Pupil-linked arousal biases evidence accumulation towards desirable percepts during perceptual decision-making

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Abstract

People are biased towards seeing outcomes 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 sensory perception. However, it remains unclear whether arousal would enhance or reduce motivational biases. Here we measured pupil dilation as a measure of arousal while participants performed a visual categorization task. We used monetary bonuses to motivate participants to see one category over another. Even though the reward-maximizing strategy was to perform the task accurately, participants were more likely to report seeing the motivationally desirable category. Furthermore, higher arousal levels were associated with making motivationally biased responses. Analyses using computational models indicated that arousal enhanced motivational effects by biasing evidence accumulation in favor of motivationally desirable percepts. These results suggest heightened arousal biases people towards what they want to see and away from an objective representation of the environment.

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? This work examines 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, as 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 towards desirable percepts, and that modulating arousal levels could be a promising approach in reducing motivational biases in decision-making.

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 perceptual outcomes. Some outcomes are better than others, and people are *motivated* to see those percepts over alternatives. Evidence from a number of studies suggest that wanting to see a desirable outcome biases people towards seeing that outcome, a phenomenon known as motivated perception (Balcetis et al., 2012; Balcetis & Dunning, 2006; 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 towards 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 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; de Gee et al., 2017; Keung et al., 2019; Markovic et al., 2014; Mather et al., 2016; Urai et al., 2017). How might arousal be related to the processes underlying motivated perception?

The existing literature on arousal suggests that arousal processes dynamically modulate motivational biases during perceptual decision-making, but has been inconsistent about the directionality of the bias. For example the "glutamate amplifies noradrenergic effects" (GANE) model (Mather et al., 2016) proposes that arousal-related norepinephrine release interacts with local glutamate levels to selectively enhance the perception and memory of motivationally salient stimuli (see also Markovic et al. 2014 for a similar model). Consistent with this account, emotional stimuli are preferentially detected and remembered than neutral stimuli (Anderson, 2005; Kensinger et al., 2007). While the GANE model has not been applied to perceptual decision-making paradigms, the model predicts that perceptual features associated with desirable outcomes would be motivationally salient, and thus preferentially processed. This account predicts that arousal *enhances* motivational biases during perceptual decision-making.

In contrast, recent studies examining the effects of arousal on perceptual decision-making have found arousal to be associated with a reduction in decision biases (de Gee et al., 2017; de Gee et al., 2014; Krishnamurthy et al., 2017, but see Keung et al. 2019). For example, de Gee and colleagues (2017) had participants judge whether a faint sensory pattern was embedded within a noisy background. On average, participants exhibited an intrinsic bias to report the absence of the pattern, and often failed to detect the pattern even when it was present. Heightened arousal was associated with a reduction in participants' intrinsic bias in a trial-by-trial manner, suggesting that the arousal system performs a critical role in suppressing decision biases. These results would predict that arousal *reduces* motivational biases during perceptual decision-making. These past studies, however, do not examine the role of arousal in a context where participants are

motivationally biased to see one percept over another. It is thus unclear if and how arousal modulates motivational biases in perceptual decision-making.

In the current work, we combined psychophysics, computational modeling and pupillometry to examine the relationship between arousal and motivational biases in 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 instructing them they would win extra money if the block contained more images from one category. Using a drift diffusion model (Ratcliff & McKoon, 2007), we modeled participants' responses as the stochastic accumulation of sensory evidence towards a decision threshold. We then assessed if pupil diameter was associated with either or both motivational biases 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.

Methods

Participants

Forty-one participants were recruited from the Berkeley community (sample of convenience), for a targeted sample size of 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 US$20 and $30 depending on their performance on the task. Data from three participants were excluded due to unsuccessful eye-tracker calibration, yielding an effective sample size of thirty-eight participants (15 male, 23 female, 18-40 years of age, mean age = 21 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 consists of 25 grey-scale images comprising a mixture of a face image and a scene image in varying proportions. Pilot data (n = 30) indicated that participants were equally likely to categorize an image as face-dominant or scene-dominant when the face-scene proportion was 48% scene and 52% face (i.e. point of subjective equivalence; Fig. S1). Thus, images with greater than 48% scene were considered face-dominant while images with less than 48% scene were considered scene-dominant. Half of the stimulus sets contained more scene-dominant images (1 x 33% scene, 3 x 43% scene, 16 x 48% scene, 3 x 53% scene, 2 x 63% scene), while the other half contained more face-dominant images (2 x 33% scene, 3 x 43% scene, 16 x 48% scene, 3 x 53% scene, 1 x 63% scene). All stimuli were created to be isoluminant. Face images were frontal photographs posing a neutral expression, and were taken from the Chicago Face Database (Ma et al., 2015). Stimuli were presented using MATLAB software and the Psychophysics Toolbox (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 3s and participants had to respond during this time. Participants earned 5 cents for each correct categorization. During the inter-trial interval (ITI; 3-6s), a scrambled image with the same average luminance was presented to minimize luminance change on screen. Participants performed 12 blocks of 25 trials. In four of the blocks, we motivated participants to see face-dominant images by instructing 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 instructing 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*).

