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Martin Hůla, Jaroslav Flegr

There is no doubt that people find flowers beautiful. Surprisingly, we know very little about the actual properties which make flowers so appealing to humans. Although the evolutionary aesthetics provides some theories concerning generally preferred flower traits, empirical evidence is largely missing. In this study, we used an online survey in which residents of the Czech Republic (n = 2006) rated the perceived beauty of 52 flower stimuli of diverse shapes and colors. Colored flowers were preferred over their uncolored versions. When controlling for flower shape, we found an unequal preference for different flower colors, blue being the most and yellow the least preferred. In the overall assessment of beauty, shape was more important than color. Prototypical flowers, i.e., radially symmetrical flowers with low complexity, were rated as the most beautiful. We also found a positive effect of sharp flower contours and blue color on the overall rating of flower beauty. The results may serve as a basis for further studies in some areas of the people-plant interaction research.

What flowers do we like? The influence of shape and color on the rating of flower beauty

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Abstract

There is no doubt that people find flowers beautiful. Surprisingly, we know very little about the actual properties which make flowers so appealing to humans. Although the evolutionary aesthetics provides some theories concerning generally preferred flower traits, empirical evidence is largely missing.

In this study, we used an online survey in which residents of the Czech Republic (n = 2006) rated the perceived beauty of 52 flower stimuli of diverse shapes and colors. Colored flowers were preferred over their uncolored versions. When controlling for flower shape, we found an unequal preference for different flower colors, blue being the most and yellow the least preferred. In the overall assessment of beauty, shape was more important than color. Prototypical flowers, i.e., radially symmetrical flowers with low complexity, were rated as the most beautiful. We also found a positive effect of sharp flower contours and blue color on the overall rating of flower beauty.

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1. Introduction

People across cultures find flowers beautiful. The aesthetic appreciation of flowers is manifested in many ways. We grow flowering plants in our apartments and gardens, horticulturists put much effort into breeding new types of ornamental flowers, and floral motifs are often present on paintings, fabrics, china or jewelry (Appleton, 1996; Eibl-Eibesfeldt, 1989). Flowers also serve as traditional and highly esteemed gifts (Haviland-Jones, Rosario, Wilson & McGuire, 2005). This human attitude towards plants and flowers is known as phytophilia (Eibl-Eibesfeldt, 1989).

Many aspects of people-plant relationships have been explored in past years, especially the effects of plants and flowers on the human psyche. Some researchers have suggested that the presence of plants positively affects mood (Larsen, Adams, Deal, Kweon & Tyler, 1998; Shibata & Suzuki, 2002; Haviland-Jones et al., 2005) and attention (Herzog, Black, Fountaine & Knotts, 1997; Kaplan & Kaplan, 1995; Kaplan, 1995; Lohr, Pearson-Mims & Goodwin, 1996; Raanaas, Evensen, Rich, Sjøstrøm & Patil, 2011; Tennessen & Cimprich, 1995), reduces stress (Cackowski & Nasar, 2003; Grahn & Stigsdotter, 2010) and even decreases recovery time after surgery (Ulrich, 1984).

The perceived beauty of flowers might influence the psychological benefits they provide to humans. It is thus reasonable to ask if there exist any common human flower preferences or whether the perceived beauty of flowers depends solely on the individual taste. Below we describe several theories and hypotheses from evolutionary aesthetics which suggest that some flower traits should be generally preferred more than others. We then present the design and results of our study, which aimed to test these hypotheses.

1.1. Preferred flower colors

Some evolutionary psychologists regard flowers as important signs that could have helped our ancestors find a suitable habitat for living. The ability to choose a rich and safe habitat was essential for the survival of our ancestors, thus an innate preference for signs of such a habitat (and the avoidance of opposite signs) was highly adaptive. It is for this reason that we perceive these signs as beautiful. Flowers signal a rich environment and promise the presence of edible bulbs or fruits (Heerwagen & Orians, 1993; Orians & Heerwagen, 1995; Pinker, 1999). Flower signs have to be visible from a distance, so we should mainly prefer their vivid and contrasting colors.

General color preference may also influence the beauty of many objects with the same color, including flowers. Green and blue colors should be preferred because they signal a rich and safe habitat (lush vegetation, water, clear sky). Brown or yellow are connected with barren land, drought, dead vegetation or feces and should be avoided (Orians & Heerwagen, 1995, pp. 567-569; Palmer & Schloss, 2010). On the other hand, edible fruits and nuts are often yellow or brown, so the predicted avoidance of these colors is somewhat dubious. Red color may signal edible fruits, sexual arousal or blood (Humphrey, 1976). Red objects should be regarded as stimulating, but whether as beautiful is uncertain.

Some studies targeting the behavior of florist shop customers reported red and pink flowers as the most preferred and blue and yellow flowers as the least preferred (Behe, Nelson, Barton, Hall, Safley & Turner, 1999; Yue & Behe, 2010). A study examining the beauty of street flowers found equal preference for diverse flower colors (Todorova, Asakawa & Aikoh, 2004). When people rated their favorite color of a tree canopy, they most preferred red (Kaufman & Lohr, 2002; Heerwagen & Orians, 1993). However, in another study, a red canopy was the least preferred and blue had the highest rating (Müderrisoğlu, Aydin, Yerli & Kutay, 2009).

People who rated the beauty of diverse birds appreciated the presence of blue and yellow coloration and overall lightness (Lišková & Frynta, 2013). Similar results were found in the case of parrots (Frynta, Lišková, Bültmann & Burda, 2010), while blue and green were the most preferred colors of pita birds (Lišková, Landová & Frynta, 2014).

Studies examining overall color ranking have usually described blue and red as the top colors (blue was usually preferred slightly more by men and red by women) and yellow near the bottom (Camgöz, Yener & Güvenç, 2002; Ellis & Ficek, 2001; Hurlbert & Ling, 2007; Schloss, Strauss & Palmer, 2013; Zemach, Chang & Teller, 2007). Color preferences also seem to be culturally dependent. For example, East Asian cultures have a preference for white color (Saito, 1996), while members of the African Himba tribe highly esteem yellow and do not like blue (Taylor, Clifford & Franklin, 2013).

