Perceptual biases, camouflage patterns, and the origin of sexual signals

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Abstract

Natural and sexual selection can be in conflict in driving the evolution of sexual ornamentation. Sexual selection typically favors detectability to potential mates, whereas natural selection penalizes detectability to avoid predators. Considering signal efficiency in addition to detectability, however, suggests that natural and sexual selection need not be antagonistic. In the visual domain, considerable evidence supports a "processing bias" by which people prefer images that match the spatial statistics of natural scenes, likely because the brain has evolved to process such scenes efficiently. A direct but untested prediction of this bias is that background-matching camouflage can be favored by natural and sexual selection. We conducted an online experiment where we show for the first time human preference for camouflaged patterning and confirm a preference for the average image statistics of natural scenes. Because many of the underlying visual mechanisms are shared across vertebrates, our results suggest that camouflage patterns can serve as evolutionary precursors of sexual signals.

Introduction

Sexual ornamentation in animals is often pulled in opposite evolutionary directions. Sexual selection driven by mate preferences is generally thought to lead to detectability or conspicuousness, to draw the attention of potential mates [1], whereas natural selection should lead to the opposite, favoring camouflage over detectability to avoid attracting predators [2]. Evidence for such a conflict has been shown in guppies, *Poecilia reticulata,* in which female preferences are biased towards detectable orange colouration [3–5] and males develop more intense orange colouration when predation is relaxed [6,7]. While conflicts between natural and sexual selection are generally thought to play an important role in shaping sexual signal diversity [8–10], many of the best examples are based on ornament color [11]. However, sexual signals also include patterns, which for visual images describe the

spatial organization of features, including colors and also shades of gray. Although visual patterns are receiving increased attention in research on sexual signals [12,13], the question of whether and to what extent they are shaped by conflicts between natural and sexual selection has so far remained little explored.

One problem is that conflicts between natural and sexual selection in the evolution of communication signals are primarily framed as a problem of signal *detection*, perhaps because of a historic focus on color. However, the attractiveness of a signal depends on more than its ability to be detected; it also depends on the ease with which the signal is processed by the brain [14–17]. This "processing bias" [18] may stem from the well-supported adaptation of the visual system to efficiently process natural statistics of the environment [19,20]. For visual signals, efficiency is achieved by matching signal design with the sensitivity (i.e., tuning) of visual neurons [21]. As a result, stimuli that resemble the underlying spatial patterns of natural scenes will be processed more efficiently (i.e. more easily and at lower metabolic cost), generating a feeling of fluency that is experienced as pleasant and therefore rewarding [22]. Indeed, a preference in humans for the statistical features of natural scenes is a robust finding in experimental psychology [23].

In nature, background-matching is a type of camouflage whereby the color and pattern of an animal's phenotype mimic those of its surroundings (see e.g. *25*). Given that background-matching relies on matching visual statistics of a stimulus with those of the habitat, the processing bias hypothesis predicts that, once detected, camouflage patterns should also be attractive to the observer. Small changes that increase the detectability of background-matching patterns to conspecifics could therefore increase the attractiveness of the signaler, thus aligning natural and sexual selection. This important but as yet untested prediction suggests that naturally selected camouflage patterns could serve as evolutionary precursors of some sexual signals.

Here, using humans as a model, we test the hypothesis that camouflage patterns are intrinsically visually attractive, and thus a pattern favored by natural selection can evoke preferences which then initiate sexual selection. In a first experiment, we used a detection task to assess the effectiveness of camouflage of different circular patterned stimuli that varied in their level of background matching. The backgrounds were artificial, but with spatial statistics either similar to those of many natural scenes or manipulated away from typical values. Participants were required to click on the circular pattern ('target') as quickly as possible to assess the detectability of the stimuli. In a second and third experiment, we evaluated the attractiveness of these targets, using the same patterned stimuli as for the detection task but removing the detectability constraint. Participants were asked to indicate which of the two patterns they preferred. In the second experiment, stimuli were presented in pairs against a uniform gray background to assess the baseline attractiveness of the target stimuli, independent of the background. In the third experiment, stimuli were presented in pairs against the same patterned backgrounds as for the detection task, so that the degree of background matching varied across stimuli, but stimuli were outlined to make them easily detectable. Our experiment therefore asked whether camouflage patterns are attractive when rendered detectable.

Results and Discussion

Generating variation in camouflage effectiveness

To evaluate the attractiveness of camouflage patterns, we first needed to generate patterned visual stimuli that differ in their camouflage effectiveness. To do so, we modified the Fourier slope of white noise images to manipulate the relative distribution of their spatial frequencies (from low to high spatial frequencies, corresponding to coarse-grained and fine-grained patterns, respectively). The Fourier slope is the relationship between power and spatial frequency when plotted on log-log axes, and that slope has been observed to lie close to -2 for many natural scenes. (e.g., *26*, *27*). With this approach, we could create abstract patterns and remove potential bias that would make interpretation more difficult (e.g. color or phase manipulation effects). Moreover, the Fourier slope is one of the most documented image statistics with effects on visual processing at different levels (i.e., on preferences, fluency, and neural encoding). We created circular images ("targets") and large square ("background") images and manipulated both the slope of the targets and the slope of their corresponding background in order to create different levels of background matching (Figure 1A). We designed the detection task with targets randomly positioned onto background images.

We postulated that targets with a slope closer to the slope of the background would be better camouflaged, that is, they would be less frequently detected and require more time to detect. Our results confirmed this prediction: these targets were the hardest to find (lower detection rates and higher detection times, Spearman correlation between detection rates and detection times, $r = -0.98$, $N = 18$).
Overall, results of the first experiment corroborate previous studies showing a link between Fourier slope and camouflage effectiveness. For example, octopuses and cuttlefish in camouflage mode modify their body pattern such that the Fourier slope of their body matches that of their visual environment [27,28]. In damselfish, matching the spatial frequencies of the background reduces the likelihood of being attacked by predators [29]. Our results complement these correlative studies, showing that the Fourier slope can be manipulated to generate variation in the camouflage effectiveness of background-matching stimuli.