Crucially, the bonus in the *Face* and *Scene Bonus* blocks depended on whether there were objectively more face-dominant or scene-dominant images respectively. As such, participants would earn the most money if they ignored the motivation manipulation and categorized the images accurately. Each participant earned the $3.00 bonus on two Face-Bonus blocks and two Scene-Bonus blocks. Participants performed the blocks in a pseudo-randomized order such that they would not perform the same type of block consecutively.

Psychometric functions

We modeled participants' response data using generalized linear mixed-effects models (GLME), which allows for the modelling of all participants' data in a single model rather than fitting a separate model for each participant (Knoblauch & Maloney, 2012). We modeled participants' response (i.e. face-dominant or scene-dominant) as a function of the % scene in an image and block type (contrast coding with *Neutral* blocks as the reference condition). The model included random slopes and intercepts for % scene and block type to account for random effects

across participants (M1; see Table S1 for full model specification). Model estimation was performed using the glmer function in the lme4 package in R (Bates et al., 2015), with *p*-values computed from t-tests with Satterthwaite approximation for the degrees of freedom, as implemented in the lmerTest package (Kuznetsova et al., 2019).

Response time analyses

We ran two linear mixed effects models (LME) to examine the effect of motivation on participants' response times (RT). RTs were log-transformed and modeled as a function of participants response type, that is whether participant's response was *motivation consistent* (i.e. categorizing an image as the category they were motivated to see), *motivation inconsistent* (i.e. categorizing an image as 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 on which response type was coded as the reference group.

The first model 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 (M2; 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 (M3; Table S1). Both models controlled for whether participants categorized the image as face-dominant or scene-dominant. The models also included the absolute difference between % scene and % face 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

Pupil diameter was recorded using an EyeLink 1000 system (SR Research) at a sampling rate of 500 Hz. The eye-tracker was calibrated using a standard 5-point calibration sequence. If calibration failed when recording data from both eyes, calibration was reattempted while recording from one eye (n = 12). If calibration remained unsuccessful, pupil data were not collected, and the participant was excluded from all analyses (n = 3). The eye-tracker was recalibrated half-way through the experiment. Eye-blinks and saccades were detected using Eyelink detection algorithms with default settings. Data were linearly interpolated from 150ms before the start of each blink or saccade to 150ms after the end of the blink or saccade. The resulting data were smoothed using a zero-phase low-pass filter (third-order Butterworth, cutoff = 4Hz) (Kret & Sjak-Shie, 2019). Data recorded from both eyes were then averaged to obtain a single time course.

For each trial, we extracted the pupil time course from 500ms before stimulus onset to stimulus offset. Trials on which more than 30% of the data were missing were discarded (M = 1.8% of total trials, SE = 0.6%). We averaged the pupil diameter from -500ms to stimulus onset as the pre-trial baseline, and computed the pupil dilation at each time point as the percentage change from baseline. Pupil dilation time courses were averaged separately for trials on which participants made motivation consistent responses and trials on which participants made motivation inconsistent responses. To examine the relationship between pupil dilation and stimulus onset, we assessed if the two time courses differed from stimulus onset to 2 seconds after stimulus onset. To examine the relationship between pupil dilation and participants' decisions, we assessed if the two time courses differed in the 2 seconds prior to participants making their response.

We ran non-parametric cluster-based permutation tests to assess statistical significance and correct for multiple comparisons (Maris & Oostenveld, 2007). Briefly, a paired t-test was

performed at each timepoint to assess if the pupil dilation was different between motivation consistent and motivation inconsistent responses. Clusters were defined as contiguous timepoints where the t-test resulted in a p-value < 0.05. 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 where the maximal cluster size was greater than the observed cluster size.

Drift Diffusion Model

The drift diffusion model (DDM) is a class of sequential sampling models 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, while time unrelated to the decision process (non-decision-time; e.g., time needed for motor response) was determined by the free parameter t.

Model parameters were estimated from participants' response time distributions using the HDDM toolbox with default priors (Wiecki et al., 2013). HDDM implements hierarchical Bayesian estimation, which assumes that parameters for individual participants were randomly drawn from a group-level distribution. 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 (MCMC) sampling methods were 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 press), we estimated a mixture model where 5% of trials were assumed to be distributed according to a uniform distribution.

The HDDM package allows for 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 0.5 denoting an unbiased starting point. As such, 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. *Motivation* was coded as 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 towards the Scene threshold on Scene-Bonus blocks, and towards the Face threshold on Face-Bonus blocks. We took β_{z1} as a measure of the motivational bias in the starting point (z_{bias}).

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

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

where *Motivation* was again coded as +1 (Scene-Bonus block), -1 (Face-Bonus Block) and 0 (Neutral Block). Positive values for β_{v1} reflect a drift bias towards the Scene threshold on Scene-

Bonus blocks and towards the Face threshold on Face-Bonus blocks. We took β_{v1} as a measure of the motivational bias in drift rate (v_{bias}). β_{v2} reflects the effect of sensory evidence (i.e. percentage scene of an image) on the drift rate. We demeaned % scene prior to entering it into the model such that the intercept term, β_{v0}, would also reflect intrinsic biases in the drift rate.