1.2. Preferred flower shapes

Flower shapes may influence their perceived beauty. Humans tend to aesthetically appreciate objects that are quickly recognizable and fluently processed by their brains. The presence of such objects assures easy orientation in the environment and rapid evaluation of its potential threats and benefits. Human attraction to these environments should be highly adaptive (Humphrey, 1980; Kaplan, 1987, 1988; Reber, Schwarz & Winkielman, 2004). Objects that are fluently processed tend to be symmetrical (Enquist & Arak, 1994; Enquist & Johnstone, 1997; Jacobsen, Schubotz, Höfel & Cramon, 2006; Van Der Helm & Leeuwenberg, 1996), prototypical (Winkielman, Halberstadt, Fazendeiro & Catty, 2006), and moderately complex (Reber et al., 2004). Empirical research has confirmed that people prefer prototypical objects and animals (Hekkert, Snelders & Wieringen, 2003; Hekkert & Wieringen, 1990; Reber et al., 2004). Complexity also influences the preference for objects (Jacobsen et al., 2006; Reber et al, 2004), but not linearly. Studies have reported that objects with very low or very high complexity are preferred less than moderately complex ones (Akalin, Yildirim, Wilson & Kilicoglu, 2009; Hekkert & Wieringen, 1990).

Symmetrical objects are also considered beautiful (Jacobsen et al., 2006; Jacobsen & Höfel, 2002; Leder, Belke, Oeberst & Augustin, 2004). The processing fluency and the preference for objects increase with the number of their axes of symmetry (Evans, Wenderoth & Cheng, 2000; Tinio & Leder, 2009). On the other hand, some researchers claim humans have a very strong preference for bilaterally symmetrical objects, which may be a by-product of the selection for partner choice (Little & Jones, 2003) and partner recognition (Johnstone, 1994). According to the habitat selection approach of Heerwagen and Orians, the type of symmetry could provide information about the nutritive value of flowers. Bilaterally symmetrical flowers usually have more nectar than radially symmetrical ones and should be regarded as more beautiful (Heerwagen & Orians, 1993).

Recent studies have shown that people prefer round objects over objects with sharp contours (Bar & Neta, 2006; Leder, Tinio & Bar, 2011; Silvia & Barona, 2009, Westerman, Gardner, Sutherland, White, Jordan, Watts & Wells, 2012) According to Bar and Neta, this difference is due to the fact that objects with sharp contours evoke a subconscious feeling of danger and fear (Bar & Neta, 2007). However, another study suggested that the preference for round objects may be just a temporary fashion trend (Carbon, 2010).

1.3. Aim of the study

According to some of the mentioned theories from evolutionary aesthetics, flowers should be preferred because of their conspicuous colors. On the other hand, many studies revealed that some shape properties influence the aesthetic appreciation of an object or a person. It is very likely that flower shape also plays a role in the assessment of the flower beauty. The main objective of the study was to compare these theories with the empirical evidence, and evaluate their relative importance. We wanted to answer the following questions: Are there any general flower preferences? Is the flower color more important than the flower shape? Are some colors or shapes more preferred than others?

1.4. Hypotheses

We proposed several hypotheses based on the research mentioned above. We expected to find clear common flower preferences in our data set.

We assumed that the presence of color would influence the rating of flower beauty. We also expected differences in the beauty rating based on the specific flower color.

We hypothesized that flower beauty would increase with perceived prototypicality, that moderately complex flowers would be considered more beautiful than those with very low or very high complexity, and that round flowers would be rated as more beautiful than those with sharp contours.

We expected symmetry would play an important role in the evaluation of flower beauty, but it was not clear whether bilateral or radial symmetry should be more preferred.

2. Materials and Methods

To test our hypotheses, we conducted two independent online surveys targeted to the Czech population. Both surveys were based on the rating of photographs of flowers. First, we describe how we obtained the flower stimuli. Then we present the design of both surveys. The dataset and flower stimuli are available via this link: https://figshare.com/s/7306f12659f68f7f3d9d

2.1. Flower Stimuli

We wanted to create a set of flower stimuli that would reflect the diversity of flower shapes and colors. However, it had to remain sufficiently small and easy to work with. For these reasons, we created a primary set of flowers that met the following conditions:

1. The plant is native to the Czech Republic.
2. The plant has no strong cultural connotations in the Czech environment (e.g. rose is symbolic of love, etc.)
3. The size of the flower is between 1 and 4 cm in diameter.
4. Each flower can be clearly distinguished.

These conditions allowed us to reduce the immense number of flowering plants while maintaining a high morphological diversity. The flowers were not absolutely unknown or notoriously familiar to the respondents, as both of these situations could possibly lead to biased results. The flower size limit guaranteed that the shape of the real flowers could be normally seen with the naked eye. The preparation of the flower stimuli set also included the conversion of photographs to a single size, and it was desirable to keep the converted flower size close to the real one. The last condition eliminated possible problems with compact inflorescences, because it is arguable whether we should distinguish the appearance of single flowers in the inflorescence or treat the whole inflorescence as a single flower. The only exceptions to the last condition were the inflorescences of the aster family (*Asteraceae)*. We included aster family members in the stimuli set because they are very common and the vast majority of people (laypersons) perceive their inflorescences as single flowers.

We found all the Czech flowering plant species in the Key to the Flora of the Czech Republic (Kubát, Hrouda, Chrtek, Kaplan, Kirschner & Štěpánek, 2002). When the flowers met the inclusion criteria, we included them in the working flower set. In the case of genera with very similar species (e. g., *Rubus, Taraxacum*), we included the flower of just one species in the working set. The working set comprised flowers of 199 species, which we divided into 26 groups according to their shape. From each group we selected two flowers with different color (e. g., Fig. 1A) and added them to the final flower set (see Appendix).

We found freely available high quality photographs of each flower on the internet. To properly illustrate the true shape of the flowers, we used three photographs for each flower. These photographs were displayed together. The photograph in the center showed the flower from above (or *en face* in the case of bilaterally symmetrical flowers), while the photographs on the left and right sides depicted flowers that were turned slightly to the left and to the right, respectively (Fig 1B, 1C).

We used Corel Photo Paint X7 to replace the original flower background by a neutral black color. The black background did not favor any flower (flowers are usually seen on a green, brown, grey or blue background) and provided enough contrast for the clear distinction of the flowers. We then centered the flowers and placed them in the same position, the top petal or tepal pointing directly upwards. Finally, we converted all of the flowers to the same size, optimal for displaying on most computer screens (flower = 150 pixels, flower + background = 200 pixels, the three photographs next to each other = 600 pixels). We also copied the final flower set and converted the photographs in it to a sepia tone (Fig. 1B). This new set was thus devoid of colors. The new set helped us to test the influence of color on the rating of flower beauty. We did not use a conversion to a greyscale because grey photographs on a black background seemed somehow gloomy, which could negatively influence their rating.

