The origin of fixed, history-independent choice biases of rodents in perceptual decision making tasks

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Abstract

Perceptual decision making is typically described with classical models (Signal Detection, Bayesian Decision, and Drift Diffusion Models) that distinguish modules for sensory processing, decision making and additional post-decisional processes with separate bias terms for each module. At the behavioral level, animal and human decision making 2-AFC studies provide ample evidence for choice-biases during such tasks. A subset of these biases are history-dependent and can be directly linked to the rewards, responses and stimuli, but the origin of the other subset of fixed history-independent biases in these tasks is still largely unknown. Here, we investigated whether these fixed biases could originate from the decision module as defined by the classical models or they must be related to post-decisional processes. We designed an interaural amplitude discrimination task with rodents, with the amplitude difference and the maximum intensity level modulated simultaneously, and found that the performance of all rats decreased asymmetrically at the two response sides as a function of decreasing intensity level. Through computational analyses, we show that these fixed biases cannot be explained within the decision module and are only compatible with post-decisional biases.

Keywords: post-decision choice bias, perceptual decision making, lapse rate, sensory uncertainty

Introduction

Perceptual decision making is widely investigated by 2-AFC tasks. A general finding is that during such experiments, observers show a number of deviations from optimal decisions. Some of these deviations have been traced back to the effect of stimuli, decisions and reward history and can produce either positive or negative biases (Fritsche, Mostert, & de Lange, 2017). Some other biases have been linked clearly to motor origin (Wichmann & Hill, 2001). However, there exists a well-known and prominent subset of biases, encountered mostly in rodent behavioral experiments, the origin of which has not been identified yet. These are called fixed biases since they cannot be directly associated with the stimuli or reward of the individual trials, they typically do not change across sessions, and they seem to be specific to the individual. Despite their abundance, these fixed biases were not investigated systematically in the literature, rather they were treated as a nuisance that needed to be eliminated by adaptive balancing of the stimuli (Piet, Hady, & Brody, 2018). While such a treatment is reasonable, identifying the origin of these biases is necessary for a deeper understanding of decision making processes. As a first step, we investigated whether the fixed bias originates from decision processes or it is related to post decisional-processes.

In order to investigate the origin of fixed biases, we selected the three most widely used computational frameworks for treating perceptual decision making: Signal Detection Theory (SDT), Bayesian Decision Theory (BDT), and Bounded Evidence Accumulation (BEA) or Drift Diffusion Model (DDM). All of these frameworks (in their basic forms) make three key assumptions about decision making. (1) The observer abstracts the task relevant information of the stimuli (e.g. contrast difference in a contrast discrimination task) and transforms it into sensory evidence (which is the abstracted and transformed task relevant information of the stimulus) through a transduction function. (2) The representation of the sensory evidence is inherently noisy. (3) There is a decision process that forms decisions based on the sensory evidence. In most cases, this process assumes that the transduction function is either linear or follows a power function, and that the noise on the sensory evidence is Gaussian (Palmer, Huk, & Shadlen, 2005). In all three frameworks, the decision process follows a deterministic rule, in which the observer sets a criterion for the minimal amount of sensory evidence (which is equivalent to MAP decision in the Bayesian framework) that is needed to choose a certain response alternative (below which the alternative is not selected). BEA models the temporal dynamics of the process, while SDT and BDT do not, but from the perspective of accuracy data in 2-AFC tasks (which we consider here), the three frameworks have very similar predictions. Assuming Gaussian noise on the sensory evidence, and a transduction function $F(S)$ the probability of choosing category one given the stimulus (the psychometric curve) is:

$$\mathcal{P}(\mathrm{R} = 1 \mid S) = \Phi(F(S) - \lambda) \tag{1}$$

where Φ is the cumulative normal distribution function, S is the stimulus, $F(S)$ is the transduction function, and λ is the decision criterion parameter, which contains the prior knowledge and loss function in the Bayesian frameworks. In the BEA framework we need to assume an unbounded accumulation of evidence for *Eq.*1 as observed in fixed-duration stimulus categorization in rodents, (Brunton, Botvinick, & Brody, 2013).