For each of the bias parameters (z_{bias} and v_{bias}), 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 if either of the biases were sufficient for explaining the data, we fit two additional comparison models in which only *z* or only *v* was biased by motivation. As a baseline for comparison, we also fit a *null* model in which neither the starting point nor drift rate were biased by motivation. While HDDM models are commonly compared using 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 measure (DIC_c) that penalizes twice the number of effective parameters (Ando, 2011):

$$DIC = deviance + pD$$

$$DIC_c = DIC + pD$$

where *pD* denotes the number of effective parameters, with lower DIC_c values indicating better model fit. Model recovery simulations indicated that DIC_c accurately identifies the true model from simulated data (*Supplemental Results,* Fig. S2).

Next, we assessed how trial-by-trial fluctuations in pupil dilation relate to the two biasing mechanisms. We computed the pupil dilation on each trial as the average pupil dilation in the 1s leading up to participants making their response. This corresponded to the significant cluster prior to choice where pupil dilation was higher on motivation consistent trials than on motivation

inconsistent trials. To examine the effect of pupil dilation on motivational bias, we generated a regressor that was the interaction between pupil dilation and the motivation consistent category:

$$pupil * mot = \begin{cases} pupil\ dilation \text{ if Scene Bonus Block} \\ 0 \text{ if No Bonus Block} \\ pupil\ dilation\ * -1 \text{ if Face Bonus Block} \end{cases}$$

We allowed the starting point to vary as a function of pupil*mot:

$$z = \frac{1}{1 + \exp(-\ (\beta_{z1}\text{pupil} * \text{mot} +\ \beta_{z0}))}$$

Positive values for β_{z1} would indicate that pupil dilation has a positive relationship with the starting point (i.e. closer to the Scene threshold) on Scene Bonus blocks, and a negative relationship (i.e. closer to the Face threshold) on Face Bonus blocks.

In the same model, we modeled the drift rate as a function of pupil*mot:

$$v = \beta_{v1} pupil * mot + \beta_{v2}\ \%scene + \beta_{v0}$$

Positive values for β_{v1} would indicate that pupil dilation has a positive relationship with the drift rate (i.e. increase bias towards the scene threshold) on Scene Bonus blocks, and a negative relationship (i.e. increase bias towards the face threshold) on Face Bonus blocks. We fit three additional comparison models in which only *z*, only *v* or neither parameters were modulated by pupil*mot. We compared the four models using DIC_c.

Model convergence of all models 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 non-convergence. In addition, we examined each trace to check that there were no drifts or large

jumps, which would also suggest non-convergence. We report model convergence metrics, posterior means and 95% credible intervals of all parameters in Tables S2 and S3.

Posterior predictive checks

For each model, we simulated 100 datasets with parameter values sampled from the posterior distribution estimated by the model. Each simulated dataset comprised the same number of participants performing the same number of trials as the real dataset, and reflect the pattern of choice and response time data if the behavior of participants' in our task were perfectly described by the model. We overlay the response time distribution generated by a model where motivation biased both the starting point and drift rate with the true response time distributions, separately for face and scene responses and for each block, as a posterior predictive check to assess model fit (Fig. S2). The effect of a biased starting point and that of a biased drift rate can be visually distinguished by comparing response proportions across the different blocks at different response time quartiles (conditional response time functions, White & Poldrack, 2014). We computed the conditional response time functions of data simulated using models where either or both the starting point and drift rate were biased by motivation, and compared them to the conditional response time function of the observed data to assess which model best captured qualitative patterns in participants' behavior (*Supplemental Results*, Fig. S3).

To assess how well the models reproduced the relationship between pupil dilation and motivationally biased responses, we simulated response and response time data given the observed pupil dilation values using models where pupil dilation modulated both the starting point and the drift rate, either of the parameters, or neither parameter. For each model, we averaged the pupil dilation separately for trials on which the model predicted a motivation consistent response and

for trials on which the model predicted a motivation inconsistent response, and performed paired t-tests to assess if mean pupil dilation was different between the two types of trials. The same analysis was then repeated with the empirical data for comparison.

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. In Face Bonus blocks, participants received a $3 category bonus if there were more face-dominant images in the block. In Scene Bonus blocks, participants received a $3 category bonus if there were more scene-dominant images in the block. In Neutral blocks, participants did not receive a category bonus. As such, 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 on 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.