The final set of flower stimuli consisted of 26 pairs of photographs, the flowers in each pair having a similar shape but a different color. There was also a sepia tone set of flower stimuli.

2.2. Determination of flower traits

Symmetry

We distinguished radially symmetrical flowers (40 in total; e.g., Fig. 1B, 1C, 1D) and bilaterally symmetrical flowers (12 in total; e.g., Fig. 1A), respecting the usual convention (for more details see, e.g., Judd, Campbell, Kellogg, Stevens & Donoghue, 2010, pp.: 66-67). We considered the inflorescences of the aster family (*Asteraceae*) as single radially symmetrical flowers.

Angularity

We followed the approach of Bar and Neta (2006) when determining flower angularity. We divided flowers into three groups according to the curvature of their contours. There were flowers with round contours (21 in total), sharp contours (15 in total) and both round and sharp contours (17 in total). See Fig. 1D.

Color

First we determined whether the flower had only a single color (22) or more colors (30). We also identified a dominant flower color (occupying at least 2/3 of the flower surface).
To determine the dominant flower color, we cut a 30 x 30 pixels square (or its equivalent) from the area with the dominant color in each flower photograph. We then computed its average value in the hue-lightness-saturation (HLS) color space. The hue values correspond to the angles of a color wheel, where certain angles are associated with certain colors. We adopted the hue ranges published by Newsam (2005). To properly distinguish flower color, we had to avoid overlaps between the hue ranges of pink and purple. We set the range for purple to 270° - 315° and the range for pink to 316°- 350°. White, grey, and black colors can be defined by setting empirical thresholds of lightness (L) and saturation (S) values (Lišková et al., 2014; Newsam, 2005). L and S can vary from 0 to 100. In our case, we defined white color as having $L > 70$ and $S < 35$. This combination of L and S values best matched the flowers perceived as white. With the described procedure, we defined the following color groups, which were later used in color preference analysis (the numbers in brackets represent the number of flowers within each group): white (14), yellow (8), blue (9), purple (8) and pink (7). Six flowers had a unique dominant color (*Hieracium aurantiacum* – orange, *Atropa bella-donna* – brown, *Arctium tomentosum* – green) or no dominant color (*Epipactis palustris*, *Galeopsis speciosa, Kickxia elatine*), and we excluded them from further color preference analysis.

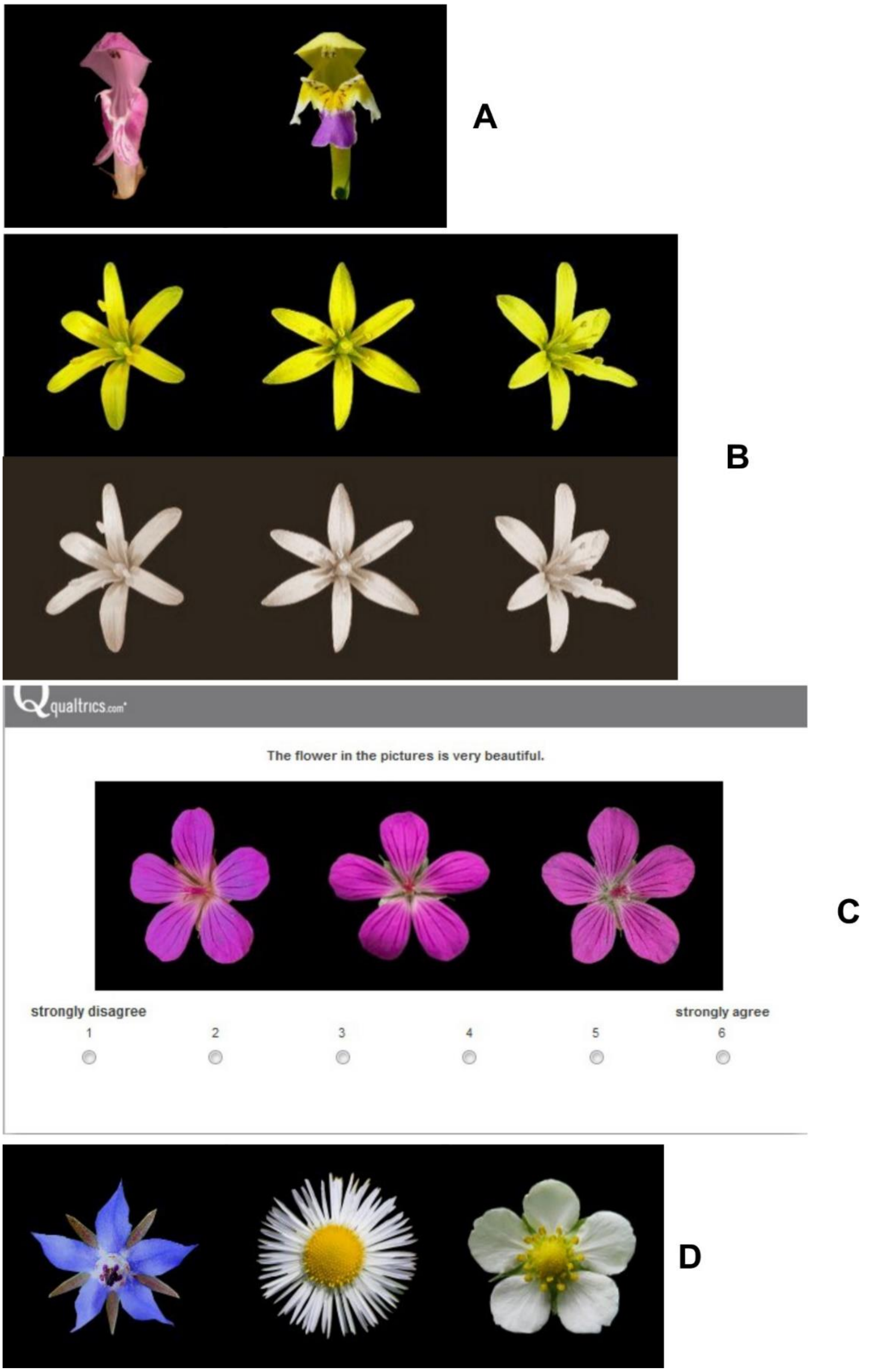


Fig. 1. Flower stimuli **A:** examples of bilaterally symmetrical flowers with similar shape (left: *Lamium maculatum,* right: *Galeopsis speciosa)* – only the *en face* photographs; **B:** colored flower stimulus and its sepia tone version (*Gagea lutea*); **C:** example of a rating question setting (*Geranium palustre*); **D:** Flowers with different angularity levels. Left: sharp (*Borago officinalis*), center: mixed (*Erigeron annuus*), right: round (*Fragaria viridis*).

