Title
Pupil-Linked Arousal Biases Evidence Accumulation Toward Desirable Percepts During Perceptual Decision-Making

Permalink
https://escholarship.org/uc/item/9m73z4z1

Journal
Psychological Science, 32(9)

ISSN
0956-7976

Authors
Leong, Yuan Chang
Dziembaj, Roma
D'Esposito, Mark

Publication Date
2021-09-01

DOI
10.1177/09567976211004547

Peer reviewed

Pupil-Linked Arousal Biases Evidence Accumulation Toward Desirable Percepts During Perceptual Decision-Making

Yuan Chang Leong[1] , Roma Dziembaj[2], and Mark D'Esposito[3,4]

[1]Department of Psychology, The University of Chicago; [2]Department of Management Science and Engineering, Stanford University; [3]Helen Wills Neuroscience Institute, University of California, Berkeley; and [4]Department of Psychology, University of California, Berkeley

Abstract

People's perceptual reports are biased toward percepts they are motivated to see. The arousal system coordinates the body's response to motivationally significant events and is well positioned to regulate motivational effects on perceptual judgments. However, it remains unclear whether arousal would enhance or reduce motivational biases. Here, we measured pupil dilation as a measure of arousal while participants (*N* = 38) performed a visual categorization task. We used monetary bonuses to motivate participants to perceive one category over another. Even though the reward-maximizing strategy was to perform the task accurately, participants were more likely to report seeing the desirable category. Furthermore, higher arousal levels were associated with making motivationally biased responses. Analyses using computational models suggested that arousal enhanced motivational effects by biasing evidence accumulation in favor of desirable percepts. These results suggest that heightened arousal biases people toward what they want to see and away from an objective representation of the environment.

Imagine playing a heated tennis match and hitting a shot that might or might not have grazed the sideline. Would your motivation to win the point make you more likely to see the ball as having stayed within bounds? For most real-world perceptual decisions, people are not neutral observers indifferent to different outcomes. Some outcomes are better than others, and people are motivated to see those percepts over alternatives. Evidence from a number of studies suggests that wanting to see a desirable outcome biases people toward seeing that outcome, a phenomenon known as *motivated perception* (Balcetis & Dunning, 2006; Balcetis et al., 2012; Leong et al., 2019; Voss et al., 2008). For example, when presented with a visually ambiguous line drawing, participants were more likely to report seeing the percept associated with a desirable outcome (Balcetis & Dunning, 2006). Motivated perception has been shown to impair perceptual decision-making by biasing people toward

what they want to see and away from the objective representation of external stimuli (Leong et al., 2019). Although previous studies provide growing evidence that motivation influences perception, it is not yet known how the interaction between motivation and sensory processing occurs.

The arousal system is well positioned to mediate motivational influences on perceptual processes. The level of physiological arousal performs an important role in coordinating the body's response to motivationally significant events, such as the opportunity to obtain potential rewards or the appearance of an imminent threat (Lang & Bradley, 2010). Motivationally relevant

Corresponding Author:
Yuan Chang Leong, The University of Chicago, Department of Psychology
Email: ycleong@uchicago.edu

stimuli activate arousal circuits and trigger an autonomic nervous system response that includes changes in heart rate, pupil dilation, and skin conductance. Fluctuations in arousal are thought to be regulated by the locus coeruleus norepinephrine system (Sara & Bouret, 2012) and have been shown to impact sensory processing, memory encoding, and decision-making (Aston-Jones & Cohen, 2005; Markovic et al., 2014; Mather et al., 2016). Furthermore, recent studies have shown that arousal influences both the accumulation of sensory information and response biases during perceptual decision-making (de Gee et al., 2020; Keung et al., 2019; Krishnamurthy et al., 2017; Murphy, Vandekerckhove, & Nieuwenhuis, 2014; Urai et al., 2017). These past studies, however, did not examine the role of arousal in a context in which participants are motivationally biased to see one percept over another. It is thus unclear whether and how arousal modulates motivational biases in perceptual decision-making.

How might arousal be related to the processes underlying motivated perception? According to the glutamate amplifies noradrenergic effects (GANE) model (Mather et al., 2016), arousal-related norepinephrine release interacts with local glutamate levels to selectively amplify the neural representation of physically or emotionally salient stimuli (see also Markovic et al., 2014). Consistent with this account, results of some studies have shown that salient stimuli are preferentially perceived and remembered under heightened arousal (Kensinger et al., 2007; Lee et al., 2018). Building on this past work, we hypothesized that otherwise neutral stimuli become motivationally salient when participants are motivated to see them and that arousal selectively biases sensory processing in favor of these stimuli. Thus, we predicted that arousal would be associated with stronger motivational biases during perceptual decision-making.

In the current work, we combined psychophysics, computational modeling, and pupillometry to examine the relationship between arousal and perceptual decision-making. Participants were presented with visually ambiguous images and were rewarded for correctly categorizing the image into one of two categories. Pupil diameter was recorded during the task as a proxy measure for physiological arousal (Bradley et al., 2008). In different experimental blocks, we motivated participants to see one category over another by informing them that they would win extra money if the block contained more images from one category. Using a drift-diffusion model (DDM; Ratcliff & McKoon, 2007), we modeled participants' responses as the stochastic accumulation of sensory evidence toward a decision threshold. We then assessed whether pupil diameter was associated with either or both motivational biases

Statement of Relevance

When confronted with an event of motivational significance (e.g., an opportunity to earn a huge reward), people often experience a strong arousal response that includes increased sweating, faster heart rate, and larger pupils. Does this arousal response help individuals make more accurate decisions, or does it instead bias and impair decision-making? In this work, we examined the effects of arousal on how people decide what they see when they are motivated to see a particular outcome. We found that heightened arousal, measured by larger pupils, was associated with a bias in how participants accumulated sensory evidence to make their decisions. As a result, participants became more likely to report seeing an ambiguous visual image as the interpretation they were motivated to see. Our results suggest that arousal biases perceptual judgments toward desirable percepts and that modulating arousal levels could be a promising approach to reducing motivational biases in decision-making.

in the starting point and rate of evidence accumulation. By combining physiological markers of arousal with computational modeling, our study provides a mechanistic account of how arousal and motivation interact to change the way we perceive the environment. Our results help refine existing theories on arousal and provide new insights into the role of affective states in regulating human cognition.

Method

Participants

Forty-one participants were recruited from the Berkeley community (sample of convenience) for the study. The target sample size was 36, which a power analysis with effect estimates obtained from a previous study (Leong et al., 2019) indicated had greater than 80% power to detect a difference in psychometric curves between conditions. All participants provided informed consent prior to the start of the study. Participants were paid between $20 and $30 (U.S.) depending on their performance on the task. Data from three participants were excluded because of unsuccessful eye-tracker calibration, yielding an effective sample size of 38 participants (15 male, 23 female; age: M = 21 years, range = 18–40 years). All experimental procedures were approved by the University of California, Berkeley, Committee for the Protection of Human Subjects.

Stimuli

For each participant, 12 sets of composite face-scene stimuli were created. Each stimulus set consisted of 25 gray-scale images, and every image in a set mixed a face and a scene in a different proportion. Results of a pilot study ($N = 30$) indicated that participants were equally likely to categorize an image as face dominant or scene dominant when the image contained 48% scene information and 52% face information (i.e., point of subjective equivalence; see Fig. S1 in the Supplemental Material available online). Thus, images with less than 48% scene information were considered face dominant, whereas images with more than 48% scene information were considered scene dominant. Half of the stimulus sets contained more scene-dominant images (1 × 33% scene, 3 × 43% scene, 16 × 48% scene, 3 × 53% scene, 2 × 63% scene), whereas the other half contained more face-dominant images (2 × 33% scene, 3 × 43% scene, 16 × 48% scene, 3 × 53% scene, 1 × 63% scene). All stimuli were created to be isoluminant. Face images were frontal photographs in which the subject had a neutral expression and were taken from the Chicago Face Database (Ma et al., 2015). Stimuli were presented using MATLAB (Version 2014A; The MathWorks, Natick, MA) and the Psychophysics Toolbox (Version 3; Brainard, 1997).

Experimental task

On each trial, participants were presented with a face-scene composite image and had to categorize whether the image was face dominant or scene dominant (Fig. 1a). The image was presented for 3 s and participants had to respond during this time. Participants earned $0.05 for each correct categorization. During the inter-trial interval (range = 2–6 s, M = 3.5 s), a scrambled image with the same average luminance was presented to minimize luminance change on screen. Participants performed 12 blocks of 25 trials each. In four of the blocks, we motivated participants to see face-dominant images by informing them that they would win a $3.00 bonus if the block had more face-dominant images (face-bonus blocks). In another four blocks, we motivated them to see scene-dominant images by informing them that they would win a $3.00 bonus if the block had more scene-dominant images. In the remaining four blocks, participants performed the task without a motivation manipulation (neutral blocks).