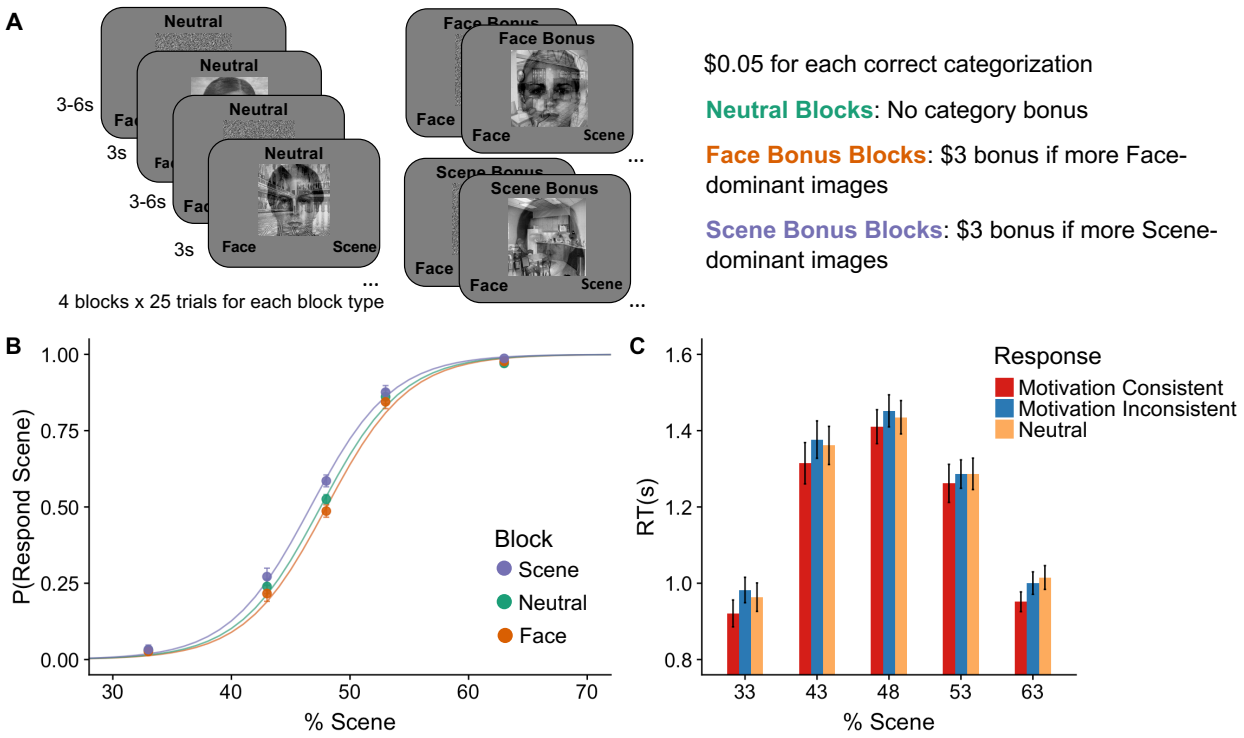

Figure 1. Motivation biased perceptual judgments. A. Experimental Design. Participants were rewarded for correctly categorizing ambiguous face/scene morphs as face-dominant or scene-dominant. On Face and Scene Bonus blocks, participants received a bonus if there were more face- or scene-dominant images in the block respectively. **B. Psychometric curves**. For the same level of objective evidence (% Scene) participants were more likely to categorize an image as scene-dominant on Scene Bonus Blocks and face-dominant on Face Bonus Blocks than on Neutral Blocks. **C. Response Times.** Responses that were motivation consistent (e.g., categorizing an image as face-dominant in a Face Bonus block) were faster than responses that were motivation inconsistent. Error bars indicate between-participant standard error of the mean.

Motivation biased perceptual judgments

To assess the effects of the category bonuses on perceptual judgments, we estimated participants' psychometric function separately for each block type (Fig. 1B). Statistical comparisons between the curves were performed using generalized linear mixed effects models (GLME). Relative to Neutral blocks, participants were more likely to categorize an image as face-dominant in Face Bonus blocks ($z = 2.10$, $p = 0.037$, b = 0.15, 95% CI = 0.01 to 0.28), and scene-

dominant in Scene Bonus blocks (z = 3.21, p = 0.001, b = 0.25, 95% CI = 0.09 to 0.40). Thus, for the same face vs. scene proportion, participants were more likely to categorize the image as the category they were motivated to see.

Next, we assessed if motivation affected participants' response times (Fig. 1C). Participants' were faster to categorize an image as 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(35.7) = 3.56, p = 0.001, b = 0.045, 95% CI = 0.020 to 0.070). Response times were faster for motivation consistent responses than on trials in the Neutral blocks ((t(37.0) = 3.09, p = 0.004, b = 0.029, 95% CI = 0.010 to 0.047), but were not significantly different between motivation inconsistent responses and trials in the in the Neutral blocks (t(41.2) = 1.51, p = 0.140, b = 0.016, 95% CI = -0.004 to 0.037).

Motivation biases both starting point and rate of sensory evidence accumulation

We fit a drift diffusion model (DDM) to participants' response time distributions. The DDM assumes that each perceptual judgment arises from the noisy accumulation of sensory evidence towards 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 participants were motivated to see. A bias in the starting point reflects an *a priori* bias towards a particular category irrespective of the evidence, while a bias in the drift rate reflects a bias in how evidence accumulates over time. Both biases increase the proportion of motivation consistent responses, but have distinguishable effects on the distribution of response

times (Leong et al., 2019; White & Poldrack, 2014; Fig. 2A). We estimated the extent to which each bias contributed to participants' behavior by fitting the model to participants' responses and response times (see *Methods*).