2.3. Survey design

Each survey consisted of a single questionnaire created in a Qualtrics environment.

In the first questionnaire the respondents rated a set of photographs of flowers by their beauty. The questionnaire also contained several sets of questions concerning basic information about the respondents, their attitude towards plants, color preferences and psychological characteristics.
Because the number of the flower stimuli was quite high (52 flowers in color and sepia tone), we decided to show each respondent only half of them (the first flower of each pair in color and in sepia tone, i.e., subset 1, or the second flower of each pair in color and sepia tone, i.e., subset 2). Although the flower stimuli in each subset remained the same, we randomized their display order. To prevent the respondents from rating the colored flower stimuli under the influence of the sepia tone stimuli and vice versa, we randomized the display order of the colored and sepia tone stimuli and also separated their rating by a set of questions.
For each flower stimulus, respondents expressed their agreement with the statement "The flower in the pictures is very beautiful". The respondents were choosing one point on a six-point scale, where 1 meant "strongly disagree" and 6 meant "strongly agree" (Fig. 1C). The respondents moved to the next flower stimulus by clicking on the "next" button. Once the new flower stimulus appeared, it was no longer possible to change the rating of the previous ones (this fact was clearly explained before the start of the rating procedure).

In the second questionnaire the respondents rated the same set of photographs as in the previous questionnaire, but this time by their prototypicality and complexity. There was also a set of questions concerning basic information about the respondents and their attitude towards plants.
The second questionnaire contained fewer questions than the previous one, and it was also not necessary to rate the sepia tone flower stimuli. This allowed us to present each respondent with the whole set of flower stimuli (subset 1 and subset 2 together). We separated the rating of flower complexity and prototypicality by a set of questions and randomized the display order of each rating. The order of flower stimuli in each rating was also randomized. The rating instructions explained what flower complexity and prototypicality meant. For illustration, we also added two examples of the complexity and prototypicality rating of birds and butterflies. The rating procedure was the same as for the determination of flower beauty, but this time, the respondents expressed their agreement with the statements "This is how I imagine a complex flower." and "This is how I imagine a typical flower."

There was a break of several months between the start of the first and second surveys.
We distributed the link to both surveys mainly via the Facebook group *Pokusní králíci* (Guinea Pigs, www.facebook.com/pokusnikralici), which is administered by the members of our laboratory. The link was also displayed on other web pages; anyone could share the link.

Respondents gave their informed consent to the data collection by proceeding with the questionnaire (this fact was clearly explained on the first page of the questionnaire). Both surveys were completely anonymous. The research was approved by the IRB of the Charles University, Faculty of Science (Approval number: 2015/31).

2.4. Characteristics of the respondents

The first questionnaire, in which flower beauty was determined, was completed by 2013 people (1489 women, 523 men and one person of unknown sex). Fifty percent of the respondents were between 23 and 33 years old; the youngest respondent was 12 and the oldest 74. Forty-five percent of the respondents lived in towns with more than 50 thousand inhabitants. Fifty percent of the respondents had a college education, while twenty-eight percent of the respondents studied or worked in the field of biology.

The second questionnaire, in which flower complexity and prototypicality were determined, was completed by 582 people (427 women, 153 men and two people of unknown sex). Fifty percent of the respondents were between 25 and 38 years old. The youngest respondent was 10 and the oldest 88. Forty-three percent of the respondents lived in towns with more than 50 thousand inhabitants. Fifty-three percent of the respondents had a college education, while twenty-five percent of respondents studied or worked in the field of biology.

Color blind respondents were excluded from the data set.

The characteristics of the respondents were very similar in both questionnaires, and it is likely that many people completed both questionnaires. We can thus assume that the ratings from both questionnaires are mutually relevant and comparable.

2.5. Statistical analyses

We analyzed the data using R software, version 3.1.3. The significance level α was set to 0.05 in all tests.

We computed the scores of the mean beauty, complexity and prototypicality rating of each flower from all respondents. The scores could theoretically vary from 1 to 6 points. The score of flower beauty represented the dependent variable. In the color preference analysis, we computed the difference between the beauty scores of each colored flower and its sepia tone version. The difference could theoretically vary from, -5 to +5 points. This difference then served as the dependent variable.

To determine the relationship between beauty, complexity and prototypicality, we used Pearson's correlation test (for normal distributions) or Spearman's rank correlation. We used the partial Kendall's correlation (R package 'ppcor') when it was necessary to filter the effect of a confounding variable. When comparing the means of two groups, we used Student's t-test (for normal distributions) or Wilcoxon's rank sum test. We also created general linear models to determine the relative importance of flower traits in the rating of flower beauty. We simplified the initial full model by stepwise backward elimination in order to ensure that the final reduced model could not differ significantly from the initial full model.

2.6. Comparison of stimuli subsets

We wanted to determine if there were any beauty score differences between the subsets of stimuli that were not caused by the different flower colors in each stimuli pair. We used a paired t-test to compare the beauty scores between the members of each pair (sepia tone version). No significant differences were found (mean difference = 0.017 point, 95 % CI [-0.18, 0.21], $t = 0.18$, $df = 25$, $p = 0.86$, Cohen's $d = 0.035$). We also found a strong positive correlation between the beauty scores of subset 1 and subset 2 (r = 0.63, 95 % CI [0.32, 0.82], t = 4.00, df = 24, $p < 0.001$). For this reason, we pooled the data from both subsets and analyzed them together.

3. Results

3.1. Flower color

We used a paired t-test to compare the mean beauty rating of colored and sepia tone flowers. Colored flowers had a significantly higher rating than the sepia tone ones (mean difference = [illegible], 95 % CI [0.07, 0.22], t = 4.02, df = 51, p < 0.001, Cohen's d = 0.56). There was a strong positive correlation between the beauty rating of colored flowers and their sepia tone versions (ρ = 0.85, 95 % CI [0.75, 0.91], S = 3609.1, $p < 0.001$).