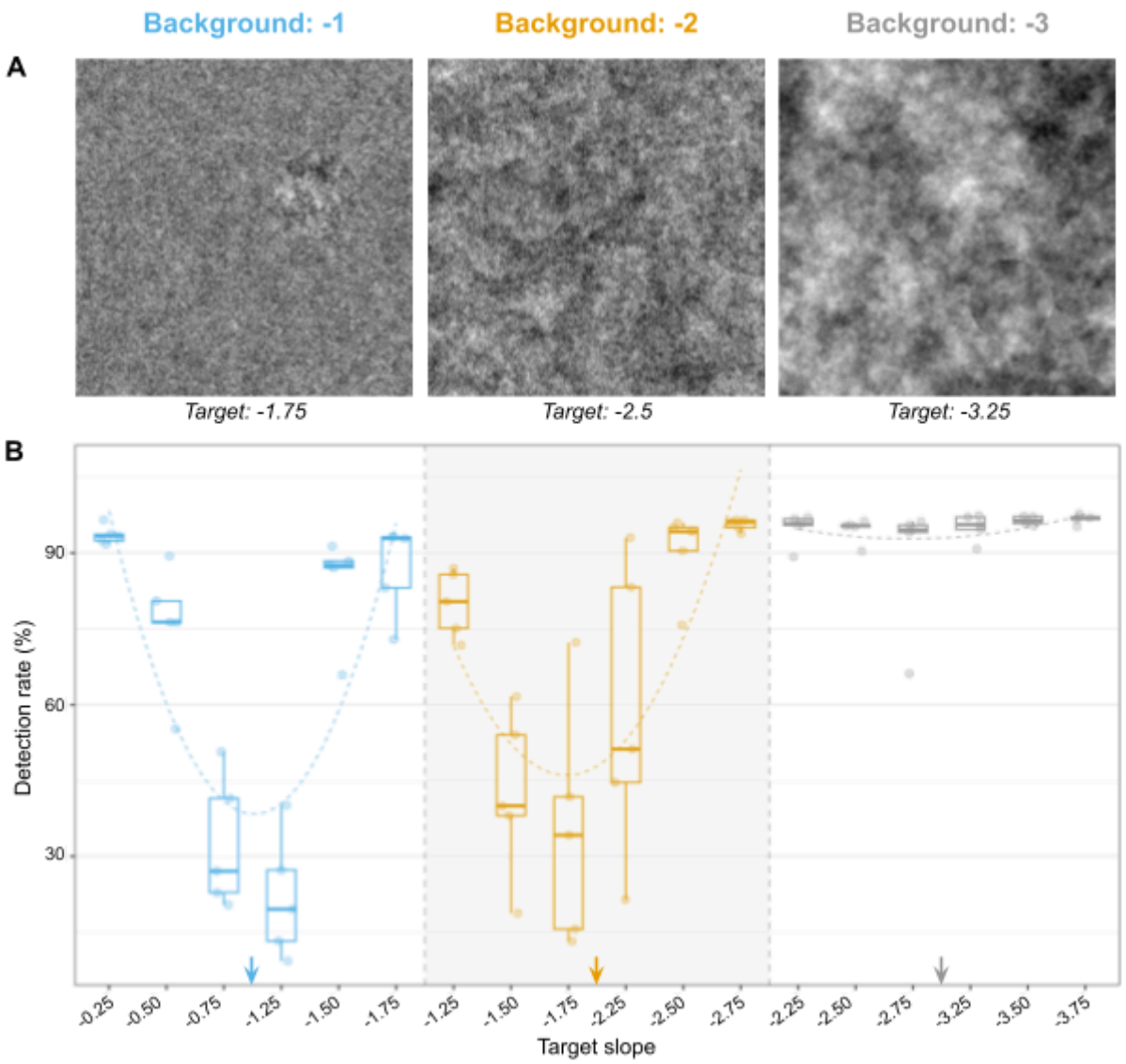

Figure 1: Detection task. *(A) Exemplars of presented stimuli with target values indicated below each image. (B) Detection rate (%) for the different conditions, computed as the number of trials for which the target was detected divided by the total number of presented trials. Each condition (i.e. one combination of background slope and target slope) is represented by five closed circles (made more visible using jittering) corresponding to five different stimuli versions (see Methods). Thin box plots indicate the amount of within-condition variation in detection rates between the stimuli versions. Background slope values are color-coded: blue for -1, orange for -2, and grey for -3. Dashed lines represent a quadratic fit to the data for each background separately (-1, -2, and -3). Arrows indicate the corresponding background value.*

Preference for natural statistics in abstract visual patterns

Our second experiment tested whether the patterns we generated for the targets in the first experiment also varied in their attractiveness. In a two-alternative forced-choice task (2-AFC), we assessed participants' preferences for the targets used in the detection task. The targets in this experiment were presented in pairs against a uniform grey background (Figure 2A). We calculated a preference score for each target using the Élő rating method, an iterative algorithm that performs pairwise comparisons and is commonly used to measure

preference (see e.g. *31*, *32*). All stimuli are then ranked based on their performance in paired comparisons, thereby obtaining a preference score.

Targets with differing Fourier slopes elicited markedly different preferences (Figure 2B). The resulting data can be fitted with a simple quadratic model (ranking~slope + slope²), which predicts a preference peak for a target slope of -2.36 (fit adjusted R^2: 0.9136). This preference peak matches the preferred peak value reported in previous studies (see e.g. [23]). The most widely accepted explanation for this value is that it matches the dominant Fourier slope of the natural visual environment (between -1.81 and -2.4 depending on the study, as reported by (*33*)).

To confirm that the slope with the peak preference score in our second experiment corresponds with the dominant slope of natural scenes, we estimated the slope of 4,319 images of the Landscape Pictures dataset [33], which contains images of different types of landscapes (e.g. mountain, beach, desert). Methods of Fourier slope calculation vary across the literature, thus any comparison of slope values across datasets must be based on the same calculation. We found an average slope of -2.39 (SD: 0.31) for those images. This is very similar to the preference peak inferred from our experiment on a gray background (-2.36), further corroborating the general finding that people prefer the Fourier slope of natural scenes. This result, combined with those from the detection task, validate the use of the Fourier slope to manipulate both the camouflage effectiveness and the attractiveness of stimuli. They also indicate a baseline pattern preference that must be accounted for when considering a preference for camouflaged stimuli in the third preference task.