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 ($p(z_{bias} > 0) > 0.999$, mean = 0.100, 95% credible interval = 0.053 to 0.145; Fig. 2B), indicating that the starting point was biased towards the scene threshold when participants were motivated to see scene-dominant images, and biased towards the face threshold when participants were motivated to see face-dominant images.

The drift rate was similarly modeled using linear regression. As the drift rate also depends on the amount of sensory evidence available in the image, we included the percentage scene in an image as an additional predictor. Motivation had a positive effect on the drift rate ($p(v_{bias} > 0) = 0.976$, mean = 0.048, 95% credible interval = 0.0004 to 0.094, Fig. 2C), indicating that sensory evidence accumulated more quickly for the motivation consistent category. As expected, percentage scene had a positive effect on the drift rate ($p(v_{scene} > 0) > 0.999$, mean = 1.446, 95% credible interval = 1.325 to 1.569), indicating that sensory evidence accumulation was biased towards the scene threshold at high scene proportion and biased towards the face threshold at low scene proportion.

To examine if either biasing mechanism was sufficient to account for participants' data, we fit additional models where motivation biased only the starting point (*z* model) or only the drift rate (*v* model). Model fits were then compared using DIC_c, with lower values indicating better fit (see Methods). Model recovery simulations confirm that DIC_c accurately recovers the true model

from simulated data (*Supplemental Results*, Fig. S2). The model in which motivation biased both the starting point and drift rate yielded the lowest DIC_c value (DIC_c - *z & v*: 26862, *z*: 26869, *v*: 26892, null: 26995; Fig. 2D). Furthermore, simulated data generated by parameterizing the *z & v* model with best-fit parameter values aligned well with participants' data, and matched qualitative patterns in the data better than the alternative models (*Supplemental Results,* 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.

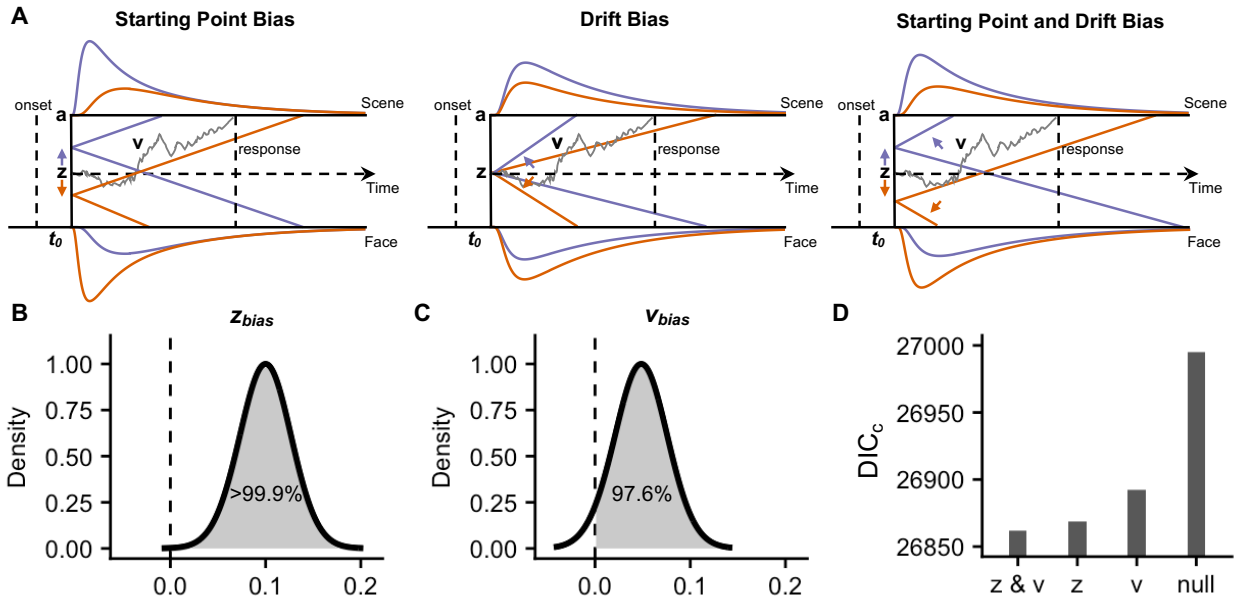

Figure 2. Motivation biased starting point and rate of evidence accumulation. A. Schematic depiction of biasing mechanisms. Biases in starting point and drift rate have distinguishable effects on the shape of response time (RT) distributions. Grey line: example trajectory of evidence accumulation on a single trial. Purple line: mean drift and resulting RT distribution when motivated to see scene-dominant images; Orange line: mean drift and resulting RT distribution when motivated to see face-dominant images. *z* = starting point, *v* = drift rate, *a* = threshold, t_0 = non-decision time. **B. Posterior distribution of model-estimated starting point bias (z_{bias})**. Dashed line indicates 0 (no bias). **C. Posterior distribution of model-estimated drift bias (v_{bias}).** Dashed line indicates 0 (no bias). **D. Model comparison based on DIC_c**. Model where motivation biased both the starting point and drift rate (*z & v*) yielded a lower DIC_c score than models where motivation biased only the starting point (*z*), only the drift rate (*v*) or neither parameters (*null*).