To determine whether the dominant flower color (hue) influenced its beauty rating, we created a general linear model in which the difference between the beauty score of each colored flower and its sepia tone version was the dependent variable. As explanatory variables we used the flower traits that could theoretically influence this difference. These were: dominant flower color (hue), lightness of the dominant flower color, saturation of the dominant flower color, number of colors in each flower, and flower prototypicality, symmetry and angularity. The initial full model (adjusted $R^2 = 0.56$) showed a significant effect of dominant flower color and symmetry. However, the final model (Table 1) consisted of only one explanatory variable – the dominant flower color (hue) - and was highly significant (adjusted $R^2 = 0.49$, $F_{4, 41} = 11.91$, $p < 0.001$). Tukey-Krammer's post hoc test revealed that blue color was the most preferred. The mean difference between the rating of blue flowers and their sepia tone versions was 0.40 ~~point~~. Blue was followed by purple (0.25 point) and pink (0.23 point). White color had no significant effect, and yellow flowers were rated even worse than their sepia tone versions (-0.17 point). See Fig. 2 and Table 2 for details.

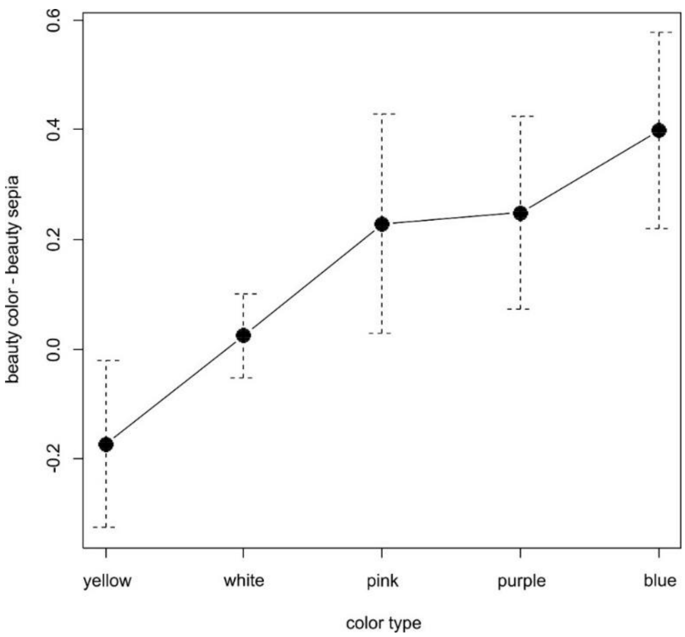
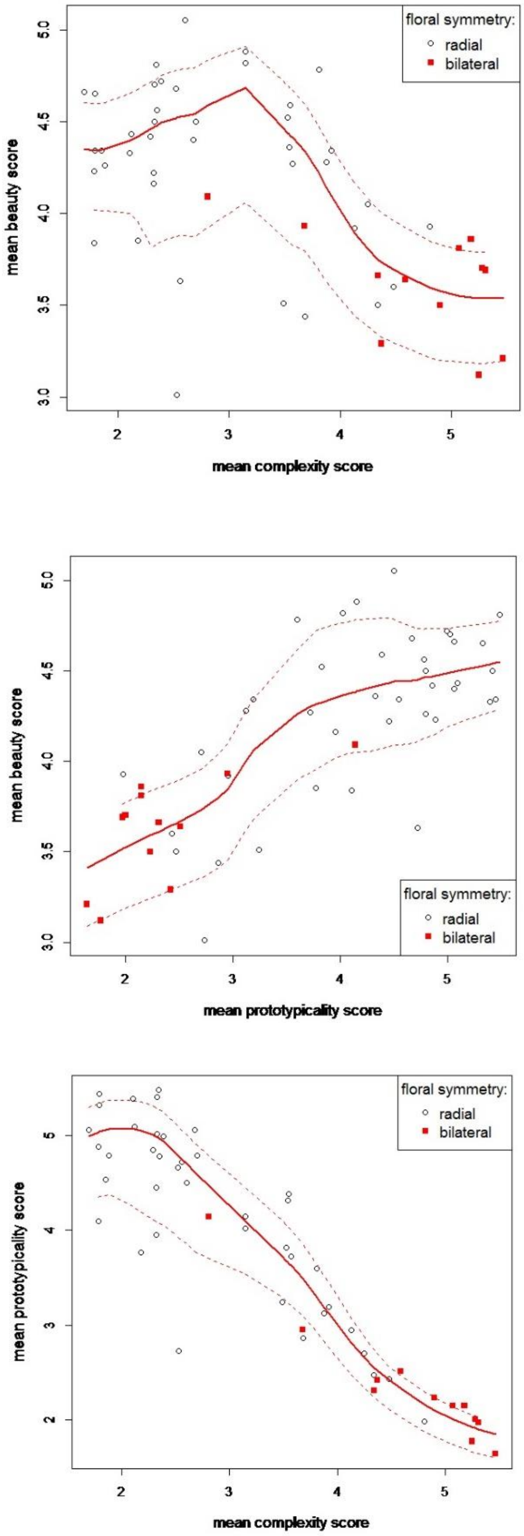


Fig 2. Effect of flower color on the estimation of beauty. **X axis**: different flower colors (hues), **Y axis:** difference between the mean beauty rating of the colored flowers and their sepia tone versions. **Error bars** represent the 95 % CI.

3.2. Beauty scores and flower traits

We determined the relationship between the scores of flower beauty, complexity and prototypicality. There was a significant positive correlation between the beauty and prototypicality scores ($\rho = 0.75$, S = 36660.39, $p < 0.001$; Fig. 3A). We found a significant negative correlation between the flower beauty and complexity scores ($\rho = -0.56$, S = 5750.47, $p < 0.001$; Fig. 3B). There was, however, a very strong negative correlation between the complexity and prototypicality scores ($r = -0.91$, $t = -15.61$, df = 50, $p < 0.001$, 95 % CI [-0.95, -0.85]; Fig. 3C). For this reason, we also computed the Kendall's partial correlation between the beauty and complexity scores, when controlling for prototypicality (and vice versa). There was still a significant positive correlation between the beauty and prototypicality scores when we excluded the effect of complexity ($z = 4.13$, df = 50, $p < 0.001$, $\tau = 0.40$), but there was no correlation between the beauty and complexity scores when we excluded the effect of prototypicality ($z = 0.41$, df = 50, $p = 0.68$, $\tau = 0.040$).

