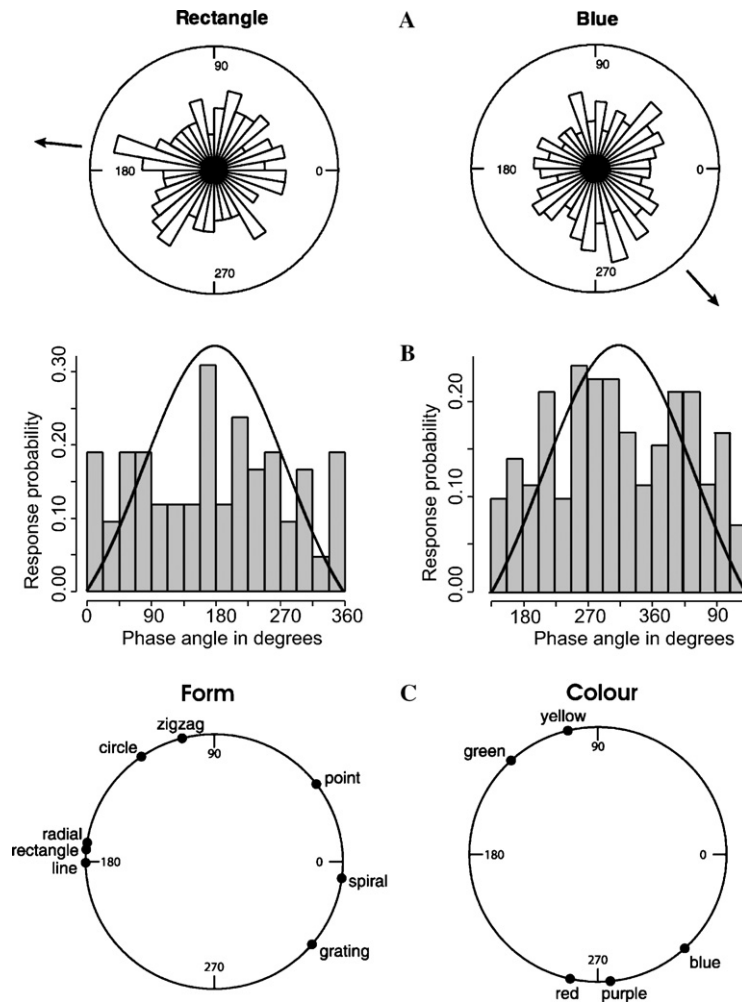


Fig. 8. (A) Circular diagrams indicating the distribution of response times expressed in terms of phase in the flicker frequency cycle for subjective rectangles and subjective blue. A rotation of 360° on the circle (in the counter-clockwise direction) correspond to one flicker frequency cycle (e.g., for 10 Hz, 50 ms of light followed by 50 ms of darkness). 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 colors. Details are given in the main body of the text.

similar frequency ranges. Should the opponent colors be coded in a similar frequency range, the problem arises as how to temporally separate the two different colors. One possibility would be the coding in phase. Different phases in the coding the different colors might be brought about by the variation of temporal resolution within the L/M pathway. Zrenner (1983) showed that in rhesus monkey parvocellular ganglion cells the M+/L- pathway have the highest temporal resolution, while the L+/M- pathway is about 20% slower. Therefore, even though a single (or at least similar) frequency is responsible for coding the opponent colors, 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 color 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.

4. General discussion

The aim of the work presented here was to study subjective colors and forms induced by flickering light. Based upon free reports during stimulation with flickering light, Experiment 1 revealed a number of classes of subjective forms and colors. The ranges of flicker frequencies were calculated over which these subjective experiences are reliably induced while patterns of co-occurrences of these experiences were also calculated. These analyses suggest that while subjective experiences are reported in quite specific frequency ranges, the probability of their appearance may depend on the appearance of other subjective experiences during the same stimulation period, although the precise patterns of association, and if temporally discrete, the transformational rules, accompanying the co-occurrences of subjective forms and colors remain to be determined. Additionally, Experiments 2 and 3 revealed that the onset of both, subjective color and form experiences, is related to the phase of the intermittent stimulation, while the particular phases at which the experiences evolve seem to represent a possible temporal coding strategy of the visual system for intra-opponent colors (and to a certain extent, forms).

For subjective forms there are not only similarities to visual hallucinations (corresponding to patterns of neuronal activation) predicted by computational models of epileptic neuronal activity in the brain (Tass, 1995), but also similarities to descriptions of a migraine aura phenomenon, the so-called scintillating scotoma (see, for example, Dahlem & Chronicle, 2004). Interestingly, the rate of flicker of the scintillating scotoma has been described to lie between 3 and 42 Hz (Crotono, Feindel, & Wilkinson, 2001), a frequency range that has been shown to be most effective in inducing subjective experiences in our experiments. Physiological correlates of the observed subjective experiences need to be further investigated, for example, by measures of electrophysiological activity allowing precise temporal registration of brain activations. Shevelev et al. (2000) presented very interesting results showing that visual illusions (circle, spiral, and grid) may be the equivalent to alpha waves traveling across the cortex when the eyes are stimulated with flicker in the alpha frequency range.

The subjective experiences described here correspond to conscious visual experiences of forms and colors that relate solely to temporal patterning in the flow of spatially unstructured light. In fact, they are experiences of visual form and color that are entirely independent of the presence of particular spatial structure or color in the distal stimulus. That conscious visual states corresponding to the experience of complex visual forms and colors can arise from flickering light is surprising enough; however flicker-evoked subjective experiences also vary very precisely with frequency. They are significantly likely to occur across a narrow bandwidth, while their precise occurrence in time may relate to a particular phase of the stimulation frequency. In addition, the occurrence of a given subjective experience is strongly dependent on the occurrence of other subjective experiences at the same stimulation period. This offers a very strong indication that the temporal characteristic of the internal response is alone sufficient for the emergence into consciousness of various

spatial structures and colors. This may be achieved by a dynamic organization at the neuronal level, which seems to operate as a self organizing system generating relations between perceptual contents (expressed by the patterns of co-occurrence of subjective experiences). The data presented here suggests that this dynamic system is tuned to some specific frequency ranges of optimal processing (shown by the pronounced relation of subjective experiences to the stimulation frequency) and that the dynamic states of the system themselves in some way interact to determine the precise structure of the subjective experiences. The stimulus-related and intra-subjective dynamics seem very promising avenues for further research into the temporal factors that seem to play a major role in the development of coherent visual experiences.

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