Pupil-linked arousal was higher when making 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 i. stimulus onset (Fig. 3A) and ii. choice (Fig. 3B). Task-evoked pupil dilation was then computed as the percentage change from a pre-trial baseline (-500ms to image onset), and averaged across participants 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, likely reflecting an increase in arousal driven by the start of the trial. This is followed by a brief recovery before a second increase that peaks around 1s post-choice. Pupil diameter was higher on trials where participants made motivation consistent responses than on trials where they made motivation inconsistent responses (from 400 ms after stimulus onset until 1s after stimulus onset, cluster p = 0.037, Fig. 3A; from 1s prior to choice until choice, cluster p = 0.015, Fig. 3B), suggesting that pupil-linked arousal was associated with motivational biases in perceptual judgments.

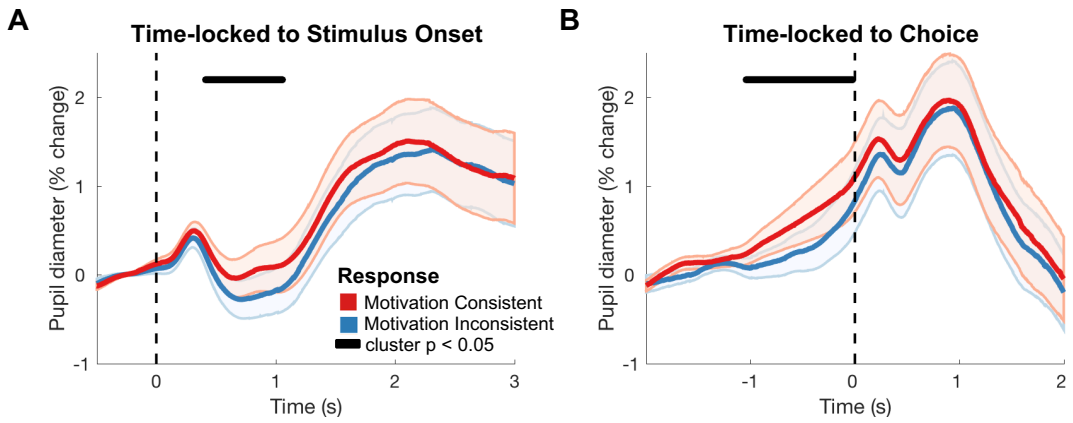

Figure 3. Motivation consistent responses are associated with greater pupil dilation. Percentage change in pupil diameter over the course of a trial, time-locked to **A.** stimulus onset and **B.** choice. Baseline pupil diameter was computed as the average pupil diameter from -500ms to stimulus onset. Solid lines denote average pupil time course for trials on which participants made motivation consistent responses (red) and motivation inconsistent responses (blue). Shaded error bars denote between-participant S.E.M. Black horizontal bars indicate time points where pupil dilation was different between the two types of trials (cluster $p < 0.05$), based on cluster-based permutation tests (Maris & Oostenveld, 2007).

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

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 modulations of the starting point and drift rate. Instead of estimating a fixed starting point or drift rate across trials, we allowed the two parameters to vary on each trial according to the pupil dilation and motivation consistent category on that trial.

The pupil dilation on each trial was computed as the average pupil dilation in the 1s leading up to choice. To model the effects of pupil dilation on motivational biases, we generated a regressor that was the interaction between pupil dilation and the motivation consistent category (*pupil*mot*; see Methods). A positive regression coefficient for *pupil*mot* indicates that pupil dilation was

associated with an increase in bias towards the motivation consistent category. We fit participants' data to a model where both the starting point and drift rate were allowed to vary as a function of *pupil*mot*. There was no effect of *pupil*mot* on the starting point ($p(z_{pupil*mot} > 0) = 0.285$, mean = -0.002, 95% credible interval = -0.010 to 0.006; Fig. 4A), indicating that pupil dilation was not associated with motivational biases in the starting point. In contrast, there was a positive effect of *pupil*mot* on the drift rate ($p(v_{pupil*mot} > 0) = 0.986$, mean = 0.008, 95% credible interval = 0.001 to 0.013; Fig. 4B), indicating that pupil dilation was associated with a bias in evidence accumulation towards the scene decision threshold when participants were motivated to see scene-dominant images and towards the face decision threshold when they were motivated to see face-dominant images.