We used a Wilcoxon rank sum to determine the differences in the complexity and prototypicality scores of bilaterally and radially symmetrical flowers. To reveal the difference in beauty scores between bilaterally and radially symmetrical flowers, we used a two sample t-test. Radially symmetrical flowers scored higher in beauty (mean difference = 0.65 points, 95 % CI [0.37, 0.93], $t = 4.65$, $p < 0.001$, Cohen's $d = 2.00$) and prototypicality (median bilateral = 2.19 points, median radial = 4.42 points, $W = 447.5$, $p < 0.001$, Hodges-Lehmann estimator = 2.02, 95 % CI [1.25, 2.56]). Bilaterally symmetrical flowers had higher scores in complexity (median bilateral = 4.99 points, median radial = 2.55 points, $W = 30$, $p < 0.001$,
Hodges-Lehmann estimator = -1.93, 95 % CI [-2.61, -1.26]). All significant results remained significant also after performing the Bonferroni correction for multiple tests.



A

B

C

Fig. 3. Correlation between the mean beauty, complexity and prototypicality ratings. Each variable could vary from 1 (least beautiful/complex/prototypical) to 5 (most beautiful/complex/prototypical). A LOESS fitted line is shown (full line). Dashed lines represent the function spread (±SD) **A:** Correlation between the beauty and complexity scores. S = 36660.39, $p < 0.001$, **ρ = -0.56**, 95 % [-0.72, -0.34]; **B:** Correlation between the beauty and prototypicality scores. S = 5750.47, $p < 0.001$, **ρ = 0.75**, 95 % [0.60, 0.85]; **C:** Correlation between the prototypicality and complexity scores. t = -15.61, df = 50, $p < 0.001$, **r = -0.91**, 95 % CI [-0.95, -0.85].

To determine the relative importance of different flower traits for rating their beauty, we created a general linear model in which the flower beauty scores served as the dependent variable. We wanted to include the dominant flower color (hue) in the model. At the same time, we also wanted to use the information contained in those flowers with a unique or uncertain dominant color (hue), which were deleted from the dataset in the previous color analysis. For this reason, we converted the factor variable dominant color (hue), which had five levels, into five binary variables (with levels of *no* and *yes*): white, yellow, purple, pink and blue. We also used the same procedure with the variable angularity. This step allowed us to gain information from the whole dataset and avoid reducing the degrees of freedom. As further explanatory variables we used the following flower traits: prototypicality, the number of colors in each flower, symmetry, lightness of the dominant flower color and saturation of the dominant flower color (or the most common color in the case of flowers with an uncertain dominant color). We did not include complexity in the model because of its very strong correlation (r = -0.91) with flower prototypicality.

The initial full model ($R^2 = 0.75$, adjusted $R^2 = 0.68$) revealed a significant effect of prototypicality, blue color, angularity and saturation. The final reduced model (Table 3) confirmed only the effect of prototypicality, blue color and sharp contours (adjusted $R^2 = 0.70$, $F_{3, 48} = 39.81$, $p < 0.001$). All three of these variables had a significant positive effect on the mean flower beauty rating. The most important was prototypicality, followed by blue dominant color and sharp flower contours (Table 4).

As a control, we also created another linear model in which the flower hues were represented as levels of a single factor variable and the flowers with a unique or uncertain dominant color were deleted from the dataset. The final reduced model was very similar to the model in which no flowers were excluded from the data set (adjusted $R^2 = 0.64$, $F_{7, 38} = 12.50$, $p < 0.001$), and it contained the same variables with similar significant effects (prototypicality: estimate = 0.32, SE = 0.046, 95 % CI [0.23, 0.42], t = 7.02, $p < 0.001$; dominant blue color: estimate = 0.35, SE = 0.13, 95 % CI [0.09, 0.62], t = 2.72, $p = 0.010$; sharp contours: estimate = 0.30, SE = 0.11, 95 % CI [0.076, 0.53], t = 2.70, $p = 0.010$).

	df	Sum of Squares	F	*p*
hue	4	1.72	11.91	< 0.001
residuals	41	1.48		

Table 1. ANOVA table of the general linear model. ANOVA table of the final reduced model is shown. The difference between the mean beauty scores of the colored and sepia tone flowers was used as the dependent variable. See sections 2.2., 2.5. and 3.1. for details of the explanatory variables.

	Coefficients Estimate	95 % CI	t	*p*
intercept (hue = white)	0.025	[-0.077, 0.13]	0.49	0.62
hue = yellow	-0.20	[-0.37, -0.02]	-2.35	0.024
hue = pink	0.20	[0.026, 0.38]	2.32	0.026
hue = purple	0.22	[0.054, 0.39]	2.66	0.011
hue = blue	0.37	[0.21, 0.54]	4.61	< 0.001

Residual standard error = 0.19, df = 41, adjusted R^2 = 0.49, p-value = 1.64e-06

Table 2. Coefficient estimates of the general linear model. Coefficient estimates of the final reduced model are shown. The difference between the mean beauty scores of the colored and sepia tone flowers was used as the dependent variable. All effects remained significant after backward sequential correction for multiple tests. See sections 2.2., 2.5. and 3.1 for details of the explanatory variables.

	df	Sum of Squares	F	*p*
prototypicality	1	7.48	96.37	< 0.001
hue = blue	1	1.18	15.20	< 0.001
angularity = sharp	1	0.61	7.88	0.0072
residuals	48	3.72		

Table 3. ANOVA table of the general linear model. ANOVA table of the final reduced model is shown. The mean beauty score of the colored flowers was used as the dependent variable. See sections 2.2., 2.5. and 3.2. for details of the explanatory variables.

	Coefficients Estimate	95 % CI	t	*p*
intercept	2.84	[2.58, 3.11]	21.74	< 0.001
prototypicality	0.31	[0.24, 037]	9.30	< 0.001
hue = blue	0.35	[0.14, 0.56]	3.33	0.0017
angularity = sharp	0.25	[0.07, 0.43]	2.81	0.0072

Residual standard error = 0.28, df = 48, adjusted R^2 = 0.70, p-value = 4.53e-13

Table 4. Coefficient estimates of the general linear model. Coefficient estimates of the final reduced model are shown. The mean beauty score of the colored flowers was used as the dependent variable. All effects remained significant after backward sequential correction for multiple tests. See sections 2.2., 2.5. and 3.2. for details of the explanatory variables.