Prior to the start of the experiment, participants were given explicit instructions that "the category bonus is based on the actual number of face-dominant or scene-dominant images in the block, and not on the categorizations that [they] make" and that "to earn more money, [they] should be as accurate as possible." The

instructions were delivered verbally by the experimenter and also in written form on screen at the beginning of the experiment. Because the instructions were intuitive and explicit, it is unlikely that participants misunderstood the task (for additional discussion, see the Supplemental Material). At the end of each face-bonus or scene-bonus block, participants received feedback on whether there were more face-dominant or scene-dominant images in the block and whether they earned the $3.00 bonus. For each participant, two face-bonus blocks contained one more face-dominant image, whereas the other two contained one less face-dominant image. Similarly, two scene-bonus blocks contained one more scene-dominant image, whereas the other two contained one less scene-dominant image. Thus, each participant earned the $3.00 bonus on two face-bonus blocks and two scene-bonus blocks. Participants performed the blocks in a pseudorandom order so that they would not perform the same type of block consecutively.

Behavioral analyses

We modeled participants' response data using generalized linear mixed-effects models, which allow for the modeling of all participants' data in a single model rather than fitting a separate model for each participant (Knoblauch & Maloney, 2012). We modeled each participant's response (i.e., face dominant or scene dominant) as a function of the percentage of scene information in an image and block type (contrast coding with neutral blocks as the reference condition). The model included random slopes and intercepts for the percentage of scene information and for block type to account for random effects across participants (Model 1; for full model specification, see Table S1 in the Supplemental Material). Models were estimated using the glmer function in the *lme4* package (Version 1.1-18.1; Bates et al., 2015) in the R programming environment (Version 3.5.1; R Core Team, 2018); p values were computed from t tests with Satterthwaite approximation for the degrees of freedom, as implemented in the *lmerTest* package (Version 3.1-0; Kuznetsova et al., 2019).

We ran two linear mixed-effects models to examine the effect of motivation on participants' response times (RTs). RTs were modeled as a function of the participant's response type, that is, whether the participant's response was *motivation consistent* (i.e., categorizing an image as belonging to the category they were motivated to see), *motivation inconsistent* (i.e., categorizing an image as belonging to the category they were motivated to not see), or neutral (i.e., trials in neutral blocks). Both models coded response type using contrast coding but differed in terms of which response type was coded as the reference group. The first model
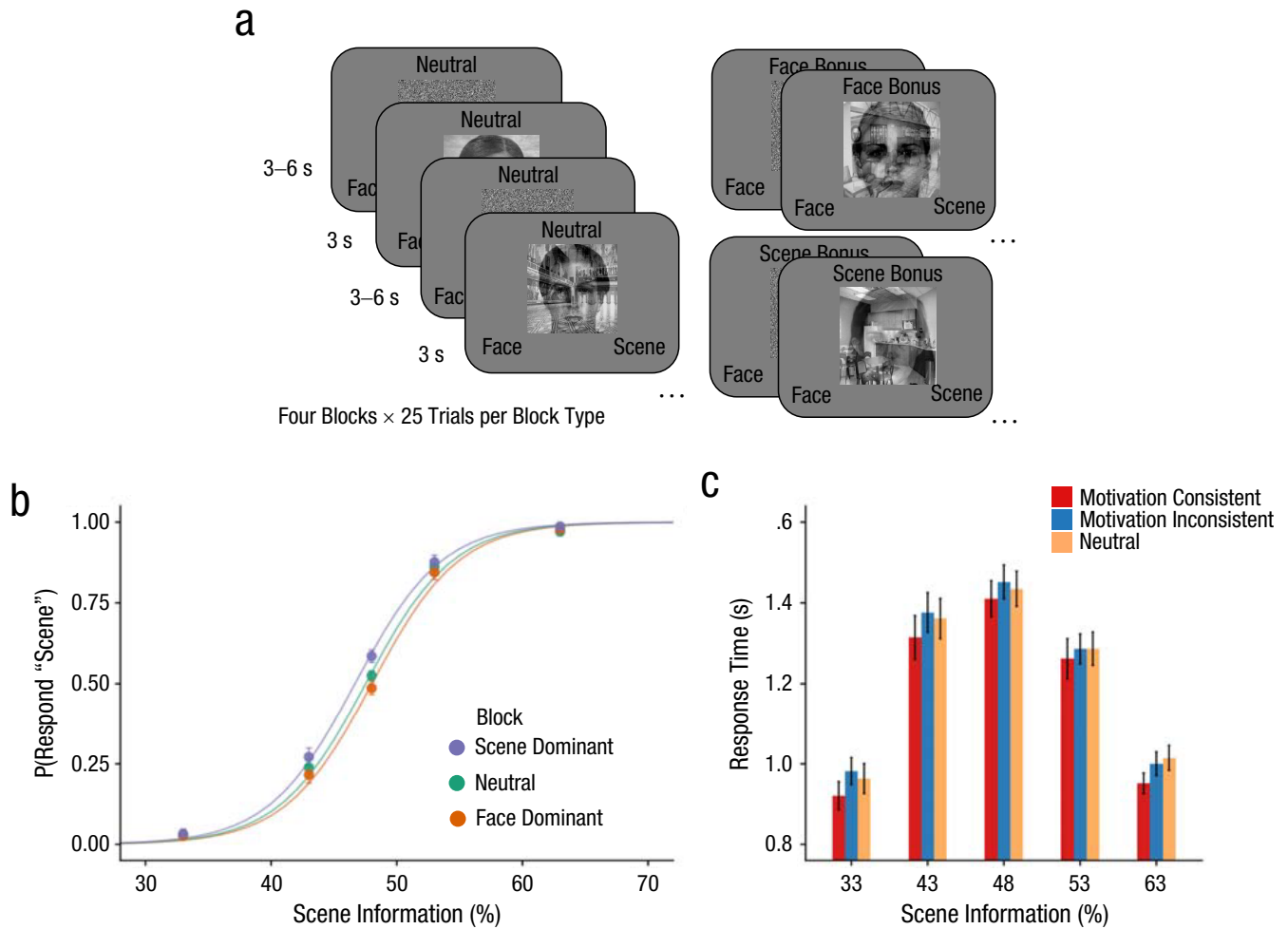
Fig. 1. Experimental design, psychometric curves, and behavioral data. On each trial (a), participants had to categorize ambiguous face-scene morphs as either face dominant or scene dominant and were awarded $0.05 for each correct categorization. On face- and scene-bonus blocks, we motivated participants to see more face- and scene-dominant images, respectively, by telling them they would receive a $3.00 bonus if there were more face- or scene-dominant images in the block. Psychometric curves (b) show the proportion of participants who categorized stimuli as having more scene information as a function of the actual percentage of scene information and block type. Mean response time (c) is shown for trials with various percentages of scene information, separately for trials on which participants responses were consistent and inconsistent with what they were motivated to see, as well as for neutral blocks. Error bars indicate between-participants standard errors of the mean.

coded motivation-consistent responses as the reference group and tested whether RTs were significantly different for motivation-consistent responses than for motivation-inconsistent and neutral responses (Model 2; see Table S1). The second model coded neutral responses as the reference group and tested whether RTs were significantly different for neutral responses than for motivation-consistent and motivation-inconsistent responses (Model 3; see Table S1). Both models controlled for whether participants categorized the image as face dominant or scene dominant. In both models, we also included the absolute difference between the percentage of scene information and the percentage of face information in an image as a covariate of no interest to control for trial difficulty, as well

as random intercepts and random slopes for all predictor variables.

Pupillometry analyses

Pupil diameter was recorded using an EyeLink 1000 eye tracker (SR Research, Kanata, Ontario, Canada) at a sampling rate of 500 Hz. The eye tracker was calibrated using a standard 5-point calibration sequence. For 12 participants, calibration failed when data from both eyes were being recorded, so we reattempted calibration while recording from one eye. For three of these participants, calibration remained unsuccessful, so pupil data were not collected, and the participant was excluded from all analyses. The eye tracker was

recalibrated halfway through the experiment. Eye blinks and saccades were detected using EyeLink detection algorithms with default settings. Data were linearly interpolated from 150 ms before the start of each blink or saccade to 150 ms after the end of the blink or saccade. The resulting data were smoothed using a zero-phase low-pass filter (third-order Butterworth, cutoff = 4 Hz; Kret & Sjak-Shie, 2019) and z scored for each eye and each participant. Data recorded from both eyes were then averaged to obtain a single time course.

We then extracted the time points of interest for each trial (stimulus-locked response: 500 ms before stimulus onset to 2 s after stimulus onset; decision-locked response: 2 s prior to decision). Trials on which more than 30% of the data were missing were discarded ($M = 1.8\%$ of total trials, $SE = 0.6\%$). For each participant, we modeled each time point using the following general linear model:

$$\text{pupil response} = \beta_0 + \beta_1 \text{motivation consistency}$$
$$+ \beta_2 \text{RT} + \beta_3 \%\text{scene} + \beta_4 \text{response}$$
$$+ \beta_5 \text{baseline},$$

where motivation consistency was coded 1 for motivation-consistent responses (e.g., categorizing an image as scene dominant in a scene-bonus block) and 0 for motivation-inconsistent responses (e.g., categorizing an image as face dominant in a scene-bonus block). Response was coded 1 for scene-dominant responses and 0 for face-dominant responses. Baseline denotes the average pupil diameter in the 500 ms before stimulus onset and was included to account for trial-by-trial differences in baseline pupil diameter when the model assessed the pupil response. The regression coefficients for motivation consistency thus reflect the extent to which the pupil response at a given time point was different when participants made motivation-consistent responses than when they made motivation-inconsistent responses, controlling for RT, percentage of scene information in an image, whether participants categorized the image as face dominant or scene dominant, and baseline pupil diameter.

