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This misconception might have arisen because holoparasites are extremely conspicuous and are celebrated by botanists, while hemiparasites could be overlooked as they appear superficially similar to other autotrophic plant species.

What is there still to learn? Many clades of parasitic plants are poorly studied and there is little known about their systematic relationships, their species diversity, and their development and evolution. Even well-studied clades lack genetic resources such as well-annotated genome sequences and reliable genetic transformational protocols. While great strides have been made into understanding parasitism genes, there are major open questions as to the actual genetic changes necessary for parasitism, how (and when) these genes are expressed, and the way these genes interact to form haustoria and initiate attachment. There is also much to learn about host–parasite interactions, including the mechanistic details of the host immune response and parasite immune suppression, and how this understanding can be translated into commercially successful parasite-resistant crops.

SUPPLEMENTAL INFORMATION

Supplemental Information contains two tables and can be found with this article online at https://doi.org/10.1016/j.cub.2018.06.030.

Where can I find out more?

Irving, L.J., and Cameron, D.D. (2009). You are what you eat: interactions between root parasitic plants and their hosts. Adv. Bot. Res. *50*, 87–138.

Joel, D.M., Gressel, J., and Musselman, L.J. eds. (2013). Parasitic Orobanchaceae (Berlin Heidelberg: Springer-Verlag).

Press, M.C., and Phoenix, G.K. (2005). Impacts of parasitic plants on natural communities. New Phytol. *166*, 737–751.

Westwood, J.H., Yoder, J.I., and Timko, M.P. (2010). The evolution of parasitism in plants. Trends Plant Sci. *15*, 227–235.

Yang, Z., Wafula, E.K., Honaas, L.A., Zhang, H., Das, M., Fernandez-Aparicio, M., Huang, K., Bandaranayake, P.C.G., Wu, B., Der, J.P., *et al*. (2015). Comparative transcriptome analyses reveal core parasitism genes and suggest gene duplication and repurposing as sources of structural novelty. Mol. Biol. Evol. *32*, 767–790.

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Primer

Aesthetics

Aenne A. Brielmann[1,*] and Denis G. Pelli[1,2,*]

Our everyday lives are full of aesthetic experiences. We wake up and frown at an overcast sky, or smile at the sight of the sun. Myriad decisions depend on the aesthetic appeal of the available options like which shirt to wear, which route to take to work, or where to eat. Even life-changing decisions, like where to live or who to live with, are partly based on their aesthetic appeal.

The term *aesthetics* was coined by the German philosopher Alexander Baumgarten (1714–1762) to denote the science of what is sensed and imagined. Today, the *Oxford English Dictionary* (*OED*) defines 'aesthetic' as "concerned with beauty or the appreciation of beauty" and more specifically as "giving or designed to give pleasure through beauty." Unlike this beauty-centric definition, however, the field of *empirical aesthetics* — the scientific study of aesthetics — is mostly concerned with the perception and evaluation of art. It is quantitative and acknowledges the primacy of beauty, as expressed by the *OED* above, but goes beyond the feeling of beauty, to also consider interest, being moved, and even repulsion. It is closely connected to cognitive and affective psychology and neuroscience.

The field of empirical aesthetics has yet to settle on a single definition of *aesthetics*. One of the clearest definitions comes from the neuroscientist Anjan Chatterjee: "The term aesthetics is used broadly to encompass the perception, production, and response to art, as well as interactions with objects and scenes that evoke an intense feeling, often of pleasure". This definition and the field of empirical aesthetics deemphasize beauty. This veers away from the *OED* and popular usage; the most commonly used aesthetic descriptor for art, landscapes, faces, cars, and clothing is 'beautiful'. Unlike philosophy, studies in empirical aesthetics often just use terms like 'beauty', 'liking', and 'pleasure' in their methods, without specifying meanings.

We discern two main foci of empirical aesthetics, one broad — research on beauty, aesthetic pleasure, and preference — and one narrowly focused on art — research on the perception, evaluation, and creation of art. We take the broader focus, and include art as one of many stimuli that elicit aesthetic responses.

A brief history

Our scope here is the scientific topic of aesthetics, which begins with the birth of psychology in the 19th century. However, philosophers have written thoughtfully about beauty for millennia. For example, one of Plato's Socratic dialogs, *Hippias Major*, tentatively defines beauty as pleasure through eye or ear. And Kant theorized that beauty is a free play of imagination with understanding, which sounds a lot like modern neuroaesthetics.