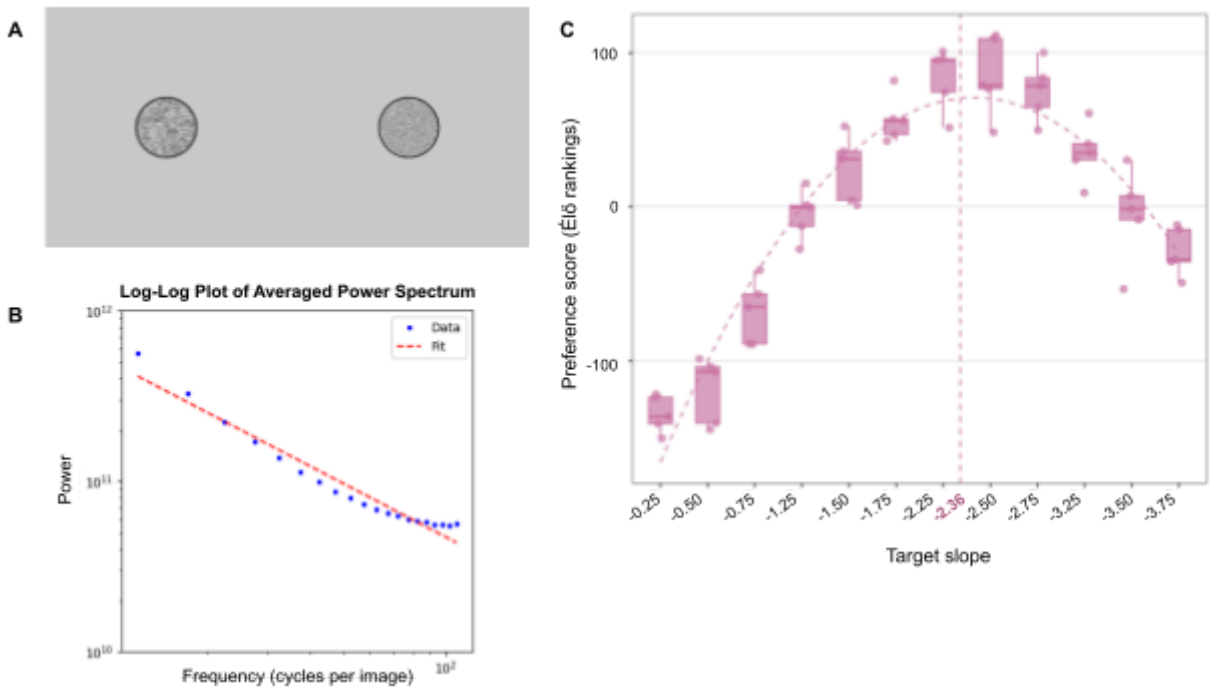

Figure 2: Preference task on gray background. *(A) Exemplar of a presented stimulus. Target slopes are -1.25 for the left target and -0.25 for the right one. For display reasons, the background color here is lighter than that of the stimuli used in the experiment (see Methods). (B) Log-log plot of the averaged power spectrum from which the Fourier slope of an image is derived (red regression line), here representing the averaged Fourier slope of images from the Landscape Pictures dataset.*

(C) Élő rankings for the 2-AFC task with a grey background. Each condition (i.e. target slope values) is represented by five closed circles (made more visible using jittering) corresponding to five different stimuli versions. Dots indicate the mean ranking values for each of the five stimuli versions of each condition (indicated on the x-axis). Thin box plots give the variability of preference scores across those versions. The dotted line indicates a quadratic fit of the data.

A preference for the Fourier slope of natural scenes has been reported in numerous studies in experimental psychology. In a particularly compelling study, Spehar and collaborators [23] showed that stimuli to which people have the highest sensitivity (i.e. absolute detection, discrimination, and contrast sensitivities) are also the most attractive. Their result emphasizes the influence of efficient processing on visual preferences: patterns whose properties coincide with visual sensitivity are processed more efficiently by the visual system and are generally preferred over patterns that are further away from visual sensitivity peaks. These and our own results are therefore consistent with the processing bias hypothesis [18], which posits that the spatial statistics of natural scenes are attractive because they are the easiest to process by the brain. They also help explain a large body of results in empirical aesthetics, which show that visual artwork imitates natural spatial statistics [34,35]. For example, faces painted by portrait artists across time and cultures tend to have a slope value matching that of natural landscapes even though real faces typically do not, suggesting that artists increase the attractiveness of their work by unconsciously mimicking the spatial statistics of natural scenes [36].

A preference for the Fourier slope of natural scenes is not only limited to humans. Hardenbicker and Tedore [37] recently discovered that peacock jumping spiders prefer images with the Fourier slope of natural scenes over two other options. In addition, in several fish species, Hulse and collaborators [38] found a correlation between the Fourier slope of species-typical habitats and the sexual signaling patterns of males (but not females). That study did not measure preferences, so whether fish are attracted to natural Fourier slopes remains to be tested, but a correlation between the spatial statistics of male sexual signals and their habitat is reminiscent of studies that demonstrate a correlation between the Fourier slope of human artwork and natural scenes.

Hidden preference for camouflage patterns

In our third experiment, we assessed the attractiveness of patterns that varied in their degree of background matching. We used the same stimuli as for the detection task (i.e., targets were displayed in front of a patterned background, rather than a gray background as in the second experiment), but we removed the detectability constraint by circling and centering the targets (Figure 3A). All targets therefore were assumed to be equally conspicuous. We assessed participants' preferences for different levels of background-matching patterns with a 2-AFC task and computed a preference score for each combination of background matching using the Élő-ranking method.

To explore the relationship between preference scores and background matching, we used linear regression to model preference scores as a response variable and the difference between target slope and background slope, as a measure of background matching, as an explanatory variable. We also included target slope and a quadratic term for background slope as additional potential explanatory variables. We found an effect of the difference between target slope and background slope on preference scores (estimate: -120.292 ±

12.015; t = -10.012, df = 89.413, p = 0.000, see Table S2). Stimuli with the lowest slope difference between target and background, i.e., with the highest background matching, tended to have higher preference scores. Similar significant effects were also obtained when data for each background were analyzed separately (Table S3). This, the main result of this study, indicates that targets that were more effectively camouflaged in the detection experiment were also more attractive when rendered detectable in the third preference experiment.

We also fitted a simple quadratic model (ranking~slope + slope^2) to find the target slope that predicts the highest attractiveness ranking for each background (data shown in Figure 3B). For a background slope of -1, a target slope of -1.92 predicts the highest ranking (77.67, fit adjusted R^2: 0.9993). For a background slope of -2, a target slope of -2.14 predicts the highest ranking (44.06, fit adjusted R^2: 0.9418). For a background slope of -3, a target slope of -2.51 predicts the highest ranking (80.32, fit adjusted R^2: 0.9943). These results indicate that preferences for visual patterns can be shifted away from a general baseline value (for Fourier slope -2.36, as determined in the second experiment) and toward the value of the background (Figure 3C), as predicted by a preference for background-matching stimuli and the processing bias hypothesis.

Notably, a similar modulation of visual attractiveness by background statistics was shown for human faces. Menzel and collaborators [39] varied the Fourier slope of the background against which faces were presented and asked participants to rate their attractiveness. They found that participants rated faces as more attractive when those faces were presented against a background that was closer to the Fourier slope of both natural scenes (-2) and faces (-3) compared to other background slopes (-1 and -4).