Significance testing and correction for comparisons over multiple time points were then conducted using nonparametric cluster-based permutation tests (Maris & Oostenveld, 2007), separately for the stimulus-locked time points and the decision-locked time points. At each time point, a one-sample t test was conducted to assess whether the regression coefficient was different from zero across participants. Clusters were defined as contiguous time points where the t test resulted in a p value less than .05. Cluster size was computed as the sum of t values in the cluster. A null distribution of

maximal cluster sizes was generated by repeating the cluster-forming procedure 10,000 times with data where the labels for motivation-consistent and motivation-inconsistent responses were randomly shuffled. Family-wise error-rate-corrected p values were then determined as the proportion of the null distribution in which the maximal cluster size was greater than the observed cluster size.

To examine the separate effects of baseline and evoked pupil dilation, we defined baseline pupil dilation as the average pupil diameter in the 500 ms before stimulus onset and defined the evoked pupil response as the average change in pupil diameter from baseline in the 1 s prior to the time of choice. We modeled whether participants made motivation-consistent responses as a function of baseline pupil dilation, the evoked pupil response, RT, and trial difficulty (i.e., absolute difference between the percentage of scene information and the percentage of face information in the image) using a linear mixed-effects model (Model 4; see Table S1). This analysis allowed us to assess the relationship between each pupil signal and participants' responses while controlling for one another, RT, and trial difficulty. We assessed the relationship between pupil dilation and both trial accuracy and RT using a similar approach (Models 5 and 6; see Table S1) and ran separate analyses to test for the zero-order relationship between baseline pupil diameter and motivation-consistent responses (see the Supplemental Material).

Drift-diffusion model

The DDM is a class of sequential-sampling model commonly applied to two-alternative forced-choice paradigms (Ratcliff & McKoon, 2007). In the context of our task, a DDM assumes that participants' responses arise from the noisy accumulation of sensory information (Fig. 2a). If the level of evidence crosses one of two decision thresholds (upper bound = scene; lower bound = face), the corresponding response is made. The starting point and rate of evidence accumulation were determined by the free parameters z and v, respectively. The distance between the two thresholds was determined by the free parameter a, whereas time unrelated to the decision process (nondecision time; e.g., time needed for motor response) was determined by the free parameter t.

Model parameters were estimated from participants' RT distributions using the hierarchical drift-diffusion model (HDDM) toolbox with default priors (Wiecki et al., 2013; see the Supplemental Material). HDDM implements hierarchical Bayesian estimation, which assumes that parameters for individual participants were randomly drawn from a group-level distribution.
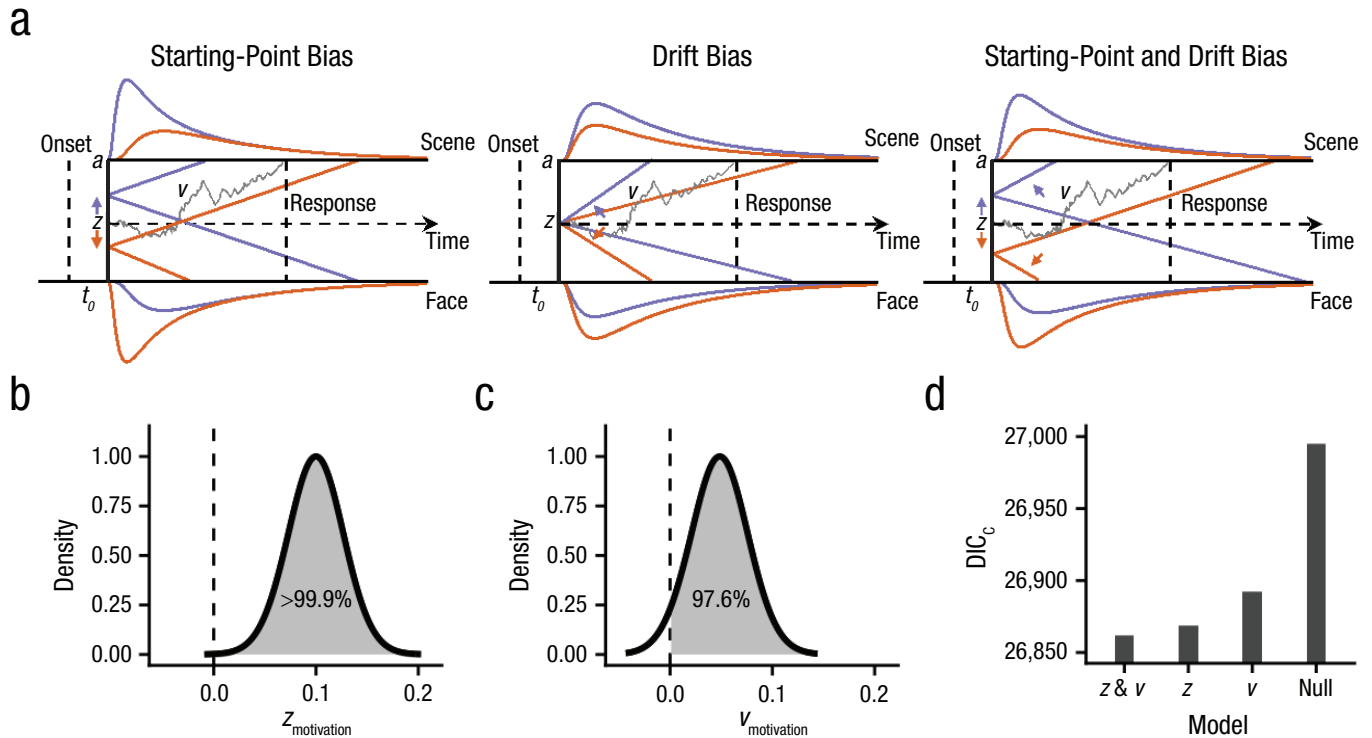
Fig. 2. Schematic depiction of biasing mechanisms (top) and model results (bottom). Biases in starting point and drift rate (a) have distinguishable effects on the shape of response time (RT) distributions. The gray lines show an example trajectory of evidence accumulation on a single trial. The purple lines show the mean drift and resulting RT distribution when participants are motivated to see scene-dominant images. The orange lines show the mean drift and resulting RT distribution when participants are motivated to see face-dominant images. The starting point and rate of evidence accumulation were determined by the free parameters z and v, respectively. The distance between the two thresholds was determined by the free parameter a, whereas time unrelated to the decision process (nondecision time; e.g., time needed for motor response) was determined by the free parameter t. Posterior distributions are shown for (b) model-estimated starting point bias ($z_{motivation}$) and (c) model-estimated drift bias ($v_{motivation}$). The dashed lines in (b) and (c) indicate 0 (no bias), and the gray shaded areas show the percentage of the distributions above 0. The corrected deviance information criterion (DIC_c) is shown separately in (d) for models containing both the starting point and drift rate (z and v) only the starting point (z), only the drift rate (v), and neither parameter (null).

We estimated group-level parameters as well as parameters for each individual participant, where each participant's parameters both contributed to and were constrained by parameters at the group level. Markov chain Monte Carlo sampling was used to estimate the joint posterior distribution of all model parameters (30,000 samples; burn-in = 3,000 samples; thinning = 2). To account for outliers generated by a process other than that assumed by the model (e.g., lapses in attention, accidental button presses), we estimated a mixture model in which 5% of trials were assumed to be distributed according to a uniform distribution.

The HDDM package allows parameters to vary according to a specified linear model. To examine the effects of motivation on the starting point, we allowed the starting point z to vary as a function of the motivation-consistent category. HDDM implements z as the relative starting point, ranging from 0 to 1, with .5 denoting an unbiased starting point. Thus, we used the

inverse logit link function to restrict z to values between 0 and 1:

$$z = \frac{1}{1 + \exp(-(\beta_{z1}\text{motivation} + \beta_{z0}))},$$

where motivation denotes the motivation-consistent category defined by the different types of experimental blocks (coded 1, −1, and 0 for scene-bonus blocks, face-bonus blocks, and neutral blocks, respectively). Positive values of β_{z1} reflect moving the starting point toward the scene threshold on scene-bonus blocks and toward the face threshold on face-bonus blocks. We took β_{z1} as a measure of the motivational bias in the starting point ($z_{motivation}$).

In the same model, we modeled the drift rate v as a function of the motivation-consistent category:

$$v = \beta_{v1}\text{motivation} + \beta_{v2}\%\text{scene} + \beta_{v0},$$

where motivation was again coded +1 (scene-bonus block), −1 (face-bonus block), and 0 (neutral block). Positive values for β_{v1} reflect a drift bias toward the scene threshold on scene-bonus blocks and toward the face threshold on face-bonus blocks. We took β_{v1} as a measure of the motivational bias in drift rate ($v_{\text{motivation}}$). β_{v2} reflects the effect of sensory evidence (i.e., percentage of scene information in an image) on the drift rate. We de-meaned the percentage of scene information prior to entering it into the model so that the intercept term, β_{v0}, would also reflect individual participants' intrinsic biases in the drift rate at 48% scene information (i.e., the point of subjective equivalence as established by pilot data).