These results indicate that trial-by-trial fluctuations in pupil dilation were associated with motivational biases in drift rate, but have no effect on biases in the starting point. If this were true, a simpler model where pupil dilation biased only the drift rate would provide a better fit to the data. Indeed, a model where only the drift rate was allowed to vary as a function of *pupil*mot* had a lower DIC_c value ($DIC_c = 26463$) than a model where both starting point and drift rate were modulated by pupil dilation ($DIC_c = 26471$), as well as models where only the starting point ($DIC_c = 26469$) or neither parameters were modulated by pupil dilation ($DIC_c = 26471$; Fig. 4C). Furthermore, data simulated from models in which pupil dilation modulated the drift rate reproduced the pattern of results where pupil dilation was higher for motivation consistent responses than for motivation inconsistent responses (empirical data: mean difference = 0.20, 95% CI = 0.01 to 0.40, $t(37) = 2.15$, $p = 0.038$; z_{pupil} & v_{pupil}: mean difference = 0.21, 95% CI = 0.11 to 0.30, $t(37) = 4.35$, $p < 0.001$; v_{pupil}: mean difference = 0.18, 95% CI = 0.08 to 0.27, $t(37) = 3.67$, $p < 0.001$). In contrast, data simulated from models in which pupil dilation modulated only the

starting point or neither parameter underestimated the difference in pupil dilation between the two types of responses (z_{pupil}: mean difference = 0.08, 95% CI = -0.01 to 0.17, $t(37) = 1.83$, $p = 0.075$; null: mean difference = 0.02, 95% CI = -0.06 to 0.10, $t(37) = 0.51$, $p = 0.615$; Fig. 4D). Together, our findings suggest that pupil-linked arousal enhances motivational biases in perceptual judgments by biasing evidence accumulation in favor of desirable percepts.

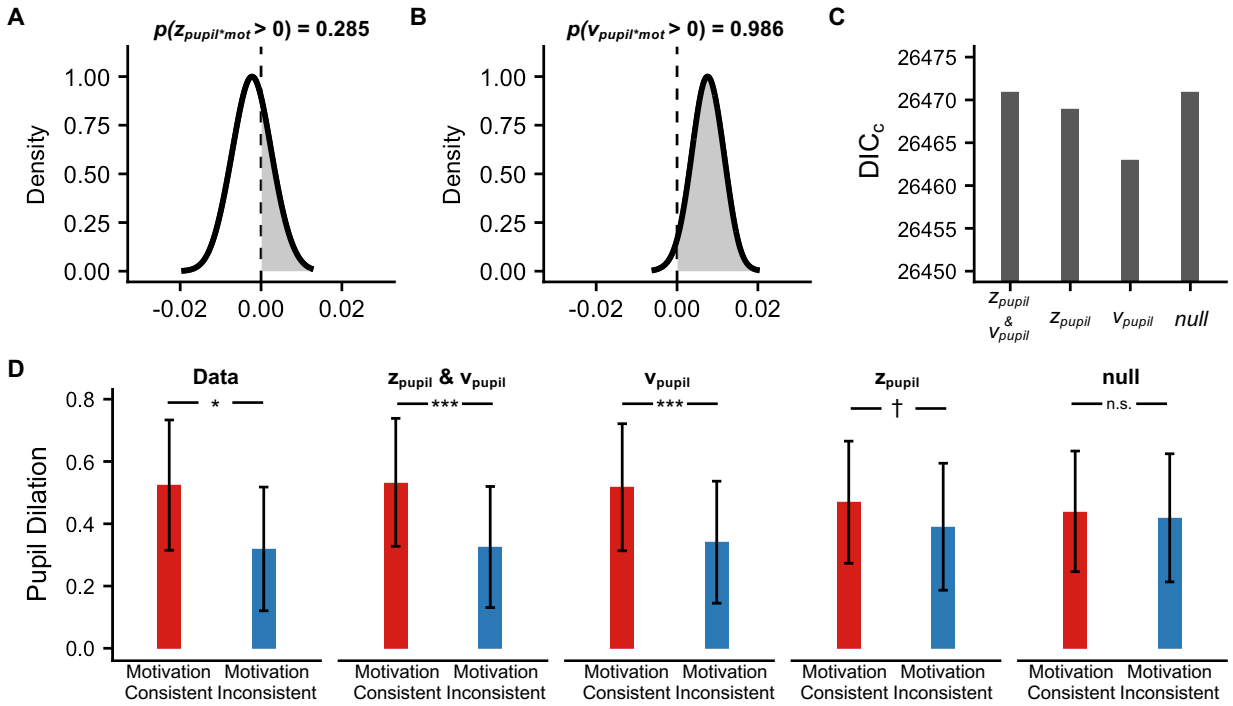

Figure 4. Trial-by-trial pupil-linked arousal modulates motivational biases in drift rate but not starting point. A. Posterior distribution for the effect of pupil dilation on motivational biases in starting point ($z_{pupil*mot}$). Dashed line indicates 0 (no effect). **B. Posterior distribution for the effect of pupil dilation on motivational biases in drift rate ($v_{pupil*mot}$).** Dashed line indicates 0 (no effect). **C. Model comparison based on DIC_c.** Model where pupil dilation modulates the drift rate (v_{pupil}) yielded a lower DIC_c score than models where pupil dilation modulated both the starting point and drift rate (z_{pupil} & v_{pupil}), only the starting point (z_{pupil}) or neither parameters (*null*). **D. Comparison between model predictions and data.** Models where pupil dilation modulated the drift rate reproduced the empirical observation that pupil dilation was higher when participants made motivation consistent responses. Error bars indicate between-subject standard error. *** $p < 0.001$, * $p < 0.05$, † $p < 0.10$.