Empirical aesthetics has only recently attracted much interest from neuroscience, psychology, and the public, but it is actually one of the oldest fields in psychology. In 1876, one of the fathers of modern psychology, Gustav Fechner, wrote the two-volume book *Vorschule der Ästhetik* (*Preschool of Aesthetics*); he claimed that, like any other psychological phenomenon, aesthetics should be studied from 'below' (empirical observation), not from 'above' (philosophical supposition). The path from 'below' for Fechner meant observing responses to individual experiences and inferring general laws from the pattern across multiple observations, much as natural sciences works today. Fechner's famous 1865 book, *Elements of Psychophysics*, defined the basic methods, still used today, of testing behavior to infer brain processes.

Fechner aimed to discover how the physical properties of the world provoke aesthetic responses: pleasure and displeasure. Note that Fechner did not restrict the application of aesthetics — liking and pleasure — to the realm of art or other 'higher' pleasures. Thus, his definition of aesthetics was broader than that of today's dictionaries. By rejecting the usefulness of an aesthetic 'from above', he also dismissed any pre-defined notions of beauty or liking and aimed to investigate the popular use of these terms. Today, most researchers still adhere to his method of empirical investigation of aesthetics — in that they record participants' responses to a range of stimuli under varying conditions — but not all subscribe to

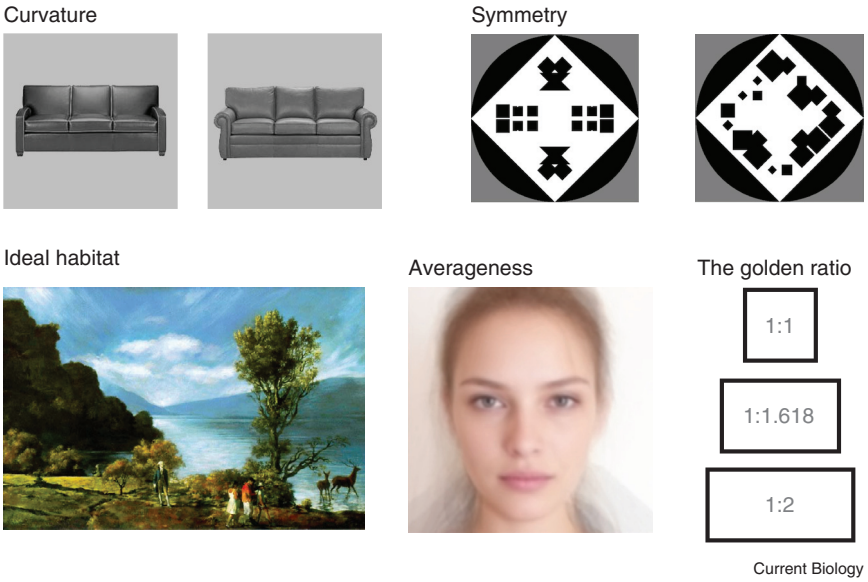

Figure 1. Examples of aesthetically pleasing stimulus properties.
Top left: curvature example from Bar *et al.* (Psychol. Sci. (2006) *17*, 645–648). Top right: symmetrical versus asymmetrical patterns as used by Bertamini *et al*. (2013). Bottom left: Komar and Melamid, *America's Most Wanted*, 1994, oil and acrylic on canvas; courtesy the artist and Ronald Feldman Gallery, New York; an ideal human habitat. Bottom center: a female average face created from 15 average-looking women by Jun'ichiro Seyama (https://www.flickr.com/photos/averageface/8270895759). Bottom right: Rectangles of different aspect ratios with the golden ratio in the middle.

this democratic notion of which objects are relevant to aesthetics.

Research on aesthetics came to a halt after Fechner, as behaviorism started to restrict psychology. Behaviorism constrained psychology to deal only with observable behavior and banned modeling of inward experiences, like feelings, that cannot be directly observed. (This was naively motivated by trying to make psychology more 'scientific', more like physics, which, ironically, at that time was making great headway with cloud chambers that were used to reach conclusions about atomic processes that cannot be directly observed.) Psychologists thus ceased to investigate phenomena like aesthetics that are inherently experiential and subjective. However, behaviorism did not inhibit writing on aesthetics beyond the psychology journals.