For each of the bias parameters ($z_{\text{motivation}}$ and $v_{\text{motivation}}$), we computed the proportion of the posterior distribution that was greater than 0. This proportion denotes the probability that the parameter had a positive value (i.e., a positive motivational effect on the parameter). To examine whether either of the biases was sufficient for explaining the data, we fitted two additional comparison models in which only z or only v was biased by motivation. As a baseline for comparison, we also fitted a null model in which neither the starting point nor drift rate was biased by motivation. Although HDDM models are commonly compared using the deviance information criterion (DIC; Spiegelhalter et al., 2002; Wiecki et al., 2013), DIC is known to favor models with greater complexity (Plummer, 2008). We thus compared the four models using a corrected DIC (DIC_c) that penalizes twice the number of effective parameters (Ando, 2011):

$$\text{DIC} = \text{posterior expectation of deviance} + pD$$
$$\text{DIC}_c = \text{DIC} + pD,$$

where pD denotes the number of effective parameters; lower DIC_c values indicate better model fit. Model-recovery simulations indicated that DIC_c accurately identifies the true model from simulated data (see Fig. S2 in the Supplemental Material).

Next, we assessed how trial-by-trial fluctuations in pupil dilation relate to the two biasing mechanisms. We computed the evoked pupil response on each trial as the average change in pupil dilation from baseline in the 1 s prior to choice. This duration corresponded to the time period during which the response-locked pupil time course was higher on motivation-consistent trials than on motivation-inconsistent trials. As was the case in our earlier analyses, baseline pupil diameter was defined as the average pupil diameter in the 500 ms prior to stimulus onset. To examine the relationship between the evoked pupil response and motivational bias, we generated a regressor that was the interaction

between the evoked pupil response and the motivation-consistent category:

$$\text{Evoked Pupil} \times \text{Motivation}$$
$$= \begin{cases} \text{evoked pupil if scene-bonus block} \\ 0 \text{ if neutral block} \\ \text{Evoked Pupil} \times -1 \text{ if face-bonus block} \end{cases}$$

We generated a similar regressor, Baseline × Motivation, to examine the relationship between baseline pupil diameter and motivational bias. We allowed the starting point to vary as a function of the Evoked Pupil × Motivation and Baseline × Motivation:

$$z = \frac{1}{1 + \exp(-(\beta_{z1}\text{Evoked Pupil} \times \text{Motivation} + \beta_{z2}\text{Baseline} \times \text{Motivation} + \beta_{z0}))}.$$

Positive values for β_{z1} or β_{z2} would indicate that the corresponding pupil signal has a positive relationship with the starting point on scene-bonus blocks (i.e., reducing the amount of evidence needed to respond "scene dominant") and a negative relationship on face-bonus blocks (i.e., reducing the amount of evidence needed to respond "face dominant"). Even though the evoked pupil response occurred after the start of the trial, it can bias the estimate of the starting point. This is because a model with a biased starting point is functionally equivalent to a model with asymmetric decision thresholds. For example, a model in which the starting point is biased toward the scene threshold is indistinguishable from a model with a lower scene threshold and an unchanged face threshold. Because the HDDM implements symmetric thresholds with a relative starting point, the effect of asymmetric thresholds can be captured only as a biased starting point. The evoked pupil response can increase participants' likelihood of making a motivation-consistent choice by reducing the corresponding decision threshold (i.e., reducing the amount of evidence needed to make that response). Including Evoked Pupil × Motivation in the model allowed us to test this possibility.

To examine the relationship between pupil dilation and motivational biases in the drift rate, we modeled the drift rate as a function of Evoked Pupil × Motivation and Baseline × Motivation:

$$v = \beta_{v1}\text{Evoked Pupil} \times \text{Motivation} + \beta_{v2}\text{Baseline} \times \text{Motivation} + \beta_{v3}\%\text{scene} + \beta_{v0}.$$

Positive values for β_{v1} and β_{v2} would indicate that the corresponding pupil signal has a positive relationship

with the drift rate (i.e., faster accumulation toward the scene threshold) on scene-bonus blocks and a negative relationship (i.e., faster accumulation toward the face threshold) on face-bonus blocks.

Model convergence was formally assessed using the Gelman-Rubin $\hat{R}$ statistic (Gelman & Rubin, 1992), which runs multiple Markov chains to compare within-chain and between-chain variances. Large differences ($\hat{R} > 1.1$) between these variances would signal nonconvergence. In addition, we examined each trace to check that there were no drifts or large jumps, which would also suggest nonconvergence. We report model-convergence metrics, posterior means, and 95% credible intervals of model parameters in Table S2 in the Supplemental Material. We also conducted posterior predictive checks by comparing participants' behavior with data simulated with parameter values sampled from the posterior distribution estimated by each model (see the Supplemental Material).

Results

Thirty-eight participants were presented with visually ambiguous images created by averaging a face image and a scene image in different proportions and were rewarded for correctly categorizing whether the image was face dominant or scene dominant (Fig. 1a). Participants performed the task in blocks of 25 trials each. In face-bonus blocks, participants received a $3.00 category bonus if there were more face-dominant images in the block. In scene-bonus blocks, participants received a $3.00 category bonus if there were more scene-dominant images in the block. In neutral blocks, participants did not receive a category bonus. Thus, participants were motivated to see more face-dominant images in face-bonus blocks and scene-dominant images in scene-bonus blocks. Crucially, the category bonuses were determined by the objective composition of images in each block and not by participants' responses. To earn the most money, participants should ignore the category bonus and categorize the images accurately. Nevertheless, participants' categorizations might be biased by what they were motivated to see.

Motivation biased perceptual judgments

To assess the effects of the category bonuses on perceptual judgments, we estimated participants' psychometric functions separately for each block type (Fig. 1b). Statistical comparisons between the curves were conducted using generalized linear mixed-effects models. Participants were more likely to categorize an image as face dominant in face-bonus blocks ($z = 2.09$, $p = .037$, $b = 0.15$, 95% confidence interval [CI] = [0.01, 0.28]) and as scene dominant in scene-bonus blocks ($z = 3.21$, $p = .001$, $b = 0.25$, 95% CI = [0.09, 0.40]), relative to neutral blocks. Thus, for the same face-versus-scene proportion, participants were more likely to categorize the image as the category they were motivated to see.

Next, we assessed whether motivation affected participants' RTs (Fig. 1c). Participants were faster to categorize an image as belonging to the category they were motivated to see (motivation-consistent responses, e.g., categorizing an image as face dominant in face-bonus blocks) than as the category they were motivated not to see (motivation-inconsistent responses), $t(36.1) = 2.90$, $p = .006$, $b = 0.043$, 95% CI = [0.006, 0.054]. RTs were faster for motivation-consistent responses than for responses in neutral blocks, $t(36.1) = 2.48$, $p = .018$, $b = 0.031$, 95% CI = [0.010, 0.047], but were not significantly different between motivation-inconsistent responses and responses in neutral blocks, $t(34.2) = 1.01$, $p = .321$, $b = 0.013$, 95% CI = [−0.012, 0.038].

Motivation biases both starting point and rate of sensory-evidence accumulation

We fitted a DDM to participants' RT distributions. The DDM assumes that each perceptual judgment arises from the noisy accumulation of sensory evidence toward one of two decision thresholds and provides a computational description of this process. Within the DDM framework, participants' motivational bias can reflect a bias in the starting point (z) and/or a bias in the rate (drift rate, v) of sensory-evidence accumulation in favor of the category that participants were motivated to see. A bias in the starting point reduces the amount of evidence needed to make a motivation-consistent response, whereas a bias in the drift rate biases the evidence-accumulation process in favor of the motivation-consistent category. Both biases increase the proportion of motivation-consistent responses but have distinguishable effects on the distribution of RTs (Leong et al., 2019; White & Poldrack, 2014; Fig. 2a; see Fig. S3 in the Supplemental Material). We estimated the extent to which each bias contributed to participants' behavior by fitting the model to participants' responses and RTs (see the Method section).

We allowed the starting point to vary according to a linear regression model with the motivation-consistent category as a predictor variable. The regression coefficient reflects the extent to which motivation affects the starting point. Motivation had a positive effect on the starting point, $p(z_{motivation} > 0) > .999$, $M = 0.100$, 95% credible interval = [0.053, 0.145] (Fig. 2b),

indicating that the starting point was biased toward the scene threshold when participants were motivated to see scene-dominant images and biased toward the face threshold when participants were motivated to see face-dominant images.

The drift rate was similarly modeled using linear regression. Because the drift rate also depends on the amount of sensory evidence available in the image, we included the percentage of scene information in an image as an additional predictor. Motivation had a positive effect on the drift rate, $p(v_{motivation} > 0) = .976$, $M = 0.048$, 95% credible interval = [0.0004, 0.094] (Fig. 2c), indicating that sensory evidence accumulated more quickly for the motivation-consistent category. As expected, the percentage of scene information had a positive effect on the drift rate, $p(v_{scene} > 0) > .999$, $M = 1.446$, 95% credible interval = [1.325, 1.569], indicating that sensory-evidence accumulation was biased toward the scene threshold when there was a high proportion of scene information in an image and biased toward the face threshold when there was a low proportion of scene information in an image.