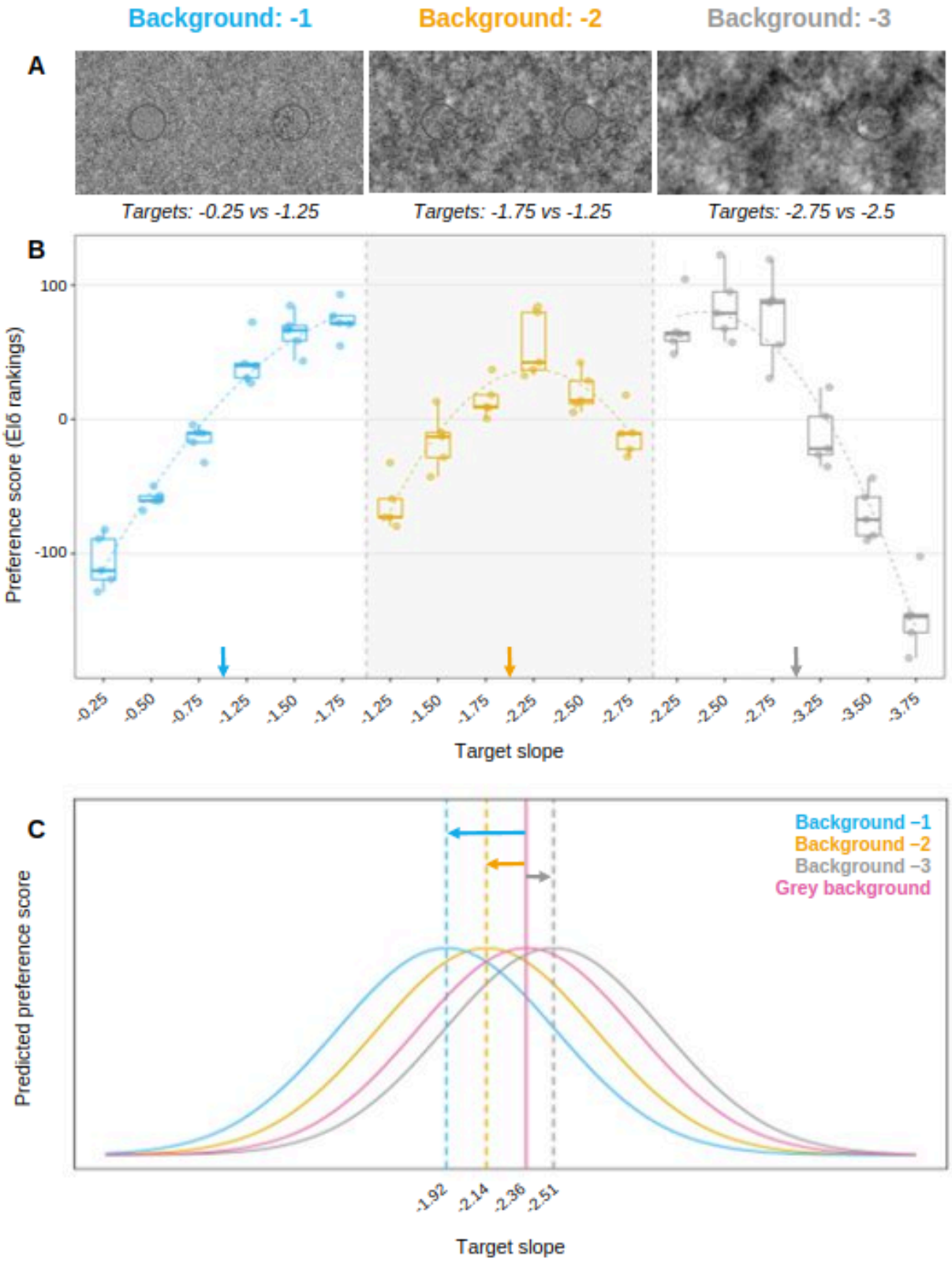

Figure 3. Preference task on a patterned background. *(A) Exemplars of presented stimuli with target values indicated below each image. (B) Élő rankings for the 2-AFC task with a patterned background. Each condition (i.e. one combination of background slope and target slope) is represented by five closed circles (made more visible using jittering) corresponding to five different stimuli versions. Thin box plots give the variability of preference scores across those 5 stimuli versions. Background slope values are colour-coded: blue for -1, orange for -2, and grey for -3. Dashed lines represent a quadratic fit to the data for each background separately (-1, -2, and -3) and*

arrows indicate the corresponding background value. C) Heuristic representation of the observed shift of preference of visual patterns away from the general baseline value of -2.36 (pink curve, a peak value obtained from Experiment 2) as a result of the modulation of the background slope.

Behavioral and evolutionary implications for animal communication

Given similarities in the early visual systems of humans and those of macaques [40], cats [41], mice [42] and birds [43], these results have important implications for animal sexual signaling. First, on a short time scale, they suggest that animals should track the pattern of the visual background against which they are displaying. If able, they should respond behaviourally or physiologically to match the statistical features of their patterns with those of the background. Similarly, if the sexual signal changes, as observed in some fish that change sex during development, individuals might choose another displaying site. Previous studies have shown that animals choose their display site in relation to their own sexual signals [44,45]. Those studies, however, focused on coloration, showing that animals gain attractiveness by maximizing the contrast with the background and the ambient light. Our results extend these findings to signal patterns, but predict that, for this signal component, animals would benefit from mimicking the visual environment.

On an evolutionary scale, our results suggest that signal patterns will be shaped by the spatial statistics of the environment. Because the visual system adapts to efficiently process the spatial statistics of natural environments, patterns that mimic those statistics will also be efficiently processed and therefore attractive [18]. This prediction of the processing bias hypothesis is an extension of ”sensory exploitation” [46] or “sensory drive,” which propose a similar mechanism for detectability, with animal signals evolving to be more easily detected [47]. The African cichlid fish *Pundamilia nyererei,* for example, lives in an environment with red-shifted light. Females exhibit an increased expression of red-sensitive photoreceptors that render red stimuli more detectable, and males exhibit more reddish coloration [48]. The sensory drive hypothesis is supported mainly by studies on coloration; our results suggest that expanding sensory drive beyond the framework of signal detection will allow us to predict the evolution of signal patterns, in addition to coloration.

Because traditional approaches to understanding the evolution of signal design are based on signal detection, natural and sexual selection are traditionally pitted in conflict along an axis of detectability. Our results suggest instead that these mechanisms can act synergistically. Natural selection generally favors camouflage, such as background-matching patterns. Due to their low detectability, the attractiveness of camouflage patterns is usually not considered, far less tested. However, if a mutation occurs that makes camouflaged patterns more easily detectable, for example by adding color or a sharp outline, their attractiveness should increase because of the efficiency with which they are processed. Hidden preferences for those efficiently processed patterns are predicted to lead to an increase in the frequency of attractive phenotypes if ecological conditions permit (Figure 4). In this way, camouflage patterns could be evolutionarily co-opted by sexual selection. This framework could therefore describe another pathway to the evolution of “magic traits” [49], i.e., traits that evolve due to divergent ecological selection and also affect mate choice.

One strategy to leverage the attractiveness of camouflage patterns might be seasonal variation in detectability. Individuals that are camouflaged most of the year could be rendered more attractive by the addition of a detectable feature during the mating season.

Male darter fish (genus *Etheostoma)*, for example, exhibit vivid and species-specific colors during the breeding season that appear to complement rather than conceal their underlying background-matching pattern (*53*, *54,* Figure 4C). Indeed, females in at least two species of darters are attracted similarly to conspecific color and pattern when these signal components are decoupled [52]. An attractive and conspicuous seasonal addition could thus enhance, and be enhanced by, the underlying attractiveness of the camouflage pattern. Aposematic patterns can also be adaptively concealed, as in frogs, for which "hidden" aposematism on the belly represents an intermediate stage in the evolution of whole-body aposematic patterning [53]. Interestingly, many aposematic patterns in frogs appear to be colorful embellishments of background-matching patterns (Figure 4B, *57*), and in *Oophaga pumilio,* for example, these patterns are attractive to the opposite sex [55]. The attractiveness of aposematic patterns therefore also may be due to a combination of color and background-matching pattern, with sexual selection and natural selection similarly aligned in the evolution of warning signals.

In sum, we provide the first evidence that camouflage patterns matching the average image statistics of natural scenes are attractive, and although demonstrated here only in humans, this result is expected to generalize to other species. By providing evidence of a processing bias, the key mechanism by which camouflage patterns can be co-opted to function as sexual signals, this study highlights the importance of considering the psychological landscape [56] of signal receivers, and of interfacing research in evolutionary biology with the vast literature in human cognitive psychology.