Discussion

In the current work, we investigated the role of physiological arousal in modulating motivational biases in perceptual decision-making. We manipulated the percept participants were motivated to see as they performed a perceptual decision-making task. Participants were more likely to categorize an image as the category they were motivated to see. This motivational bias reflected both an *a priori* bias towards the motivation consistent category, as well as a bias in how participants accumulated sensory evidence over time. Arousal, as measured by pupil dilation, was higher when participants made motivation consistent responses. Trial-by-trial fluctuations in arousal were specifically associated with faster accumulation of sensory evidence 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). Previous work suggests that motivation can bias this comparison in favor of percepts 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 presented with ambiguous face-scene image 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 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 motivationally salient stimuli (Mather et al., 2016). The GANE model builds on earlier work showing that norepinephrine increases the *gain* of neurons, such that excited neurons become even more active and inhibited neurons become even less active (Aston-Jones & Cohen, 2005; Sara & Bouret, 2012). As attention is directed towards stimulus features that are motivationally salient (Bourgeois et al., 2016; Pessoa, 2009), neurons encoding motivationally salient features would be more active than neurons encoding other information. Increasing neural gain accentuates this difference, selectively enhancing the neural representation of motivationally salient features and amplifying motivational effects on perceptual processing. Hence, the locus coeruleus norepinephrine system is a promising candidate system that might mediate the effects observed in our study. 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.

To our knowledge, the implications of the GANE model have not yet been considered in the context of perceptual decision-making, where individuals have to decide between different perceptual alternatives. Our findings highlight the consequences of arousal-related sensory biases for decision-making. Arousal does not merely facilitate the faster detection or better memory of motivationally salient stimuli – it can potentially bias individuals to report seeing ambiguous stimuli as what they want to see. This suggests that moments of heightened arousal are also moments where individuals are less objective in their perceptual judgments.

Notably, the GANE model provides a framework to reconcile our findings with other studies that have examined the effect of pupil-linked arousal processes on perceptual decision-making. Several recent studies have found that stronger pupil responses were associated with smaller decision biases (de Gee et al., 2017; de Gee et al., 2014; Krishnamurthy et al., 2017). For example, in the studies by de Gee and colleagues (2017; 2014) pupil dilation was associated with a reduction in participants' intrinsic biases to report the absence of a pattern when they had to judge whether a target pattern was embedded within a noisy sensory background. One possible explanation for the discrepancy with our study is that stimuli in these studies did not contain coherent sensory information of an alternative percept. That is, a stimulus either contained a target pattern and noise, or only noise. Increasing neural gain in this context would increase neuronal sensitivity to the target pattern, such that participants would be more likely to detect the target. Similarly, Krishnamurthy and colleagues (2017) found that pupil dilation was associated with smaller biases induced by prior expectations in a sound localization task. Increasing neural gain would again increase neuronal sensitivity to the stimulus, giving rise to decisions that depend more on the stimulus and less on participants' prior expectations.

Other studies have found that pupil dilation correlates with trial-by-trial decision variability in perceptual decisions (Keung et al., 2019; Murphy, Vandekerckhove, et al., 2014). For example, Murphy and colleagues (2014) had participants judge whether the dominant motion direction of a cloud of moving dots was leftward or rightward, and found that larger pupils were associated with greater variability in evidence accumulation. In other words, pupil dilation was associated with a leftward bias on some trials and a rightward bias on other trials. The authors interpreted these results as suggesting that pupil-linked arousal processes amplify neuronal noise, resulting in increased variability in behavior. As some dots were moving leftward while others were moving rightward, neurons coding for both directions would be active. Neuronal noise will result in the neurons coding for one direction to be more active than those coding for the other direction by chance alone. Hence, increasing neural gain would enhance activity related to one direction on some trials, and to the other direction on other trials. In contrast, participants in our task were presented with ambiguous stimuli containing two competing percepts, but one of the percepts was motivationally salient and associated with a stronger neural response. Increasing neural gain in our task would amplify the motivational enhancement, resulting in a systematic bias towards the motivationally salient percept.

Motivation has 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 wide-spread projections of norepinephrine neurons across the brain, this is certainly possible. Future studies can extend our work and examine the

relationship between arousal and motivational biases on other types of human reasoning and evaluation processes.

Author Contributions

Y.C.L., R.D., and M.D. designed the study; Y.C.L. collected and analyzed the data; Y.C.L. and M.D. wrote the manuscript, with revisions from R.D. All authors approved the final version of the manuscript for submission.

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