To examine whether either biasing mechanism was sufficient to account for participants' data, we fitted additional models in which motivation biased only the starting point (z model) or only the drift rate (v model). Model fits were then compared using DIC_c; lower values indicate better fit (see the Method section). The model in which motivation biased both the starting point and drift rate yielded the lowest DIC_c value (z and v: 26,862, z: 26,869, v: 26,892, null: 26,995; Fig. 2d). Furthermore, simulated data generated by parameterizing the z-and-v model with best-fit parameter values aligned well with participants' data and matched qualitative patterns in the data better than the alternative models (see Fig. S3). Taken together, our modeling results suggest that motivation biased both the starting point and rate of sensory-evidence accumulation in favor of the motivation-consistent category.

Pupil-linked arousal was higher when participants made motivation-consistent responses

We next investigated whether physiological arousal was associated with motivational biases in perceptual judgments. We measured participants' pupil diameter as a measure of physiological arousal. For each trial, the pupil time course was extracted around two events of interest: (a) stimulus onset (500 ms before stimulus onset to 2 s after stimulus onset; Fig. 3a) and (b) choice (2 s prior to choice; Fig. 3b). We then averaged the pupil time courses separately for trials on which participants made motivation-consistent responses and

trials on which they made motivation-inconsistent responses. The shapes of the pupil time courses were similar across the two types of trials. In particular, stimulus onset induces an increase in pupil diameter that peaks around 300 ms, reflecting an increase in arousal at the start of the trial. This is followed by a brief recovery before a second increase that peaks around 250 ms after participants make a choice.

We modeled the pupil time courses using general linear modeling (see the Method section), which allowed us to examine the relationship between motivation-consistent responses and pupil dilation while controlling for the effects of RT, percentage of scene information in an image, whether participants categorized the image as face dominant or scene dominant, and baseline pupil diameter. Using this approach, we found that pupil size was larger on trials in which participants made motivation-consistent responses than on trials in which they made motivation-inconsistent responses (from 400 ms to 1.1 s after stimulus onset, cluster $p = .028$; from 1.1 s prior to decision to time of decision, cluster $p = .008$; Figs. 3c and 3d). These results indicate that pupil-linked arousal was associated with motivational biases in perceptual judgments.

To examine the role of both baseline and evoked pupil dilation, we defined baseline pupil dilation as the average pupil diameter in the 500 ms before stimulus onset and defined the evoked pupil response as the average change in pupil diameter from baseline in the 1 s prior to the time of choice. We then entered both measures into linear mixed-effects models to assess their relationship with motivation-consistent responses, accuracy, and RT (see the Method section). Reproducing the time-course analyses, results showed that participants were more likely to make motivation-consistent responses on trials with higher evoked pupil response ($z = 2.89$, $p = .004$, $b = 0.166$, 95% CI = [0.054, 0.278]) when models controlled for the effects of RT, baseline pupil diameter, and trial difficulty. Participants were also less likely to correctly categorize the image as face dominant or scene dominant on trials with higher evoked pupil response ($z = -2.46$, $p = .014$, $b = -0.416$, 95% CI = [-0.748, -0.084]). Together, these results suggest that at higher levels of arousal, participants' perceptual judgments were more likely to be biased by the motivation manipulation and depended less on the objective information in the image.

Consistent with earlier work (de Gee et al., 2014), our analyses showed that evoked pupil responses were larger on trials with longer RTs, $t(36.9) = 2.94$, $p = .006$, $b = 0.141$, 95% CI = [0.047, 0.235]. As reported earlier, motivation-consistent responses were on average faster than motivation-inconsistent responses. If the relationship between pupil dilation and motivation-consistent
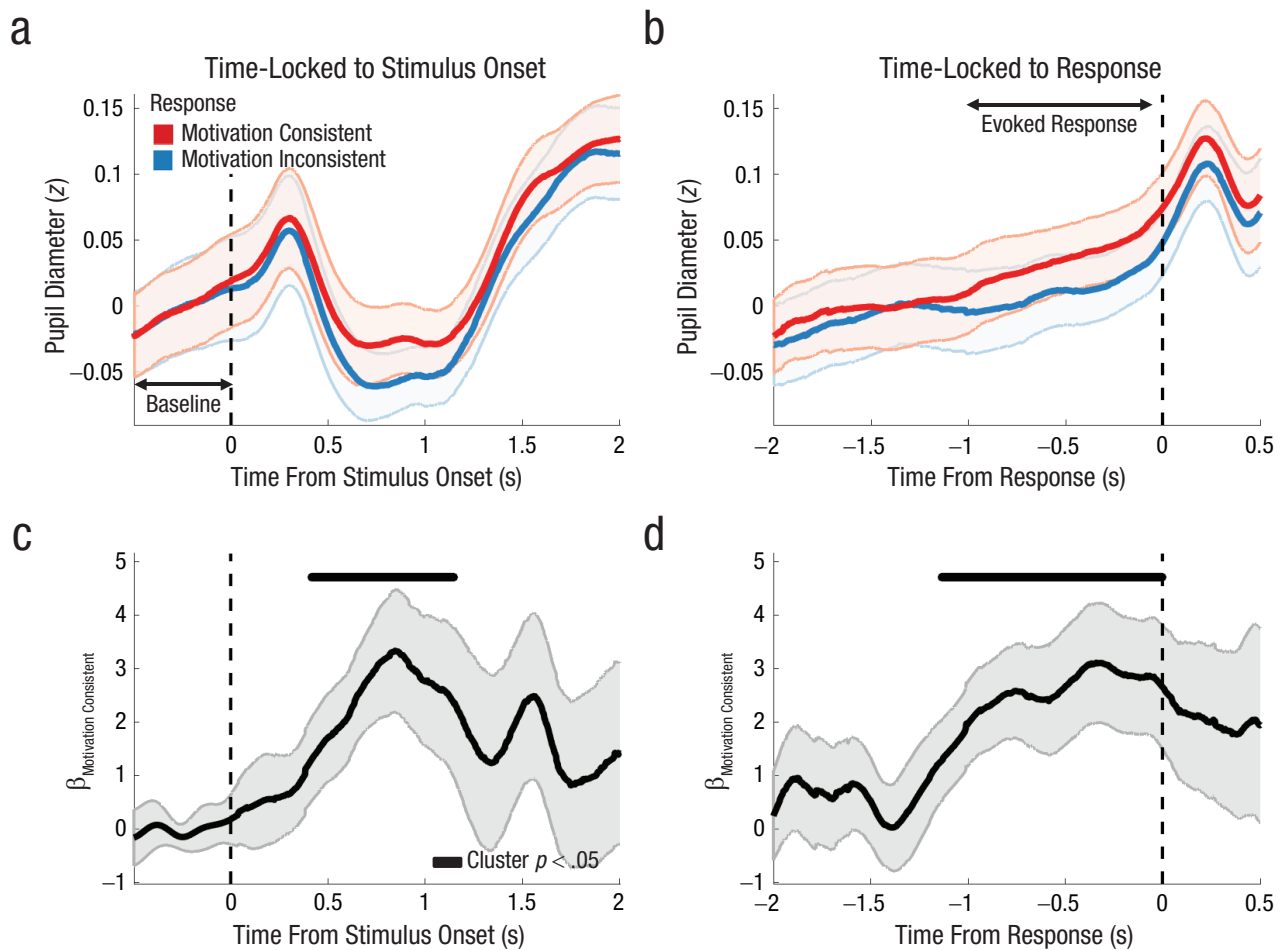
Fig. 3. Pupillometry results. The graphs in the top row show average pupil diameter over the course of a trial, time locked to (a) stimulus onset and (b) time of response. Solid lines denote the pupil time course for trials on which participants made motivation-consistent responses and motivation-inconsistent responses. Dashed lines mark stimulus onset time. Baseline pupil dilation was defined as the average pupil diameter in the 500 ms before stimulus onset, and the evoked pupil response was defined as the average change in pupil diameter from baseline in the 1 s prior to the time of response. Shaded error bands denote between-participants standard errors of the mean. The bottom row shows the relationship between making a motivation-consistent response and pupil dilation, controlling for response time, percentage of scene information, whether participants made a face-dominant or scene-dominant categorization, and baseline pupil diameter, time locked to (c) stimulus onset and (d) time of response. Shaded error bands denote standard errors of the estimate. Black horizontal bars indicate time points when regression coefficients were significantly different from 0 on the basis of cluster-based permutation tests.

responses were driven solely by RT effects, the shorter RTs on motivation-consistent responses should have led to a smaller evoked pupil response, which is the opposite of what was observed. Thus, RT effects cannot explain the relationship between the evoked pupil response and motivational biases in perceptual judgments.

In contrast, baseline pupil diameter was not associated with motivation-consistent responses, $z = 0.998$, $p = .318$, $b = 0.028$, 95% CI = [−0.026, 0.082]; accuracy, $z = −0.789$, $p = .430$, $b = −0.049$, 95% CI = [−0.170, 0.073]; and RT, $t(31.3) = 1.46$, $p = .154$, $b = 0.018$, 95% CI = [−0.006, 0.043]. The preceding analyses assessed the effects of baseline pupil diameter while controlling for the evoked pupil

response and trial difficulty. We ran a separate analysis to test for the zero-order relationship between baseline pupil diameter and motivation-consistent responses, which similarly found that baseline pupil diameter was not different between motivation-consistent and motivation-inconsistent responses, $t(37.3) = −0.009$, $p = .993$, $b = 0.0002$, 95% CI = [−0.049, 0.049] (see Fig. S4 in the Supplemental Material). These results indicate that the relationship between pupil dilation and motivation-consistent responses was driven by larger evoked pupil responses during the decision period and not trial-by-trial fluctuations in the prestimulus baseline.