At the end of the 19th century, after Fechner but before behaviorism, the playwright Oscar Wilde (1854–1900) persuasively argued for the Aesthetics Movement, whose motto was: "Art for art's sake". After World War II, aesthetics as perception of art was examined in two very influential books: Rudolf Arnheim's *Art and Visual Perception* (1954/1974) and Ernst Gombrich's *Art and Illusion: A Study in the Psychology of Pictorial Representation* (1960). Arnheim (1904–2007) learned Gestalt theory in Berlin from Wertheimer and Kohler, and was president of the American Society for Aesthetics. Art historian Gombrich's (1909–2000) book argues that art "comes to life" not through its actual faithfulness, but by meeting the needs and expectations of the time. Aesthetics is a battleground in today's culture wars. Disability aesthetics and queer theory argue that accepting disability and unconventional gender roles enriches and complicates notions of the aesthetic.

Reclaiming ground from the receding tide of behaviorism, psychologist Daniel Berlyne (1924–1976) published *Aesthetics and Psychobiology* (1971). He claimed that aesthetic pleasure has an inverted-U-shaped relationship to complexity (and other qualities, including novelty), which is mediated by arousal. Like Fechner, Berlyne investigated how object properties elicit more or less aesthetic pleasure. His hypothesis that pleasure is mediated by a U-shaped dependence on arousal is still being tested in empirical aesthetics today. The evidence is controversial but tends to disconfirm Berlyne's hypothesis.

Following Berlyne, empirical aesthetics again went silent, except for research on facial attractiveness. Art and other objects of aesthetic appreciation that evoke much greater inter-individual differences remained almost uninvestigated by empirical aesthetics and were thus left to art history and criticism, notably Gombrich and Arnheim. This changed with the advent of a new approach within empirical aesthetics: neuroaesthetics.

In 1999, a shift from psychophysics to functional magnetic resonance imaging (fMRI) in aesthetics started when Semir Zeki, with his colleagues Tomohiro Ishizu, Hideaki Kawabata, and others, sought an area of the brain whose activity is correlated with beauty responses, independent of stimulus modality. This approach mirrored a greater turn in the field: away from Fechner and Berlyne's search for the relation between stimulus properties and aesthetic pleasure response and towards a universal mechanism that underlies this pleasure across stimuli. What remained, however, is the idea that aesthetics, like any topic in science, can be understood through rigorous empirical research.

Neuroaesthetics has caught the public imagination, and has stimulated much research in empirical aesthetics. Several new theories of aesthetic processing were proposed in the early 2000s: Helmut Leder's model emphasizes understanding the artwork ('cognitive mastery'); Rolf Reber suggested that aesthetic pleasure depends on the ease of stimulus processing ('fluency'); Anjan Chatterjee's neurological three-stage processing model involves sensory-motor, knowledge-meaning, and emotion-valuation neural systems; and Paul Locher's two-stage model consists of rapid initial gist extraction followed by a slow, cognitive, and evaluative stage. Other models emphasize: the importance of emotion and motivation; the distinction between beauty and interest; and transformative responses to art. As of today, these models are still being tested and there is little consensus.

We categorize the models and their underlying research by their focus on either the stimulus or the response. The *stimulus-focused* research aims to identify a set of object properties in the (usually) visual domain that contribute to aesthetic pleasure (see Stimulus-based determinants of aesthetic experience,

below). The *response-focused* research investigates the mechanisms, including their neural processes, that underlie aesthetic judgments (see Aesthetic processing, below).

Stimulus-based determinants of aesthetic experience

Some object properties contribute to aesthetic appeal. Figure 1 provides examples of various types of objects for which such properties have been assessed. The most frequently mentioned aesthetic preference may be that for symmetry over asymmetry. It has been established at least in abstract shapes, patterns, and faces. The question of a symmetry-preference in faces has been raised in a different context too, namely preference for averageness. Average face stimuli are usually generated by overlaying or morphing several faces with image-processing software, resulting in a face that is not only more average but also more symmetric. However, there is also evidence from other stimuli — for example, color patches, furniture, and surrealist paintings — that averageness in the sense of conformity with a category prototype is usually preferred over more-deviant exemplars. This greater liking for things that can be more easily categorized may also be reflected in people's general preference for figurative and representational over abstract art.