4. Discussion

We found that the presence of color generally slightly increased the beauty rating of flowers. When we compared colored and sepia tone versions of the same flowers, we found significant differences in the effects of specific colors. Blue was the most preferred, followed by pink and purple. As expected, white flowers did not differ from their sepia tone versions in their ratings, because both versions looked very similar. Yellow flowers were rated as less beautiful than their sepia tone versions. We were not able to measure the effect of red because only one genus (*Papaver*) native to the Czech Republic typically has red flowers. Our results correspond well with the habitat selection theory (Heerwagen & Orians, 1993) and also with the ecological valence theory (Palmer & Schloss, 2010) as well as with empirical research on the perceived beauty of simple colors (Camgöz et al., 2002; Ellis & Ficek, 2001; Hurlbert & Ling, 2007; Schloss et al., 2012; Zemach et al., 2006) and tree canopies (Müderrisoğlu et al, 2009). A preference for blue was also reported for pita birds, which are very similar in shape but differ in coloration (Lišková et al., 2014). We can assume that the general human color preference (as determined in American and European populations) also applies to flowers.

It is important to note that although there were differences in flower color preference, they had only a minor effect when compared to the importance of flower shape. Only the presence of blue color significantly affected the beauty rating of flowers with diverse shapes. This relative unimportance of color was also found in the beauty rating of birds, where their shape (such as the length of the tail) had the major effect. However, blue and yellow colors also affected the perceived beauty of birds (Frynta et al., 2010; Lišková & Frynta, 2013).

There is no agreement on the effect of lightness on the beauty rating of objects and organisms. Lišková and Frynta (2013) stated that the beauty rating of birds increased with the overall lightness of their coloration. Schloss and colleagues (2012) found that lightness had no effect on the rating of color squares, a negative effect on the rating of small objects (e.g., t-shirt, pillow) and a positive effect on the rating of large objects (walls). We found no effect of lightness on the beauty rating of flowers. These differences in results may be caused by the use of different procedures to determine the degree of lightness and also by differences in stimuli presentation. It is also probable that the relative importance of lightness is context dependent.

We report a very close relationship between the perceived flower prototypicality, complexity and type of symmetry. We expected to find a negative correlation between the prototypicality and complexity scores, but not as strong as our results actually indicate (r= -0.91). It would be helpful to compare the perceived complexity scores with some objective measurements. Unfortunately, it is very difficult to find an objective measurement method that could be applied to flowers with such a diversity of shapes.

The observed relationship between the flower beauty and complexity scores was very close to an inverse U shape. This finding is in accord with previous research (Akalin et al., 2009; Hekkert & van Wieringen, 1990). Overly simple objects are usually described as boring, while very complex objects are difficult to process, which could explain their low preference (Reber et al., 2004).

Bilaterally symmetrical flowers scored very low in prototypicality and very high in complexity. It is true that bilaterally symmetrical flowers are less common in the Czech Republic (and also worldwide). They often have fused floral parts and are highly three dimensional, so it might be difficult to describe their shape. These facts may account for their low prototypicality and high complexity scores.

We observed large differences in beauty scores between bilaterally and radially symmetrical flowers (radially symmetrical flowers scored higher). This supports the hypothesis that more axes of symmetry should lead to more fluent processing of the object and its higher preference (Evans et al., 2000). Our findings may also quite paradoxically support the hypothesis predicting our preference for bilateral symmetry. People tend to associate bilateral symmetry with human faces and bodies or with animals (Little & Jones, 2003). Bilaterally symmetrical flowers might be difficult to categorize. Their confounding animal- or even humanlike appearance might lead to their low preference.

Partial correlations and the linear models also revealed that prototypicality encompasses both complexity and symmetry and is the main predictor of flower beauty. When we included prototypicality in our model, complexity and symmetry had no effect on flower beauty. Prototypical flowers had high beauty and low complexity ratings and were radially symmetrical.

Angularity also had a significant effect on the beauty scores. Surprisingly, it turned out that sharp contours positively affected the flower beauty scores, while mixed contours had no effect. Our results disagree with those of previous studies (Bar & Neta, 2006; Silvia & Barona, 2009), perhaps due to the different rating methods used. Previous research used forced choice methods in which the participants had to choose between two similar objects with different contours (e.g., sofa, watch, flower, rectangle etc.). In our case, each flower was rated separately, and we created no matching pairs with different levels of angularity. We also cannot dismiss the possibility that the preference for roundness is context-specific and does not apply to flowers.

4.1. Limitations and prospects

We have already mentioned some limitations of our study. First, we cannot overly generalize the results because the survey was conducted only on a non-representative sample of the Czech population. Cultural and individual differences in the evaluation of flower beauty (such as the effect of age, education or level of expertise) should certainly be explored in the future. Another limitation of our study was the fact that the respondents rated only photographs of single flowers. We should design an experiment in which real flowers would be rated and compare the results to those of the present study.

The relationship between prototypicality, complexity and symmetry is worthy of greater interest, not only in the case of flowers, but also in general. Attention should also be paid to the effect of red color on the rating of flower beauty, possibly by repeating the study with a more heterogeneous set of flowers not native to the Czech Republic.

The existence of unequal preferences for diverse flower traits opens an interesting question concerning the effects of flowers and plants on human health and performance. We should explore whether the effects of flowers and plants on human well-being change with their perceived beauty.

5. Conclusion

Our research provides some empirical evidence for the evolutionary theories concerning the aesthetic evaluation of flowers. The results suggest that people share common preferences for certain flower traits. It seems that perceived flower beauty is influenced by flower color. In accordance with the habitat selection theory, blue color increased and yellow decreased the perception of flower beauty. However, our results also showed that flower shape is more important than color in the beauty rating and that prototypicality has a major positive effect on the perceived beauty of flowers.