In exploratory analyses, we found that baseline pupil diameter was marginally lower for neutral responses

(i.e., trials in the neutral blocks without a $3.00 category bonus) than both motivation-consistent and motivation-inconsistent responses—neutral versus motivation consistent, $t(37.1) = 1.76$, $p = .088$, $b = 0.072$, 95% CI = [−0.001, 0.152]; neutral versus motivation inconsistent, $t(37.1) = 1.86$, $p = .071$, $b = 0.072$, 95% CI = [−0.004, 0.148] (see Fig. S4). This suggests that the prospect of a category bonus induced an increase in baseline pupil diameter, although the raised baseline on its own did not bias participants to make motivation-consistent responses. Instead, they suggest that the bias was associated with a larger evoked response on top of the elevated baseline.

In summary, increased pupil dilation during the decision period was associated with participants making motivation-consistent perceptual categorizations. This relationship was not due to differences in RT or baseline pupil diameter. In addition, increased pupil dilation during the decision period was associated with lower task accuracy, suggesting that on trials with heightened arousal, participants were more biased by what they were motivated to see and relied less on the objective information in the image.

Pupil-linked arousal was associated with trial-by-trial motivational biases in drift rate

Pupil-linked arousal was associated with an increased likelihood of making motivation-consistent perceptual judgments. Our earlier modeling analyses suggested that motivational effects on perceptual judgments were driven by both biases in the starting point and rate of evidence accumulation. Was pupil-linked arousal related to either or both biasing mechanisms? To address this question, we used a linear regression approach to examine the relationship between pupil dilation and trial-by-trial fluctuations in motivational bias. Instead of estimating a fixed starting point or drift rate across trials, we allowed the two parameters to vary according to the baseline pupil diameter and the evoked pupil response on each trial.

To model the relationship between pupil dilation on motivational biases, we generated regressors that denote the interaction between pupil dilation and the motivation-consistent category (i.e., Baseline × Motivation and Evoked Pupil × Motivation; see the Method section). The coefficients on these regressors reflect the extent to which the corresponding pupil signal (i.e., baseline diameter or evoked pupil response) was associated with motivational effects on model parameters. For example, a positive regression coefficient for Evoked Pupil × Motivation on the drift rate would reflect a positive relationship between the evoked pupil response and motivational

biases in the drift rate. We fitted participants' data to a model in which the starting point and drift rate were allowed to vary as a function of Baseline × Motivation and Evoked Pupil × Motivation.

The evoked pupil response had a positive relationship with motivational biases in the drift rate, $p(v_{\text{Evoked Pupil × Motivation}} > 0) = .979$, $M = 0.069$, 95% credible interval = [0.004, 0.135] (Fig. 4a). That is to say, larger evoked pupil responses were associated with a bias in evidence accumulation toward the scene threshold when participants were motivated to see scene-dominant images and a bias toward the face threshold when they were motivated to see face-dominant images. In contrast, the evoked pupil response was not associated with motivational biases in the starting point, $p(z_{\text{Evoked Pupil × Motivation}} > 0) = .437$, $M = −0.003$, 95% credible interval = [−0.082, 0.089]. Baseline pupil diameter was not associated with motivational biases in either the drift rate, $p(v_{\text{Baseline × Motivation}} > 0) = .851$, $M = 0.018$, 95% credible interval = [−0.015, 0.058], or the starting point, $p(z_{\text{Baseline × Motivation}} > 0) = .366$, $M = −0.006$, 95% credible interval = [−0.043, 0.031]. Similar results were obtained with a model that included the motivation-consistent category as a covariate (see Fig. S5 in the Supplemental Material) and a model that included parameters for intertrial variability of the starting point, drift rate, and nondecision time (see Fig. S6 in the Supplemental Material).

Our results suggest that the relationship between pupil dilation and motivational biases arose because of a bias in drift rate associated with larger evoked pupil responses during the decision period. If this were true, a simpler model in which only the motivational bias in the drift rate varied as a function of Evoked Pupil × Motivation would provide a better fit to the data. Indeed, such a model had a lower DIC_c value than more complex models, models in which other parameters were allowed to vary with pupil dilation, and a model in which neither the starting point nor the drift rate was modulated by pupil dilation (Fig. 4b; see Table S3 in the Supplemental Material). Furthermore, data simulated from a model in which only the motivational bias in the drift rate varied as a function of Evoked Pupil × Motivation was sufficient to reproduce the empirical observation that evoked pupil responses were higher for motivation-consistent responses than motivation-inconsistent responses—empirical data: mean difference = 0.023, 95% CI = [0.002, 0.444], $t(37) = 2.24$, $p = .031$; model v_p: mean difference = 0.020, 95% CI = [0.009, 0.300], $t(37) = 3.87$, $p < .001$ (see Fig. S7 in the Supplemental Material).

Together, the estimated regression coefficients from the model and model comparison using DIC_c provide converging evidence that arousal effects on motivational biases in perceptual judgments were driven by
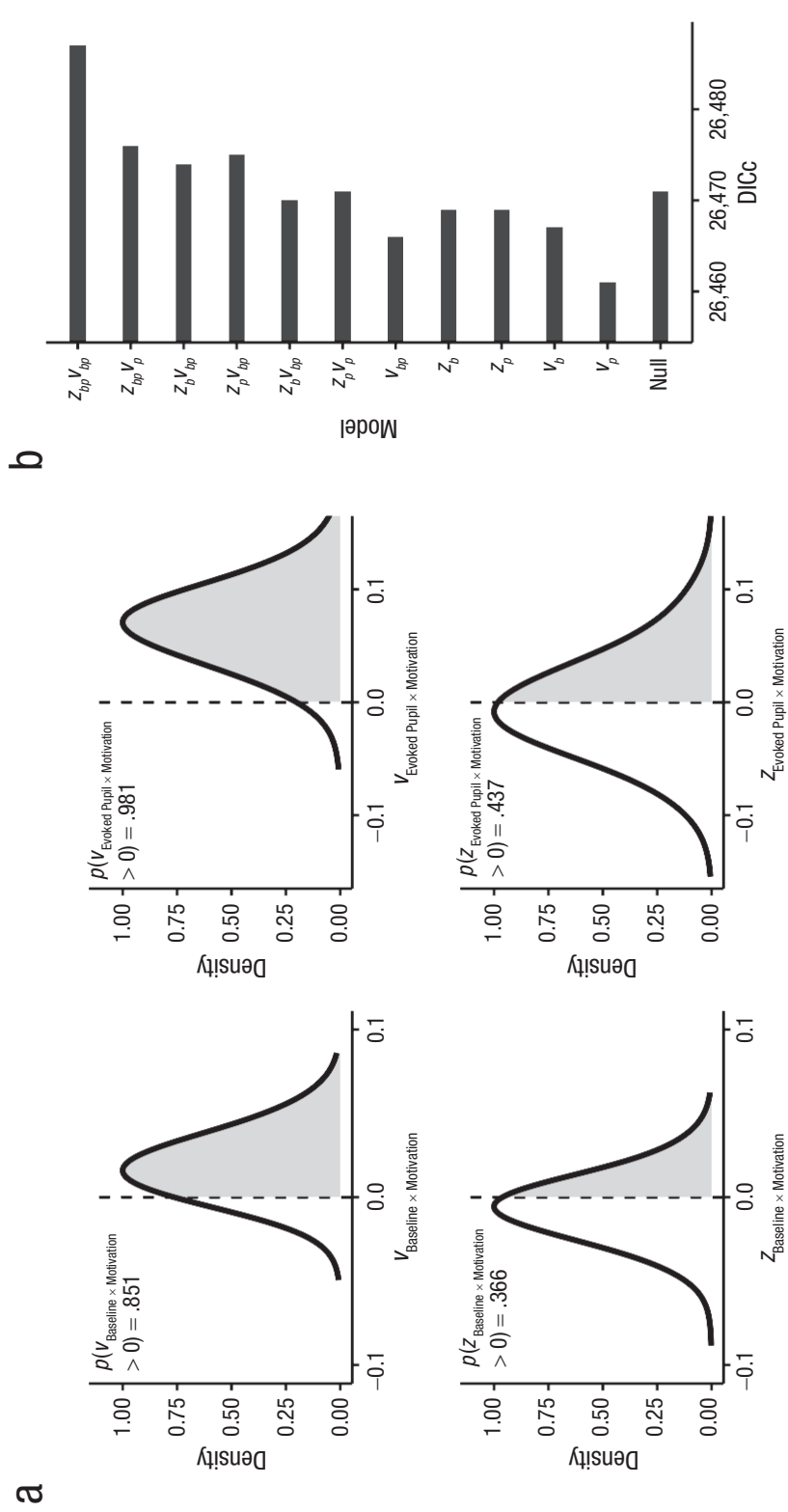
Fig. 4. Model comparisons. In (a), posterior distributions for the regression coefficients of baseline pupil diameter on drift bias ($v_{\text{Baseline} \times \text{Motivation}}$) and starting-point bias ($z_{\text{Baseline} \times \text{Motivation}}$) are shown in the left column, and posterior distributions for the regression coefficients of the evoked pupil response on drift bias ($v_{\text{Evoked Pupil} \times \text{Motivation}}$) and starting-point bias ($z_{\text{Evoked Pupil} \times \text{Motivation}}$) are shown in the right column. The dashed line indicates 0 (no effect), and the gray shaded areas show the proportion of the distributions above 0. The model comparison (b) is based on the corrected deviance information criterion (DIC_c). Models in which pupil dilation modulated starting point and drift bias are indicated by z and v, respectively. Subscript b indicates that the parameter varied with baseline pupil diameter, and subscript p indicates that the parameter varied with evoked pupil response. "Null" denotes a model in which neither the starting point nor the drift rate varied with pupil dilation.