Perhaps the most broadly established aesthetic preference is the one of curvature over angularity. People like the appearance of otherwise equivalent shapes and objects more if their contours are round rather than sharp and angular, and this is the case in various cultures across the globe.

An average preference for colors of blue-green cold hue, relatively high saturation, and lightness is quite reliably found at least in Western adult observers. This preference is, however, culture-, gender- and age-dependent.

Many researchers have studied a potential aesthetic preference for the Golden Ratio, approximately 1.6:1. The nineteenth-century results of Gustav Fechner confirming a preference for rectangles with the golden aspect ratio have repeatedly failed to replicate. The golden ratio is frequently found in nature and classical art. One lab has shown that original classical statues possessing a golden ratio between the length of the upper body versus legs are preferred to manipulated versions with altered proportions. But, just like findings on simple shapes, these are likely stimulus-, context-, and observer-dependent responses.

Thus, many lines of research have aimed to identify universally aesthetically pleasing object features. Some features seem to have universal appeal (curvature, symmetry) while others have greater contextual and individual differences (color, ratios). These findings promise prediction of the average response across a population. However, their ability to predict an *individual's* aesthetic responses is limited by individual differences, which outweigh general tendencies in most aesthetic judgments. Even for faces, which are popularly supposed to be consistently judged, individual taste accounts for about half the variance in attractiveness ratings. Depending on the kind of stimulus, the between-observer agreement ranges can be much lower; for example, for photographs of real-world scenes roughly 15% of variance in ratings is shared between observers, and less than 10% for abstract art. It is also worth bearing in mind that sometimes deliberate deviations from on-average appealing features can hold a special appeal, too. 'Beauty marks' are a famous example — a fake mole on just one side of the face breaks the symmetry, yet is often reported to be especially attractive.

Evolutionary accounts

Given the evidence for at least some aesthetic universals, one might ask why they exist. In searching for an answer, some scientists seek explanations in evolutionary psychology. The evolutionary account holds its main appeal with regard to human beauty. Many attractive face attributes, like averageness, symmetry, and a reddish skin color, may indicate health and thus higher mate quality for producing children. In the same way, aesthetic preference for women with an hourglass-shaped figure has been linked to fertility. Similarly, preference for landscapes that include water, forest, and signs of animal life has been explained as attraction to human-friendly habitats. These evolutionary accounts hold that aesthetic pleasure is an automatic, intuitive heuristic that has evolved to promote decisions that favor reproductive success. This links beauty to value.

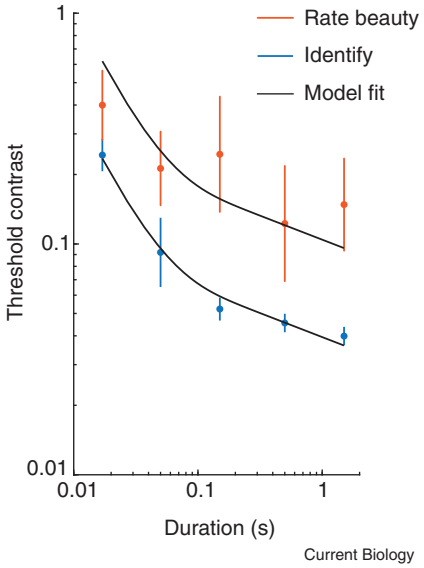

Figure 2. Comparing average threshold contrasts for face identification (blue) and judged beauty (orange).
On each identification trial, the observer was asked to indicate which face she saw by pressing a letter key corresponding to a column of faces labeled a–f. On each beauty trial, the observer was asked to rate how beautiful she found the face on this trial on a scale of 0–9. Contrast is defined relative to the original photo. Observers' ($N = 7$) threshold contrasts were measured for six very attractive faces from the Chicago Face Database (Ma *et al.*, 2015). Identification threshold criterion was 75% correct. Beauty threshold criteria were set to each individual participant's beauty judgment of the face with unrestricted viewing time minus one (on a 0–9 scale). Faces were 15 deg high. We ran separate blocks for identification and beauty. The sequence of faces and durations was randomized, and the contrast on each trial was chosen to minimize variance of the final threshold estimate. Threshold was measured in 60 trials by the QUEST adaptive Bayesian estimator. Error bars represent ± SEM in log contrast. Black lines show the fit of the model described in the main text where contrast threshold c for each duration t is given by the equation $c = a\, t^{\,b} / (1\text{-}\exp(\text{-}t/\tau))$. The parameter a varies by task (0.10 for beauty and 0.04 for identification), while τ (0.03 s) and b (–0.21) are constant.