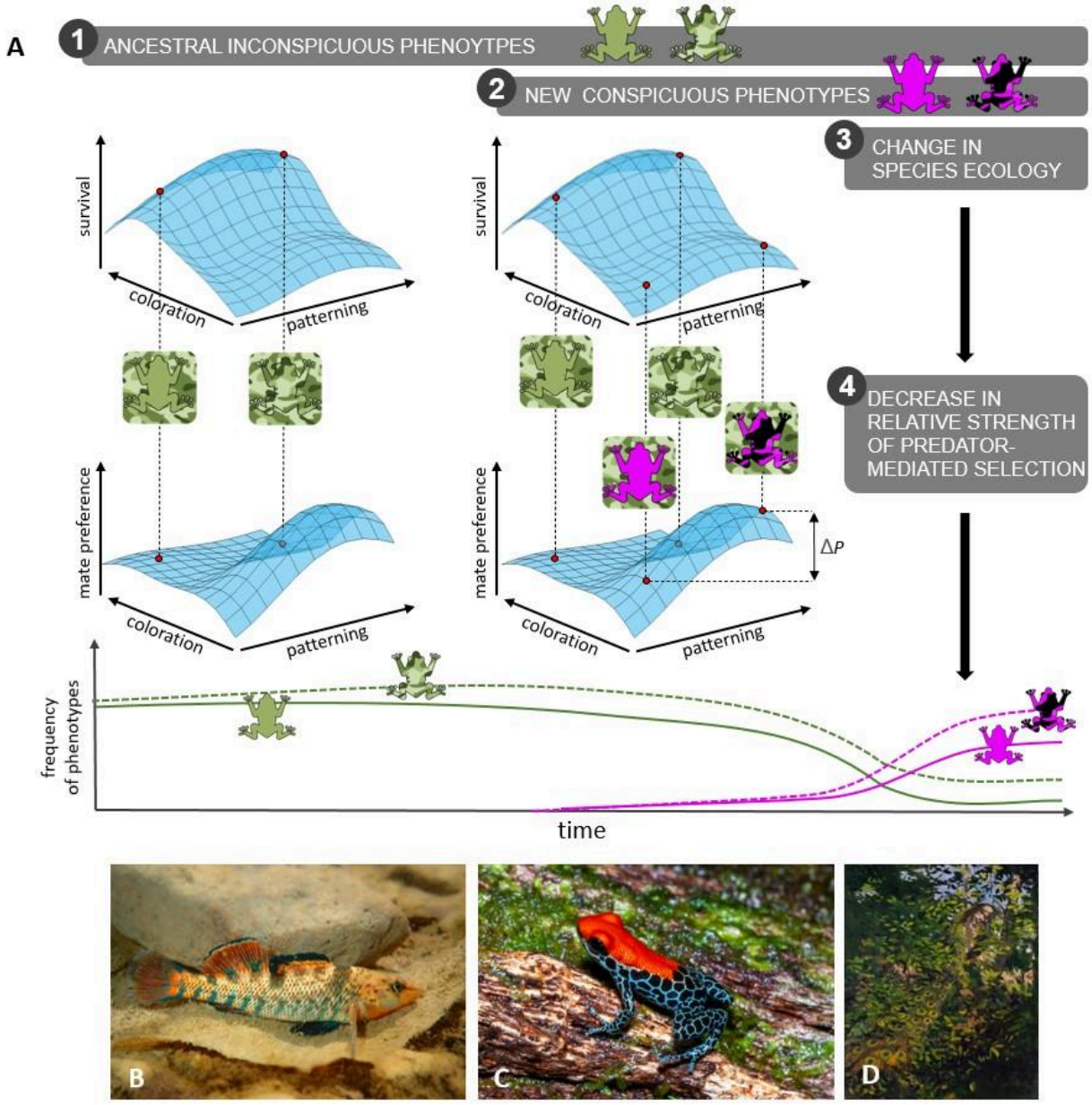

Figure 4. Evolution from camouflage to sexual signalling through the exploitation of processing bias. Panel A: 1. *Natural selection due to predation generally results in inconspicuous phenotypes. Phenotypes with a pattern that matches that of the environment ('inconspicuous pattern') are well-camouflaged and thus gradually increase in frequency in the population. Such phenotypes typically do not elicit strong preferences among conspecifics because of their low detectability.* ***2.*** *Any new mutation increasing conspicuousness should be negatively selected by predation (low survival). However, because they are highly detectable by potential mates and thus reduce their cost of mating, these phenotypes are potentially attractive. Among conspicuous phenotypes, camouflage patterns that match the visual structure of the habitat ('conspicuous patterned') should be preferred (ΔP) over those that do not ('conspicuous plain') because they are even more efficiently processed. In this study, we have provided the first empirical evidence supporting this prediction.* ***3.*** *These 'sleeping beauties' would remain negatively selected by natural selection until a change in ecological factors (e.g., colonization of habitats or regions with fewer predators, the appearance of new, alternative prey, predators' focus on new sensory cues) makes sexual selection strong enough to counteract the effects of predation on*

*phenotype evolution **4**. Thus, conspicuous phenotypes that have evolved from camouflage patterns can be evolutionarily co-opted by sexual selection. **Lower panels**: Examples of camouflage patterns underlying conspicuous color and patterns. B:* Etheostoma caeruleum *(Julien Renoult). C:* Ranitomeya reticulata *(DH Fischer). D: Painting of a peacock (*Pavo cristatus*) camouflaged in a tree by Abbott H. Thayer. Thayer, a naturalist painter of the 18th century, explored the idea that the primary function of animal patterns is camouflage. Although widely criticized at the time, Thayer's idea is consistent with the proposed framework, that even the most canonical nuptial patterns can evolve from, and continue to function at least in part as, camouflage. (Abbott Handerson Thayer, Richard S. Meryman, Peacock in the Woods, study for book Concealing Coloration in the Animal Kingdom, 1907, oil on canvas, Smithsonian American Art Museum).*

Methods

Stimulus and experimental design

Stimulus design: Sets of stimuli for the three experiments were generated with the Python programming language (Python Software Foundation, https://www.python.org/). The procedure to create each image for the different experimental conditions for the first experiment was the following: two randomly generated white noise images (650 x 650 pixels), a target image and a background image, were first created and then Fourier transformed in order to change the slope of the relationship between the log-power spectrum and the log-frequency corresponding to our different conditions (background image: slope = -1, -2, -3; target image: slope = background slope ± 0.25; ± 0.5; ±0.75). A circular selection with a radius of 80 pixels was selected from a random location of the target image and superimposed onto the background image at the same random coordinates. Targets could appear anywhere on the background, as long as they did not get cropped out of the frame. To eliminate pixelated edges, a very slight amount of blur was applied to the target edges. More specifically, a Gaussian filter (with a standard deviation of 0.5) was applied around the edge of each target before superimposing it onto the background image. Similarly, Gaussian filtering was applied to the background image at the target's location to smooth the contours around the target. This procedure had only a marginal effect on the slope of the power spectrum of the entire targets/backgrounds. The final shape and dimensions of those stimuli were a square of 650 x 650 pixels. Those dimensions are fixed and do not vary with the monitor size of participants.

Using the same procedure, for the second and third experiments we created a second set of stimuli of larger dimensions (650 x 1300 pixels) to contain two targets, one centered in each half of the stimulus. To make the targets conspicuous (i.e. easily detectable), we outlined them with a dark gray contour (linewidth: 1.5 and pixel intensity of the gray color: 64). The set of stimuli for the second experiment was created with a uniform, gray background (pixel intensity of the gray color: 128) in contrast to the patterned background of experiment 3.