1505

biases in evidence accumulation that tracked trial-by-trial fluctuations in evoked pupil response.

Discussion

In the current work, we investigated the role of physiological arousal in modulating motivational biases in perceptual decision-making. We manipulated the percept that participants were motivated to see as they performed a perceptual decision-making task. Participants were more likely to categorize an image as belonging to the category they were motivated to see. This motivational bias reflected a bias toward making motivation-consistent responses as well as a bias in how participants accumulated perceptual evidence over time. Arousal, measured by pupil dilation, was higher when participants made motivation-consistent responses. Trial-by-trial fluctuations in the evoked pupil response were specifically associated with faster evidence accumulation in favor of the motivationally desirable percept. These findings suggest that pupil-linked arousal processes mediate motivational effects on perceptual decision-making by enhancing the processing of motivationally desirable information.

Contemporary accounts of perceptual decision-making propose that perceptual decisions are determined by comparing the activity of neurons selective to different perceptual features (Gold & Shadlen, 2007; Heekeren et al., 2008). Motivation can bias this comparison in favor of percepts that participants are motivated to see by enhancing neural activity selective to desirable perceptual features in sensory regions of the brain (Leong et al., 2019). For example, when participants were presented with ambiguous face-scene morphs, face-selective and scene-selective neural activity in sensory cortices was greater when participants were motivated to see face-dominant and scene-dominant images, respectively. Participants with stronger motivational enhancement of category-selective neural activity also exhibited greater biases in model-estimated drift rate, suggesting that motivationally enhanced neural representations result from the biased accumulation of sensory information. The current findings suggest that motivational biases in sensory processing not only vary between individuals but also vary trial by trial depending on the level of arousal. When arousal is high, there is a stronger motivational bias in sensory processing, and participants are more likely to see the desirable percept. In contrast, when arousal is low, motivational effects are weaker and participants' decisions depend more on the objective sensory information in the image.

Pupil-linked arousal processes are thought to be driven by activity in the locus coeruleus norepinephrine system (Joshi et al., 2016; Murphy, O'Connell, et al., 2014). Our results are consistent with the GANE model of norepinephrine function, which posits that arousal-related norepinephrine release selectively enhances the processing of salient stimuli (Mather et al., 2016). The GANE model builds on earlier work showing that norepinephrine increases the gain of neurons; excited neurons become even more active and inhibited neurons become even less active (Aston-Jones & Cohen, 2005; Sara & Bouret, 2012). High neural gain would thus result in focused attention on the most salient features of a stimulus (Eldar et al., 2016). Here, we argue that otherwise neutral perceptual features become motivationally salient when participants are motivated to see them. Attention is directed toward these features, and neurons encoding these features would be more active than neurons encoding other features (Bourgeois et al., 2016; Pessoa, 2009). During moments of heightened arousal, high neural gain accentuates this difference, selectively enhancing the neural representation of motivationally salient features and amplifying motivational effects on perceptual processing. Novel imaging approaches now provide the opportunity to accurately and reliably measure activity in the locus coeruleus (Betts et al., 2019; Liu et al., 2017). Future work can take advantage of these approaches to simultaneously measure activity in the locus coeruleus and sensory regions of the brain to directly test the role of the locus coeruleus norepinephrine system in enhancing motivationally desirable neural representations.

Growing evidence suggests that pupil-linked arousal processes during the decision period (i.e., between stimulus onset and the participant's response) influence the accumulation of sensory evidence during perceptual decision-making (Cheadle et al., 2014; de Gee et al., 2014, 2017, 2020; Keung et al., 2019; Krishnamurthy et al., 2017). For example, in the studies by de Gee and colleagues (2014, 2017, 2020), larger evoked pupil responses were associated with a reduction in participants' intrinsic biases to report the presence or absence of a target pattern embedded in a noisy sensory background. Similarly, Krishnamurthy and colleagues (2017) found that larger evoked pupil responses were associated with the reduced influence of prior expectations in a sound-localization task. How might we reconcile the negative relationship between pupil dilation and decision biases documented in these earlier studies with our finding that larger pupil dilation was associated with stronger motivational biases? One possible explanation is that in the earlier studies, participants were motivated to be accurate in their perceptual reports and were indifferent to the different perceptual options. Thus, attention would not be biased toward any one aspect of the stimulus. The higher neural gain

associated with a larger evoked pupil response would then primarily serve to increase neuronal sensitivity to the stimulus. Thus, larger evoked pupil responses would be associated with perceptual decisions that depend more on sensory features of the stimulus and less on prior biases. In contrast, participants in our task were motivated to see one of two competing percepts present in an ambiguous stimulus. Attention directed toward stimulus features associated with the desirable percept enhances neural activity encoding that percept. Increasing neural gain in our task amplifies the motivational enhancement and biases perceptual decisions in favor of the percept that participants were motivated to see. Thus, larger evoked pupil responses would be associated with stronger motivational biases.

Prior studies have found that prestimulus arousal levels, measured by prestimulus baseline pupil diameter, can also affect the upcoming decision (Krishnamurthy et al., 2017; Murphy, Vandekerckhove, & Nieuwenhuis, 2014; Nassar et al., 2012). For example, Krishnamurthy and colleagues (2017) found that both baseline and evoked pupil dilation were associated with the reduced influence of prior expectations on perceptual decisions. In our task, baseline pupil diameter was not related to motivational biases. Our task, however, was not designed to examine pupil dilation during the prestimulus period. In particular, there was a relatively short intertrial interval between the end of one trial and stimulus onset on the next trial (mean intertrial interval = 3.5 s). Thus, the prestimulus baseline on a given trial might be contaminated by the evoked pupil response on the previous trial. Future experiments with longer intervals between trials will be necessary to determine the relationship (or lack thereof) between baseline pupil diameter and motivational bias.

Altogether, the current results expand our understanding of the role of arousal in perceptual decision-making. Whereas prior work has primarily focused on how arousal affects perceptual decision-making in "neutral" contexts in which participants are indifferent to different perceptual options, our study examined the effects of arousal-related biases when participants are motivated to see one percept over another. Our findings suggest that arousal biases evidence accumulation in favor of desirable percepts. As a result, during moments of heightened arousal, participants were more likely to be biased to see what they were motivated to see and less likely to make accurate perceptual categorizations. Given the putative relationship between pupil-linked arousal processes and the locus coeruleus norepinephrine system, our results also highlight potential neuromodulatory mechanisms driving motivational biases. Notably, motivation has also been shown to influence information processing across many domains of human cognition (Kunda, 1990). For example, people learn more from positive outcomes than negative outcomes during an instrumental-learning task (Lefebvre et al., 2017) and incorporate favorable information more than unfavorable information when updating beliefs about future life events (Sharot et al., 2011). Do pupil-linked arousal processes also modulate motivational biases beyond sensory perception? Given the widespread projections of norepinephrine neurons across the brain, this is certainly possible. Future studies can extend our work and examine the effect that the relationship between arousal and motivational biases may have on other types of human reasoning and evaluation processes.