On a different, but compatible, account, aesthetic experiences are regarded as a by-product of the fundamental set-up of human brains and senses. This view equates stimulation with pleasure and liking, so people 'like' things that stimulate brain activity.

These evolutionary accounts provide ideas about *why* aesthetic processing

occurs, but they do not specify *what* these processes are.

Aesthetic processing

In contrast to stimulus-focused research, response-focused research does not presuppose that there are stimulus properties that are universally appealing. Instead, this line of research is searching for a universal process that underlies everybody's aesthetic responses. As one of the first response-focused psychologists, Berlyne conjectured that the highest aesthetic pleasure arises from the mild arousal that is elicited by stimuli of medium complexity. However, the evidence linking arousal and complexity to aesthetic pleasure is mixed. Recent research by Manuela Marin and colleagues suggests that beauty, liking, and pleasure depend differently on complexity: inverted-U, negatively linear, and positively linear, respectively. This pattern of results emerged even though all these measures of aesthetic appeal were strongly positively correlated with one another ($0.73 \leq r \leq 0.95$).

The strong correlation between different judgments of aesthetic appeal is particularly striking when it comes to pleasure and beauty. Most philosophers claim that beauty is a kind of pleasure. In line with this notion, several studies have found that pleasure and beauty are linearly related. This leads to a very parsimonious account of beauty: It is a pleasure that is special in exceeding all other pleasures.

How does such high pleasure arise? The fluency theory states that an object is more pleasing the more easily (fluently) it can be processed. Two types of experimental result are interpreted as evidence for fluency theory by its proponents. First, increasing stimulus duration from 50 to 500 milliseconds increases aesthetic appeal, at least when the stimuli are abstract rather than natural, like faces. Second, if simple line drawings are preceded by a congruent priming stimulus — which is more or less equivalent to increasing the stimulus duration — they are liked better than when preceded by an incongruent one. In both types of studies, stimulus duration does not exceed one second, but pleasure and beauty are reported to be independent of stimulus duration over the range 1 to 30 seconds. That being said, there are many anecdotal accounts of rare experiences of great beauty that arise only after many minutes of exposure. These experiences may be too infrequent to be measured in a traditional lab paradigm. Possible accounts range from a slow cognitive process that builds a new perception over many minutes to, at the other extreme, a fixed very low independent probability of seeing the beauty in each glimpse, and the ability to retain it.

A parsimonious account for the finding that aesthetic appeal increases over the first few hundred milliseconds of stimulus presentation is that visual beauty requires vision: An aesthetic response requires successful early sensory processing. This hypothesis can be tested by comparing how the required contrast evolves with duration for both a basic visual task, such as correct identification, and for a high beauty rating (Figure 2). Natural images contain many features with various thresholds, and identification and beauty likely depend on different features, so we do not expect equal thresholds for identification and beauty. But if beauty and identification each consistently require a particular feature, then we expect similar curves, differing only by a contrast factor (assuming similar processing of both features). In a plot of threshold contrast vs duration, at short durations we expect Bloch's law, a fixed product of contrast and duration with log-log slope of –1, and at long durations expect probability summation with a shallow log-log slope of –1/3.5 (see Figure 6.13 in Watson, 1986).

Neuroaesthetics

Besides varying stimulus duration, the time course of aesthetic processing can be investigated in other ways as well. The high temporal resolution of EEG and MEG exposes some of the dynamics of the neural processing of the stimulus. Such studies consistently find differences between an early processing stage up to 300 milliseconds from stimulus onset and a late stage after 500 milliseconds or more. The early stage is mainly related to experiencing the stimulus and thus reflects the processing of the aesthetic stimulus itself, as discussed in the previous section. The late stage is mainly related to making an aesthetic evaluation of the stimulus, that is, the cognitive decision about how to judge or rate the stimulus.