For each of the three experiments, we created 5 versions of stimulus images per condition to introduce variability in the pattern design. The slope value of all five versions was identical but the resulting patterns varied in their local pixel arrangement. Thus, in total, experiment 1 had 18 different conditions (3 levels for the background variable: -1; -2; -3 and 6 levels for the difference between the background and the target slope: ± 0.25; ± 0.5; ± 0.75), each with

5 versions of the stimulus images, representing a total of 90 unique images. Experiment 2 with a patterned background had a total of 90 conditions (3 background slope values: -1; -2; -3, 2 targets with 6 slope differences each: ±0.25; ±0.5; ±0.75, and 2 sides: left or right), each with 5 stimulus versions, resulting in 450 unique images. Experiment 3 had a total of 78 conditions (1 background slope value: “gray”, 2 targets with 6 slope differences each: ±0.25; ±0.5; ±0.75, and 2 sides: left or right), each with 5 stimulus versions resulting in 390 unique images. Note that paired targets were never identical.

Fourier slope manipulation and estimation: To manipulate the Fourier slope of our white noise images, we first converted our image in the Fourier domain using the fast Fourier transform function implemented in Python. After normalizing its Fourier transform by its greatest absolute value, we separated the image into a phase matrix and an amplitude matrix. We then estimated the rotational average of the power spectrum for each frequency before estimating the slope of the power spectrum with a linear regression. To create an image with the desired slope, we first generated a residual matrix from the difference between the image and an even amplitude spectrum with the desired slope. We then applied the residuals to an amplitude matrix with the desired slope and applied it to the phase matrix before reconstructing the image with an inverse Fourier transform. The obtained output image now has the desired slope value.
To estimate the Fourier slope of an image, we fast Fourier transformed them and computed the rotational average of the power spectrum for all spatial frequencies between 10 and 110 cycles per image. This frequency selection limits edge effects and high-frequency noise. To give equal weight to all frequencies, we also binned (n=20) each power spectrum before estimating the slope value of the averaged power spectrum using a linear regression.

Experimental design: Each participant engaged in two experiments: the detection task and one of the two forced-choice tasks (gray or patterned background), which was randomly assigned. The presentation order of the two experiments was counterbalanced between participants.

Detection task (Experiment 1): Each stimulus was displayed at the center of the webpage, one at a time in a randomized order for a maximum duration of 8,000 ms. The intertrial interval was picked from a uniform distribution between 500 and 2,000 ms (in steps of 1 ms). The task contained 21 trials. Each stimulus was randomly picked from the pool of the 90 created images and presented only once, with the exception of three of the ten first trials that were repeated at the very end to check for within-participant consistency. At the end of each trial (i.e. after the participant clicked on the stimulus or when the response time limit had been reached), participants received feedback in the shape of a yellow circle, highlighting the location of the target. Prior to the experimental trials, three practice trials were presented to make sure the participant understood the task. Participants were instructed to “Click on the target as fast as possible”. Detection rates (%) were computed as the number of trials for which a target was correctly detected (i.e., clicked on) divided by the total number of trials.

Forced-choice task (Experiments 2 or 3): Stimuli were presented in a randomized order for a maximum duration of 12,000 ms. The intertrial interval was picked from a uniform distribution between 500 and 2,000 ms (in steps of 1 ms). The task contained 21 trials. Each pair of stimuli randomly picked from the pool of the 390 (gray background, Experiment 2) or 450 (patterned background, Experiment 3) created images was presented only once with the

exception of three of the ten first trials that were repeated at the very end to check for within-participant consistency. Pairs of stimuli varied on two treatment dimensions: the background slope values (-1; -2; -3 or a gray background) and the position (left-side or right-side of the image) of the target. Importantly, both targets always differed in their slope value. Participants were asked the following question, displayed above the stimuli: “Compare the patterns in the two circles, which one do you prefer?”.

Questionnaires: The participants were asked 5 questions before and 2 questions after they performed both tasks. Questions were demographic in nature and related to education level and frequency of exposure to visual art (Table S1).

Online experiment and participant recruitment: The experiment took place online on a website hosted by the Montpellier Bioinformatics Biodiversity platform (University of Montpellier, France) and is still available for demonstration purposes: http://isemsurvey.mbb.univ-montp2.fr/pattern/. The experiment was programmed using a custom HTML script (including JavaScript, CSS, and PHP) and jsPsych, a JavaScript library for creating online experiments [57], and is available to play on all standard internet browsers. The experiment must be conducted with a desktop or laptop computer, excluding smartphones and tablets.

Participants were recruited through advertisements on dedicated mailing lists and on social networks. Participants were not paid, and they had to be at least 16 years old. Approval from the French (deemed exempt, CNIL number 2-21044) and American (deemed exempt, UMBC IRB #522) ethics committees was obtained prior to the start of the experiment.

Prior to launching the online experiment, the study’s objectives and planned analyses were pre-registered following open science practices (available on https://osf.io/nujh7/).

Measure of pattern preference

Preference scores for a target with a specific slope value are expressed as a ranking, computed via the Élő score (using the EloChoice package in R, v0.29.4; [58]), an iterative algorithm traditionally used in chess games and that performs pairwise comparisons. It is now frequently used as a measure of aesthetic value and is well suited for unbalanced design as the case of our study (see [31]; [30] for similar use; [59] for a comparison of different pairwise ranking systems). Briefly, each pair of stimuli is similar to a contest where the preferred stimulus wins points and the non-preferred stimulus loses the same amount of points. As in [30], we used the elochoice function with initial Élő scores set to 0, and *k* set to 100. We ran 1000 simulations to make sure our ratings were stable. We ran the analysis image-wise, that is by considering each of five versions of a stimulus as an independent condition to account for potential variability between stimulus versions. Note that running the same code but by considering all five versions of a stimulus as the same condition did not yield different results. We estimated the minimum number of participants required to achieve stability in ratings using the raterprog function of the EloChoice package with the ratershuffle argument set to 10 to avoid a participant order effect. We found that using the data from 378 participants for images with a grey background (reliability index = 0.57, Figure S1) and from 263 participants was sufficient to reach stable ratings (reliability index = 0.59, Figure S2) for images with a patterned background.

Statistical analyses

We removed participants who did not finish the experiment and participants who took part in the experiment more than once (IP address verification procedure). In total, we kept the data of 1,757 participants out of the 2,567 participation events that were recorded (68.6%). For details on sociodemographic data, see supplementary material.

For the detection task, we removed trials where responses were faster than neurophysiological limits (i.e. below 150ms, see e.g. Thorpe et al., 1996). For the two alternative forced-choice tasks, we found no lateral bias in participants' responses: the left target was chosen in 50.5 to 51% of the trials.

Using the three repeated trials per participant, we assessed intra-respondent consistency by performing paired comparisons with t tests between the first and second repetition of those trials across participants. For the detection task, we found no difference for the detection rate (t = -0.82376, df = 177.16, p = 0.4112) and we found the detection time for the second repetition (mean: 1,576.962) to be faster than for the first repetition (mean: 1732.750) as expected (t = -6.7704, df = 13147, $p < 0.001$). For the preference tasks, we found no difference in terms of preferred stimulus, neither for the gray background (t = 0.5223, df = 7754, p = 0.6015), nor for the patterned background (t = 0.2833, df = 6034, p = 0.777). Further analyses for those experiments were conducted on the non-repeated trials only.