ORCID iD

Yuan Chang Leong [iD] https://orcid.org/0000-0003-2499-2393

Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/09567976211004547

References

Ando, T. (2011). Predictive Bayesian model selection. *American Journal of Mathematical and Management Sciences*, *31*(1–2), 13–38. https://doi.org/10.1080/01966324.2011.10737798

Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*,

28(1), 403–450. https://doi.org/10.1146/annurev.neuro.28.061604.135709

Balcetis, E., & Dunning, D. (2006). See what you want to see: Motivational influences on visual perception. *Journal of Personality and Social Psychology*, *91*(4), 612–625. https://doi.org/10.1037/0022-3514.91.4.612

Balcetis, E., Dunning, D., & Granot, Y. (2012). Subjective value determines initial dominance in binocular rivalry. *Journal of Experimental Social Psychology*, *48*(1), 122–129. https://doi.org/10.1016/j.jesp.2011.08.009

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Betts, M. J., Kirilina, E., Otaduy, M. C. G., Ivanov, D., Acosta-Cabronero, J., Callaghan, M. F., Lambert, C., Cardenas-Blanco, A., Pine, K., Passamonti, L., Loane, C., Keuken, M. C., Trujillo, P., Lüsebrink, F., Mattern, H., Liu, K. Y., Priovoulos, N., Fliessbach, K., Dahl, M. J., . . . Hämmerer, D. (2019). Locus coeruleus imaging as a biomarker for noradrenergic dysfunction in neurodegenerative diseases. *Brain*, *142*(9), 2558–2571. https://doi.org/10.1093/brain/awz193

Bourgeois, A., Chelazzi, L., & Vuilleumier, P. (2016). How motivation and reward learning modulate selective attention. In B. Studer & S. Knecht (Eds.), *Progress in brain research* (Vol. 229, pp. 325–342). Elsevier. https://doi.org/10.1016/bs.pbr.2016.06.004

Bradley, M. M., Miccoli, L., Escrig, M. A., & Lang, P. J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, *45*(4), 602–607. https://doi.org/10.1111/j.1469-8986.2008.00654.x

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Cheadle, S., Wyart, V., Tsetsos, K., Myers, N., de Gardelle, V., Herce Castañón, S., & Summerfield, C. (2014). Adaptive gain control during human perceptual choice. *Neuron*, *81*(6), 1429–1441. https://doi.org/10.1016/j.neuron.2014.01.020

de Gee, J. W., Colizoli, O., Kloosterman, N. A., Knapen, T., Nieuwenhuis, S., & Donner, T. H. (2017). Dynamic modulation of decision biases by brainstem arousal systems. *eLife*, *6*, Article e23232. https://doi.org/10.7554/eLife.23232

de Gee, J. W., Knapen, T., & Donner, T. H. (2014). Decision-related pupil dilation reflects upcoming choice and individual bias. *Proceedings of the National Academy of Sciences, USA*, *111*(5), E618–E625. https://doi.org/10.1073/pnas.1317557111

de Gee, J. W., Tsetsos, K., Schwabe, L., Urai, A. E., McCormick, D., McGinley, M. J., & Donner, T. H. (2020). Pupil-linked phasic arousal predicts a reduction of choice bias across species and decision domains. *eLife*, *9*, Article e54014. https://doi.org/10.7554/eLife.54014

Eldar, E., Niv, Y., & Cohen, J. D. (2016). Do you see the forest or the tree? Neural gain and breadth versus focus in perceptual processing. *Psychological Science*, *27*(12), 1632–1643. https://doi.org/10.1177/0956797616665578

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–472. https://doi.org/10.1214/ss/1177011136

Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annual Review of Neuroscience*, *30*(1), 535–574. https://doi.org/10.1146/annurev.neuro.29.051605.113038

Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience*, *9*(6), 467–479. https://doi.org/10.1038/nrn2374

Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, *89*(1), 221–234. https://doi.org/10.1016/j.neuron.2015.11.028

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007). Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of Memory and Language*, *56*(4), 575–591. https://doi.org/10.1016/j.jml.2006.05.004

Keung, W., Hagen, T. A., & Wilson, R. C. (2019). Regulation of evidence accumulation by pupil-linked arousal processes. *Nature Human Behaviour*, *3*(6), 636–645. https://doi.org/10.1038/s41562-019-0551-4

Knoblauch, K., & Maloney, L. T. (2012). *Modeling psychophysical data in R*. Springer.

Kret, M. E., & Sjak-Shie, E. E. (2019). Preprocessing pupil size data: Guidelines and code. *Behavior Research Methods*, *51*(3), 1336–1342. https://doi.org/10.3758/s13428-018-1075-y

Krishnamurthy, K., Nassar, M. R., Sarode, S., & Gold, J. I. (2017). Arousal-related adjustments of perceptual biases optimize perception in dynamic environments. *Nature Human Behaviour*, *1*(6), Article 0107. https://doi.org/10.1038/s41562-017-0107

Kunda, Z. (1990). The case for motivated reasoning. *Psychological Bulletin*, *108*(3), 480–498. https://doi.org/10.1037/0033-2909.108.3.480

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2019). *lmerTest: Tests in linear mixed effects models* (Version 3.1-0) [Computer software]. https://CRAN.R-project.org/package=lmerTest

Lang, P. J., & Bradley, M. M. (2010). Emotion and the motivational brain. *Biological Psychology*, *84*(3), 437–450. https://doi.org/10.1016/j.biopsycho.2009.10.007

Lee, T.-H., Greening, S. G., Ueno, T., Clewett, D., Ponzio, A., Sakaki, M., & Mather, M. (2018). Arousal increases neural gain via the locus coeruleus–noradrenaline system in younger adults but not in older adults. *Nature Human Behaviour*, *2*(5), 356–366. https://doi.org/10.1038/s41562-018-0344-1

Lefebvre, G., Lebreton, M., Meyniel, F., Bourgeois-Gironde, S., & Palminteri, S. (2017). Behavioural and neural characterization of optimistic reinforcement learning. *Nature Human Behaviour*, *1*(4), Article 0067. https://doi.org/10.1038/s41562-017-0067

Leong, Y. C., Hughes, B. L., Wang, Y., & Zaki, J. (2019). Neurocomputational mechanisms underlying motivated seeing. *Nature Human Behaviour*, *3*(9), 962–973. https://doi.org/10.1038/s41562-019-0637-z

Liu, K. Y., Marijatta, F., Hämmerer, D., Acosta-Cabronero, J., Düzel, E., & Howard, R. J. (2017). Magnetic resonance imaging of the human locus coeruleus: A systematic review. *Neuroscience & Biobehavioral Reviews*, *83*, 325–355. https://doi.org/10.1016/j.neubiorev.2017.10.023

Ma, D. S., Correll, J., & Wittenbrink, B. (2015). The Chicago Face Database: A free stimulus set of faces and norming data. *Behavior Research Methods*, *47*(4), 1122–1135. https://doi.org/10.3758/s13428-014-0532-5

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Markovic, J., Anderson, A. K., & Todd, R. M. (2014). Tuning to the significant: Neural and genetic processes underlying affective enhancement of visual perception and memory. *Behavioural Brain Research*, *259*, 229–241. https://doi.org/10.1016/j.bbr.2013.11.018

Mather, M., Clewett, D., Sakaki, M., & Harley, C. W. (2016). Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. *Behavioral & Brain Sciences*, *39*, Article e200. https://doi.org/10.1017/S0140525X15000667

Murphy, P. R., O'Connell, R. G., O'Sullivan, M., Robertson, I. H., & Balsters, J. H. (2014). Pupil diameter covaries with BOLD activity in human locus coeruleus. *Human Brain Mapping*, *35*(8), 4140–4154. https://doi.org/10.1002/hbm.22466

Murphy, P. R., Vandekerckhove, J., & Nieuwenhuis, S. (2014). Pupil-linked arousal determines variability in perceptual decision making. *PLOS Computational Biology*, *10*(9), Article e1003854. https://doi.org/10.1371/journal.pcbi.1003854

Nassar, M. R., Rumsey, K. M., Wilson, R. C., Parikh, K., Heasly, B., & Gold, J. I. (2012). Rational regulation of learning dynamics by pupil-linked arousal systems. *Nature Neuroscience*, *15*(7), 1040–1046. https://doi.org/10.1038/nn.3130

Pessoa, L. (2009). How do emotion and motivation direct executive control? *Trends in Cognitive Sciences*, *13*(4), 160–166. https://doi.org/10.1016/j.tics.2009.01.006

Plummer, M. (2008). Penalized loss functions for Bayesian model comparison. *Biostatistics*, *9*(3), 523–539. https://doi.org/10.1093/biostatistics/kxm049

Ratcliff, R., & McKoon, G. (2007). The diffusion decision model: Theory and data for two-choice decision tasks. *Neural Computation*, *20*(4), 873–922. https://doi.org/10.1162/neco.2008.12-06-420

R Core Team. (2018). *R: A language and environment for statistical computing* (Version 3.5.1) [Computer software]. Retrieved from http://www.R-project.org

Sara, S. J., & Bouret, S. (2012). Orienting and reorienting: The locus coeruleus mediates cognition through arousal. *Neuron*, *76*(1), 130–141. https://doi.org/10.1016/j.neuron.2012.09.011

Sharot, T., Korn, C. W., & Dolan, R. J. (2011). How unrealistic optimism is maintained in the face of reality. *Nature Neuroscience*, *14*(11), 1475–1479. https://doi.org/10.1038/nn.2949

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B: Statistical Methodology*, *64*(4), 583–639. https://doi.org/10.1111/1467-9868.00353

Urai, A. E., Braun, A., & Donner, T. H. (2017). Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. *Nature Communications*, *8*(1), Article 14637. https://doi.org/10.1038/ncomms14637

Voss, A., Rothermund, K., & Brandtstädter, J. (2008). Interpreting ambiguous stimuli: Separating perceptual and judgmental biases. *Journal of Experimental Social Psychology*, *44*(4), 1048–1056. https://doi.org/10.1016/j.jesp.2007.10.009

White, C. N., & Poldrack, R. A. (2014). Decomposing bias in different types of simple decisions. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *40*(2), 385–398. https://doi.org/10.1037/a0034851

Wiecki, T. V., Sofer, I., & Frank, M. J. (2013). HDDM: Hierarchical Bayesian estimation of the drift-diffusion model in Python. *Frontiers in Neuroinformatics*, *7*, Article 14. https://doi.org/10.3389/fninf.2013.00014