In contrast, fMRI has poor temporal resolution (a time constant of roughly 6 seconds) and thus studies using this technique have not revealed much about fast temporal dynamics. They have, however, identified brain regions that contribute to processing aesthetic appeal independent of stimulus modality. These studies suggest that the processing of beauty is correlated most consistently with activity in the medial orbitofrontal cortex (mOFC) and the overlapping ventromedial prefrontal cortex (vmPFC). Meta-analyses confirm that judgments and experiences of pleasant (measured as liked, beautiful, or attractive) stimuli are associated with enhanced activation of the mOFC/vmPFC across many stimulus modalities. Preliminary results suggest that activation of the medial PFC is causally related to the experience of beauty, as trans-cranial direct current stimulation (tDCS) decreases beauty — but not ugliness — of abstract paintings. This suggests that beauty experiences across various modalities share the neural network that is associated with pleasure-processing and crucially involves the mOFC/vmPFC region.

Relation to other fields of psychology and future directions

Apart from its obvious relations to cognitive and affective psychology and neuroscience, empirical aesthetics also overlaps with other sub-disciplines of psychology and neuroscience. It is linked to social and personality psychology in considering the moderating effects of emotion, personality variables, culture, and expertise on aesthetic responses. Social and even political psychology bear on long-standing questions relating aesthetic and moral goodness. Consumer psychology overlaps with aesthetics when considering the perceptual appearance of commercial products. Looking forward, there is an open question of the relation of aesthetic value to economic value, as studied in decision making and neuroeconomics. Recently, empirical aesthetics has joined computational psychology in the creation and investigation of deep-learning algorithms that aspire to create art (such as Caedmon; http://www.caedmon.it/).

The scientific study of aesthetics has matured over the past two decades. The boundaries of the field remain porous, but a core interest in beauty, pleasure, and art has crystalized. In particular, two strands of research are yielding

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insight into several aspects of aesthetic experience. Stimulus-focused studies have determined key object properties that, on average, increase or decrease the aesthetic appeal of an object, such as symmetry and curvature. Response-focused studies have started to describe the processes that underlie aesthetic pleasure and their neural correlates independent of stimulus properties. So far, research indicates that aesthetic response requires successful early sensory processing and that there is an especially tight, linear relation between beauty and pleasure responses. Neurally, parts of the ventro-medial orbitofrontal cortex play a crucial role for processing beauty across many stimulus modalities.

FURTHER READING

Bertamini, M., Makin, A., and Rampone, G. (2013). Implicit association of symmetry with positive valence, high arousal and simplicity. i-Perception *4*, 317–327.

Chatterjee, A., and Vartanian, O. (2014). Neuroaesthetics. Trends Cogn. Sci. *18*, 370–375.

Graf, L.K.M., and Landwehr, J.R. (2015). A dual-process perspective on fluency-based aesthetics: the pleasure-interest model of aesthetic liking. Pers. Soc. Psychol. Rev. *19*, 395–410.

Ishizu, T., and Zeki, S. (2011). Toward a brain-based theory of beauty. PLoS One *6*, e21852.

Jacobsen, T., and Beudt, S. (2017). Stability and variability in aesthetic experience: a review. Front. Psychol. *8*, 1–14.

Leder, H., and Nadal, M. (2014). Ten years of a model of aesthetic appreciation and aesthetic judgments: the aesthetic episode — developments and challenges in empirical aesthetics. Br. J. Psychol. *105*, 443–446.

Ma, D.S., Correll, J., and Wittenbrink, B. (2015). The Chicago face database: A free stimulus set of faces and norming data. Behav. Res. Methods *47*, 1122–1135.

Nadal, M., and Pearce, M.T. (2011). The Copenhagen Neuroaesthetics conference: prospects and pitfalls for an emerging field. Brain Cogn. *76*, 172–183.

Palmer, S.E., Schloss, K.B., and Sammartino, J. (2013). Visual aesthetics and human preference. Annu. Rev. Psychol. *64*, 77–107.

Pearce, M.T., Zaidel, D.W.W., Vartanian, O., Skov, M., Leder, H., Chatterjee, A., and Nadal, M. (2016). Neuroaesthetics: the cognitive neuroscience of aesthetic experience. Perspect. Psychol. Sci. *11*, 265–279.

Pelowski, M., Markey, P.S., Lauring, J.O., and Leder, H. (2016). Visualizing the impact of art: an update and comparison of current psychological models of art experience. Front. Hum. Neurosci. *10*, 1–21.

Redies, C. (2015). Combining universal beauty and cultural context in a unifying model of visual aesthetic experience. Front. Hum. Neurosci. *9*, 1–20.