We fitted our data with linear mixed-effects models (*lme4* package, [61]) with REML set to false. We averaged the participants' Élő scores to obtain one score per image and used it as our dependent variable. Our independent variables (fixed effects) included the value of the difference between the background slope and the target slope (0.25, 0.50, 0.75) and the sign of the difference (positive or negative, coded as 1 and -1, respectively), the interaction between the slope value of the background and of the target, and the quadratic of the background slope. We added the value and the sign of the difference between the background slope and the target slope and the stimulus version (5 versions per stimulus type) as random effects. In addition to our main model, we ran three similar models for each background separately, removing the background variables (the interaction with the target slope and the quadratic of the background slope).

Data and code availability

An OSF repository contains the code to reproduce the stimuli and the images used for the online experiment in high resolution, the preprocessed data and the code to reproduce the main analyses and figures, and the pre-registration file [https://osf.io/nujh7/].

Supplementary Information is available for this paper.

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Data and materials availability: All data and code, and materials used in the analysis are available on the following GitLab repository: https://gitlab.com/yseulthb/camo_exp.

Supplementary material

List of Supplementary Materials:

Supplementary Text: Participants recruitment and experiment questionnaire
Table S1: Experiment questionnaire and response options
Table S2: General model
Table S3: Model for each background separately
Fig. S1: Ratings stability for the 2-AFC task with a grey background
Fig. S2: Ratings stability for the 2-AFC task with a patterned background

Participants recruitment and experiment questionnaire

Recruitment: Participants were recruited through advertisements on dedicated mailing lists and on social networks. Participants were not paid, and they had to be at least 16 years old, corresponding to the legal digital majority in the EU. Prior to the experiment, participants were asked to report their month and year of birth to enforce that rule. For American citizens aged between 16 and 18 years, participants were asked to obtain their parents' verbal approval before they participated in the experiment. Participants were asked to take part in the study only once. On top of informing them of that condition prior to the experiment. The IP address of the participant was only used to enforce that rule, and was not associated with personal information, following a protocol approved by the CNIL. Collected data were stored on-site.

All research was performed in accordance with relevant guidelines/regulations. In accordance with the French legislation, the protocols for this study have been submitted and approved by the French National Commission on Informatics and Liberty (CNIL number 2-21044). The CNIL, an independent public authority affiliated to the European Data Protection Board, is responsible for ensuring that information technology ethically serves the citizen and that it does not infringe on human identity, human rights, privacy or individual or public liberties. The present research is an online experiment with volunteers interacting remotely and anonymously, thus no ethical approval was required—nor possible—from an academic or scientific comity under French legislation, as their recourse is only possible if it is compulsory. The European GDPR (General Data Protection Regulation) was fully applied, and all participants were informed of the subject of the study.

Procedure: At the beginning of an experiment, participants were offered to choose the instruction language between French, English, and Spanish. After agreeing to the study details (consent form) and answering some questions about participants' demographic details (Table S1), the experiment started.

Table S1: Experiment questionnaire and response options

Questions	*Options*
Please indicate what best describes your gender	Female (cis/trans), Male (cis/trans), Non binary, I prefer not to say, Other / I prefer to self-describe
Please indicate your birth date	Year and Month
Do you have uncorrected colour-blindness ?	Yes, No
Education: select the option that corresponds to your highest qualification	Graduate Degree, Associate Degree or Bachelors Degree, High School, Vocational training school certificate, CGE SSCE, PSC no diploma
What is your country of current residency ?	List of countries
Does your job or any of your hobbies involve visual artistic activity or visual creation?	Not at all, Sometimes, Often, Daily
How often do you go to art exhibitions (museums, galleries)?	Once a week, Once a month, Once a year, Never

Sociodemographic data

Participants whose data were included in the analysis were 61% women (n=1069), 36% men (n=629), and 3% in other categories (non-binary: 38, prefer to self-describe: 5, prefer not to say: 16). A majority of participants had graduate degrees (66%, n=1162). 35 participants were color-blind, representing less than 2% of the participants. Most participants were born after 1980, with a peak in the early 2000s, corresponding to undergraduate students who took part in the study as a way to get extra credit. When asked about their hobbies, most participants (82%) reported having hobbies that don't involve visual creativity or only rarely. Most participants go to art exhibitions once a year or less (82%). Participants were mostly located in France (46%) and in the US (29%) with an additional good representation of Western Europe and Canada. Our participants are therefore WEIRD (from Western, Educated, Industrialized, Rich and Democratic countries as described in Henrich et al., 2010), which was expected given our advertising methods (mostly academic or professional mailing lists in Western countries).

It is possible that certain demographic traits, as well as higher exposure to visual art or creativity, might influence stimulus preferences. Therefore, we looked for potential relationships between demographic variables (age, gender, education level) and the ranking scores, and between visual exposure to art (presence of visual arts activity in jobs or hobbies, and frequency of art exhibition visits) and the ranking scores. For each demographic variable of interest, we computed the ranking score for patterned and grey images for a subset of the data, corresponding to the targeted participants. We then randomly sampled from the whole participant dataset a subset of the same size and computed the ranking for those participants as well (for both patterned and grey images). After making sure the rankings of both subsets (or groups of participants) were normally distributed, we compared them using a t-test. Overall, no difference was found for any of the tested sociodemographic variables.

Linear models

Table S2: General model

Random effects

Groups name	Variance	Std.Dev.
Target slope (Intercept)	8.634e+01	9.292e+00
Stimulus version (Intercept)	3.885e-31	6.233e-16
Background slope (Intercept)	8.417e-32	2.901e-16
Residual	4.467e+02	2.113e+01

Number of obs: 90, groups: target slope, 12; stimulus version, 5; background slope, 3

Fixed effects

	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	69.334	20.105	85.947	3.449	0.000875
Slope diff. (value)	-120.292	12.015	89.413	-10.012	2.89e-16
Slope diff. (sign)	4.868	9.028	26.492	0.539	0.594279
Background slope	270.011	27.951	79.829	9.660	4.55e-15
Target slope	-263.859	22.341	27.701	-11.811	2.51e-12
(background slope)²	134.334	7.368	88.940	18.232	< 2e-16
Background slope :target slope	-133.711	7.052	34.594	-18.960	< 2e-16

Analysis of Deviance Table (Type II Wald chisquare tests)

Response: ranking

	Chisq	Df	Pr(>Chisq)
Slope diff. (value)	100.2344	1	< 2.2e-16
Slope diff. (sign)	0.2907	1	0.5898
Background slope	24.6102	1	7.018e-07
Target slope	0.0423	1	0.8371
(background slope)²	332.4018	1	< 2.2e-16
Background slope :target slope	359.4748	1	< 2.2e-16

In addition to the slope difference, our statistical model further revealed that the slope of the background against which targets are presented also significantly influenced attractiveness in the regression model run with all background conditions [estimate: 270.011 ± 27.951; t = 9.66, df = 79.829, p = 0.000] (see Table S2). Analyzing results for each background separately confirmed the link between the preference for a target and the level of background matching across backgrounds. Those models (see Suppl Table S3) further showed that preference is influenced by the target slope for both background slopes of -1 [estimate: -122.748 ± 12.811; t = -9.581, df = 26, p = 0.000] and -3 [estimate: 126.47 ± 22.67; t = 5.578, df = 26, p = 0.000], though in opposite directions, but it is not with background slope of -2. This result indicates a preference for targets with slope values closer to -2 than to any other background slope value against which the target was presented, but only when presented against a background different from -2.