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Scientific name	English name	Family	Pair	Symmetry	Beauty-color	Beauty-sepia	Complexity	Prototypicality	Angularity	Dominant color
Alisma plantago-aquatica	common water-plantain	*Alismataceae*	1	radial	3.51	3.64	3.49	3.24	mixed	pink
Sagittaria sagittifolia	arrowhead	*Alismataceae*	1	radial	4.16	3.88	2.32	3.95	round	white
Anthericum liliago	st Bernard´s lily	*Asparagaceae*	2	radial	4.34	4.32	1.85	4.54	sharp	white
Gagea lutea	yellow star of Bethelem	*Liliaceae*	2	radial	4.26	4.5	1.88	4.79	round	yellow
Anoda cristata	spurred anoda	*Malvaceae*	3	radial	4.23	4.33	1.78	4.88	round	purple
Linum austriacum	asian flax	*Linaceae*	3	radial	4.66	4.29	1.69	5.6	round	blue
Dianthus superbus	fringed pink	*Caryophyllaceae*	4	radial	3.93	4.6	4.81	1.98	sharp	white
Lychnis flos-cuculi	ragged-robin	*Caryophyllaceae*	4	radial	3.5	3.21	4.34	2.47	sharp	purple
Dianthus carthusianorum	carthusian pink	*Caryophyllaceae*	5	radial	4.68	4.45	2.52	4.66	sharp	pink
Mycelis muralis	wall lettuce	*Asteraceae*	5	radial	4.22	4.3	2.32	4.45	sharp	yellow
Aster alpinus	alpine aster	*Asteraceae*	6	radial	4.81	4.66	2.34	5.48	round	blue
Erigeron annuus	annual fleabane	*Asteraceae*	6	radial	4.5	4.32	2.33	5.41	mixed	white
Eruca sativa	salad rocket	*Brassicaceae*	7	radial	3.1	3.5	2.53	2.73	round	white
Lunaria annua	annual honesty	*Brassicaceae*	7	radial	3.84	3.2	1.78	4.1	round	purple
Erythronium dens-canis	dogtooth violet	*Liliaceae*	8	radial	4.5	3.76	4.25	2.7	sharp	purple
Lilium martagon alba	white Turk´s cap lily	*Liliaceaea*	8	radial	4.28	4.31	3.88	3.12	mixed	white
Euphrasia rostkoviana	eyebright	*Orobanchaceae*	9	bilateral	3.81	3.78	5.7	2.15	mixed	white
Melittis melissophyllum	bastard balm	*Lamiaceae*	9	bilateral	3.29	3.12	4.37	2.42	round	pink
Anemone ranunculoides	yellow anemone	*Ranunculaceae*	10	radial	4.34	4.52	1.79	5.44	round	yellow
Fragaria viridis	wild strawberry	*Rosaceae*	10	radial	4.33	4.34	2.1	5.39	round	white
Galeopsis speciosa	large-flowered hemp nettle	*Lamiaceae*	11	bilateral	3.69	3.24	5.31	1.97	mixed	NA
Lamium maculatum	spotted deadnettle	*Lamiaceae*	11	bilateral	3.12	2.68	5.25	1.77	round	pink
Convolvulus arvensis	field bindweed	*Convolvulaceae*	12	radial	3.85	3.91	2.18	3.77	round	white
Gentiana acaulis	stemless gentian	*Gentianaceae*	12	radial	4.88	4.21	3.15	4.15	sharp	blue
Althaea officinalis	marsh-mallow	*Malvaceae*	13	radial	4.42	4.13	2.29	4.85	round	white
Geranium palustre	marsh cranesbill	*Geraniaceae*	13	radial	4.65	4.37	1.79	5.32	round	purple
Geum urbanum	wood avens	*Rosaceae*	14	radial	4.36	4.83	3.54	4.32	mixed	yellow
Potentilla sterilis	barren strawberry	*Rosaceae*	14	radial	4.52	4.63	3.53	3.82	mixed	white
Crepis biennis	rough hawksbeard	*Asteraceae*	15	radial	4.4	4.37	2.68	5.6	sharp	yellow
Hieracium aurantiacum	orange hawkweed	*Asteraceae*	15	radial	4.59	4.15	3.55	4.38	sharp	NA
Hypericum perforatum	St John´s wort	*Hypericaceae*	16	radial	4.5	4.84	2.7	4.79	mixed	yellow
Rubus fruticosus agg.	blackberry	*Rosaceae*	16	radial	3.63	3.7	2.56	4.72	mixed	white
Atropa bella-donna	deadly nightshade	*Solanaceae*	17	radial	3.44	3.59	3.68	2.86	mixed	NA
Campanula rotundifolia	harebell	*Campanulaceae*	17	radial	5.5	4.87	2.6	4.5	sharp	blue
Lathyrus tuberosus	tuberous pea	*Fabaceae*	18	bilateral	3.66	3.14	4.34	2.31	round	pink
Pisum sativum	garden pea	*Fabaceae*	18	bilateral	3.64	3.66	4.59	2.51	mixed	white
Gentiana verna	spring gentian	*Gentianaceae*	19	radial	4.82	4.12	3.15	4.2	round	blue
Silene dioica	red campion	*Caryophyllaceae*	19	radial	4.27	4.12	3.57	3.72	round	pink
Viola biflora	alpine yellow-violet	*Violaceae*	20	bilateral	3.93	3.85	3.68	2.95	mixed	yellow
Viola reichenbachiana	early dog-violet	*Violaceae*	20	bilateral	4.9	3.57	2.81	4.14	round	blue
Borago officinalis	borage	*Boraginaceae*	21	radial	4.78	4.31	3.81	3.6	sharp	blue
Swertia perennis	felwort	*Gentianaceae*	21	radial	4.34	4.27	3.92	3.19	sharp	blue
Ficaria verna	lesser celandine	*Ranunculaceae*	22	radial	4.43	4.63	2.12	5.9	mixed	yellow
Xeranthemum annuum	immortelle	*Asteraceae*	22	radial	4.7	4.44	2.33	5.2	sharp	purple
Cymbalaria muralis	ivy-leaved toadflox	*Orobanchaceae*	23	bilateral	3.5	3.4	4.9	2.23	mixed	blue
Kickxia elatine	cancerwort	*Orobanchaceae*	23	bilateral	3.21	3.4	5.47	1.64	mixed	NA
Epipactis palustris	marsh helleborine	*Orchidaceae*	24	bilateral	3.86	3.74	5.18	2.15	mixed	NA
Ophrys apifera	bee orchid	*Orchidaceae*	24	bilateral	3.7	3.5	5.28	2	round	pink
Geranium pyrenaicum	hedgerow geranium	*Geraniaceae*	25	radial	4.72	4.64	2.39	4.99	round	purple
Stellaria holostea	greater stitchwort	*Caryophyllaceae*	25	radial	4.56	4.51	2.35	4.78	round	white
Arctium tomentosum	downy burdock	*Asteraceae*	26	radial	3.6	3.12	4.48	2.43	sharp	NA
Cirsium arvense	creeping thistle	*Asteraceae*	26	radial	3.92	3.67	4.13	2.95	mixed	purple

1 = least beautiful/complex/prototypical, 6 = most beautiful/complex/prototypical

Appendix. List of flower stimuli.