Watson, A.B. (1986). Temporal sensitivity. In Handbook of Perception and Human Performance, eds. Boff. K.R., Kaufman, L., and Thomas, J.P. (Wiley: New York), pp. 6/1–6/43.

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Botanical parasitism of an insect by a parasitic plant

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We report evidence of a new trophic interaction in nature whereby a parasitic plant attacks multiple species of insects that manipulate plant tissue when the two co-occur on a shared primary host plant. Most plant species are attacked by a great diversity of external and internal herbivores [1]. One common herbivore guild, gall-forming insects, induce tumor-like structures of nutrient-rich plant tissue within which immature insects feed and develop [2,3]. While the gall is made of plant tissue, its growth and development are controlled by the insect and it therefore represents an extended phenotype of the gall former [4]. Typically, parasitic plants attack other plants to gain nutritional requirements by connecting directly to the vascular system of their hosts using modified root structures called *haustoria* [5]. Here, we document the first observation of a parasitic plant attacking the insect-induced galls of multiple gall-forming species and provide evidence that this interaction negatively affects gall former fitness.

In a native scrub habitat in southern Florida, USA (27°1’ 39.9648” N; 80°6’ 33.444” W), we discovered the parasitic love vine, *Cassytha filiformis* (Lauraceae), attacking two species of gall-forming cynipid wasps on the sand live oak, *Quercus geminata* (Fagaceae). The gall wasp most commonly parasitized by *C. filiformis* was *Belonocnema treatae* (Hymenoptera: Cynipidae), which forms spherical,

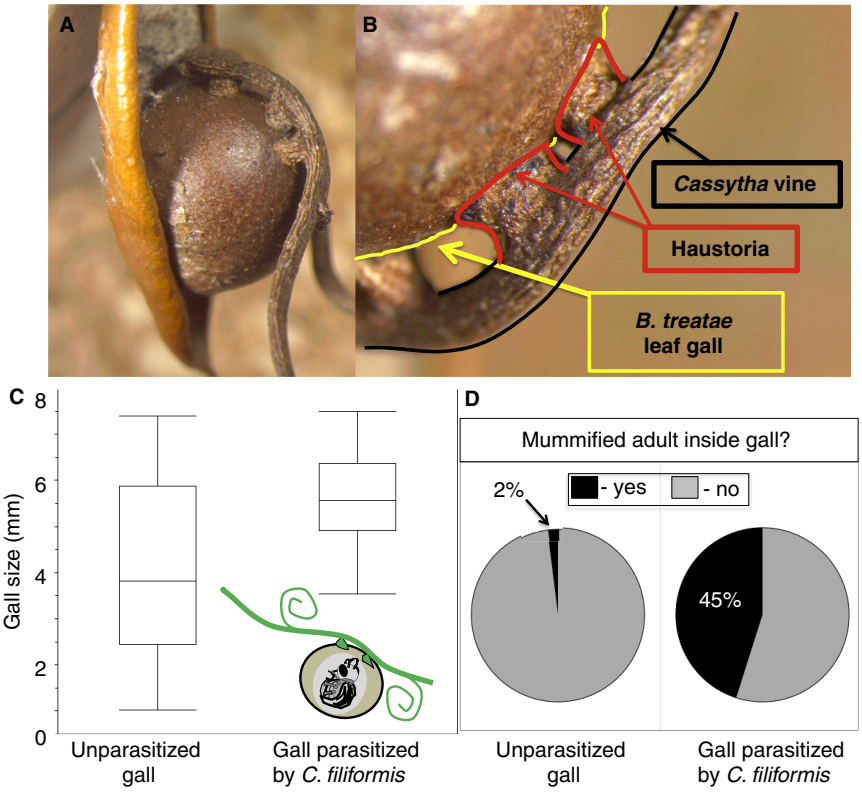

Figure 1. A trophic inversion involving a parasitic plant and a gall former.
(A) *Cassytha filiformis* vine attaching haustoria to a leaf gall induced by the wasp *Belonocnema treatae* on the underside of their host plant, *Quercus geminata*. (B) Labeled graphic of insect gall, parasitic vine, and vine haustoria. (C) Box plots of leaf gall diameter for unparasitized galls (control) and galls that have been parasitized by *C. filiformis*. (D) Proportion of *B. treatae* leaf galls that contained a dead ‘mummified’ adult for unparasitized galls (control) and galls that have been parasitized by the vine *C. filiformis*.