Table S3: Model for each background separately

Background slope: -1

Random effects

```
 Groups name                   Variance    Std.Dev.
 Stimulus version (Intercept) 1.123e-31    3.352e-16
 Residual                      2.051e+02   1.432e+01
Number of obs: 30, groups:  stimulus version, 5
```

Fixed effects

	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	-92.505	14.560	26.000	-6.353	9.96e-07
Slope diff. (value)	-60.486	12.811	26.000	-4.721	7.01e-05
Slope diff. (sign)	-1.270	6.919	26.000	-0.184	0.856
Target slope	-122.748	12.811	26.000	-9.581	5.12e-10

Background slope: -2

Random effects

```
 Groups name                   Variance    Std.Dev.
 Stimulus version (Intercept) 1.586e-31    3.983e-16
 Residual                      3.391e+02   1.841e+01
Number of obs: 30, groups:  stimulus version, 5
```

Fixed effects

	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	46.936	34.119	26.000	1.376	0.1807
Slope diff. (value)	-143.801	16.469	26.000	-8.731	3.3e-09
Slope diff. (sign)	15.397	8.895	26.000	1.731	0.0953
Target slope	-12.482	16.469	26.000	-0.758	0.4553

Background slope: -3

Random effects

```
 Groups name                   Variance    Std.Dev.
 Stimulus version (Intercept) 8.913e-32    2.985e-16
 Residual                      6.427e+02   2.535e+01
Number of obs: 30, groups:  stimulus version, 5
```

Fixed effects

	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	450.92	69.12	26.00	6.524	6.46e-07
Slope diff. (value)	-143.00	22.67	26.00	-6.307	1.12e-06
Slope diff. (sign)	-12.90	12.25	26.00	-1.054	0.302

Target slope	126.47	22.67	26.00	5.578	7.37e-06

Ratings stability and reliability index

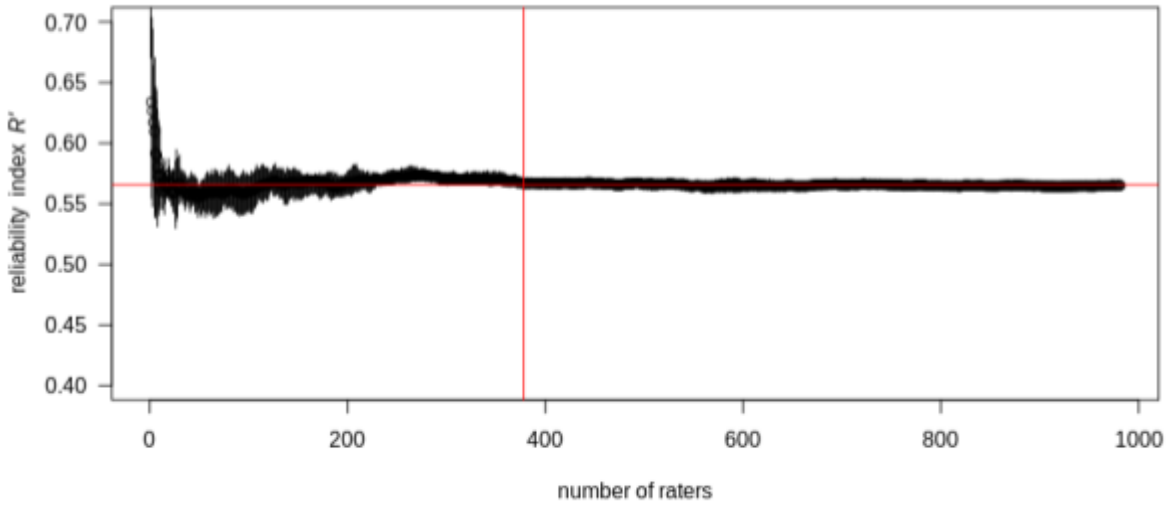

Figure S1: Ratings stability for the 2-AFC task with a grey background. *The intersection of the two red lines indicate the number of raters needed to achieve the averaged reliability index (avgRI). AvgRI is measured as the average RI between 400 and 981 participants for which we can see ratings have achieved stability. The obtained avgRI is 0.567 corresponding to 378 raters. This was averaged across all 10 simulations, which correspond to a randomised order of raters.*

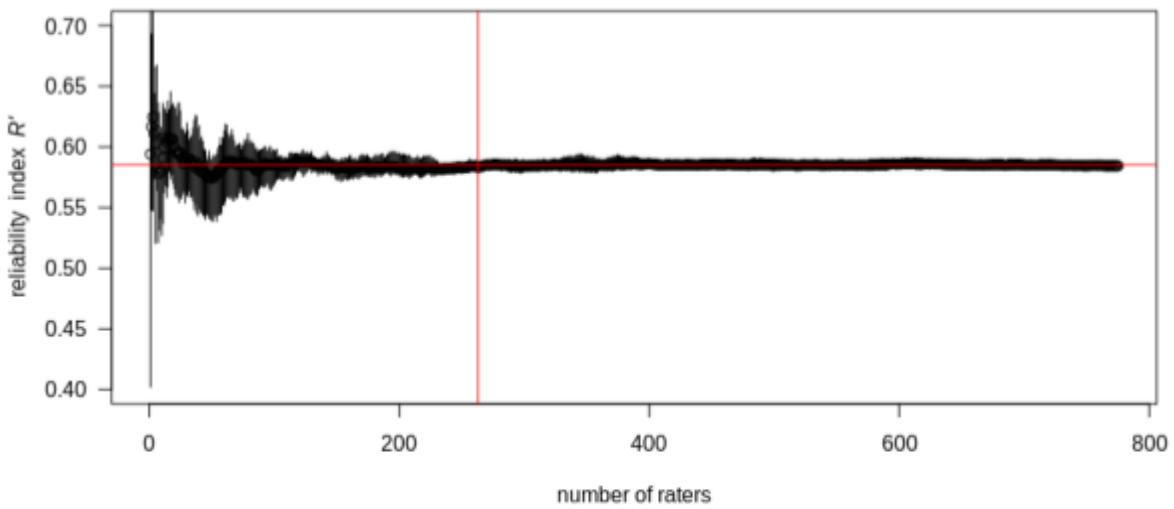

Figure S2: Ratings stability for the 2-AFC task with a patterned background*. The intersection of the two red lines indicate the number of raters needed to achieve the averaged reliability index (avgRI). AvgRI is measured as the average RI between 250 and 775 participants for which we can see ratings have achieved stability. The obtained avgRI is 0.585 corresponding to 263 raters. This was averaged across all 10 simulations, which correspond to a randomised order of raters.*