Classical choice biases can have sensory or decisional origin. Sensory biases can emerge for example when the $F(S)$ transduction function is asymmetric at the low and high end of the sensory dimension. Under the assumptions of the classical models, these biases modulate the mean value of the sensory evidence, therefore their effect on the performance can be captured by a lateral shift in the psychometric curve. Biases related to decision are represented by a single decision criterion parameter (λ) which, similarly to sensory biases, can only shift the psychometric curve horizontally. Therefore, the classical formalism implies that all choice biases (not related to post-decisional processes), including prior knowledge, decision criterion, and loss functions reflecting the history of the rewards, costs, responses, stimuli, and the frequency of the categories in the task at hand can produce only shifts in the psychometric curve. It is unclear how fixed biases enter this picture. If they tend to scale rather than shift the psychometric curve, they would not be possible to integrate in the classical framework. Instead, these fixed biases then might be related to post-decisional processes such as biases during translation of the decision into motor response (Erlich, Brunton, Duan, Hanks, & Brody, 2015). This conjecture is supported by the fact that the fixed choice bias, by definition, is not related to the history of the task parameters, and thus it is different from the effects typically summarized in λ of the decision process. In this study, we hypothesize that rats fixed choice biases are, indeed, related to post-decisional and not to decisional processes. In order to test this, first, we extended the classical models (*Eq.*1) with a post-decision bias term, and compared the classical and the extended version of the models in terms of their ability to shift vs. scale the psychometric curve. Second, we collected data with rodents using a 2-AFC task measuring rather than compensating for fixed biases, and investigated whether the classical or the extended model could predict the experimental results better.

We extended the classical models by adding a post-decision bias term that influences only the response without influencing the category of the stimulus, the decision rule, or the sensory evidence (Fig.1). Since ω representing the fixed

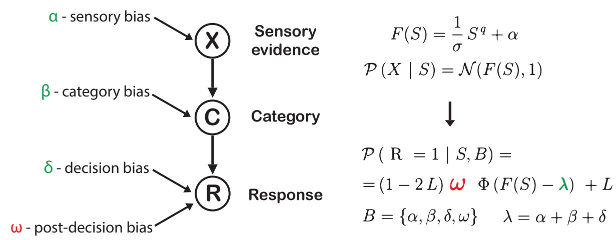

Figure 1: Extended model. $F(S)$ is the transduction function, σ is the sensory noise, $\mathcal{N}$ represents the Normal distribution, and L is the lapse rate. ω the pos-decision bias scales while the rest of the biases (λ) shifts the psychometric function.

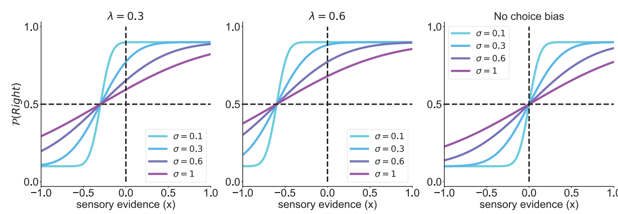

Figure 2: Modulation of accuracy as a function of increasing choice bias (λ) in the classical models at four different levels of sensory uncertainty (σ). Lapse rate = 0.1.

bias in this model is separated from the decision module, the extended module, in principle, is better suited for capturing the scale effect of the psychometric curve. In practice however, it is very hard to distinguish between the classical and extended models using accuracy data due to the fact that the scaling of the psychometric curve can be attributed not only to post-decision bias (ω) but to lapse rates (errors independent of sensory evidence). In order to compare the two models, we turned to the fact that, the psychometric curve can scale asymmetrically, and while this can be achieved by both lapse rates and fixed biases, the underlying constraints of such a scaling are different in the two models. Specifically, if the sensory noise (σ in Fig.1) is modulated during the experiment, it will modulate the psychometric curve symmetrically at both response alternatives assuming no post-decision bias (Fig.2), while the same curve will be modulated asymmetrically at the two response alternatives if a post-decision bias exists (Fig.3).

Methods of the behavioral task

Rats performed 2-AFC interaural amplitude discrimination task (Fig.4), in which they had to decide whether the left or the right speaker produced a louder noise. In the experiment, we simultaneously modulated the ratio of the left-right amplitudes ($20\log_{10} A_R/A_L$) and the maximum intensity level

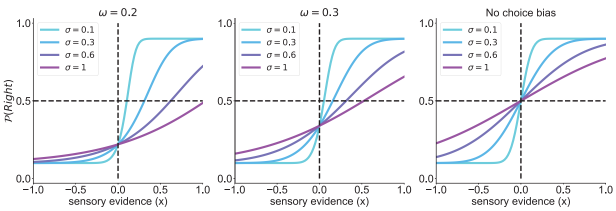

Figure 3: Modulation of accuracy as a function of increasing post-decision bias (ω) in the extended at four different levels of sensory uncertainty (σ). Lapse rate = 0.1.

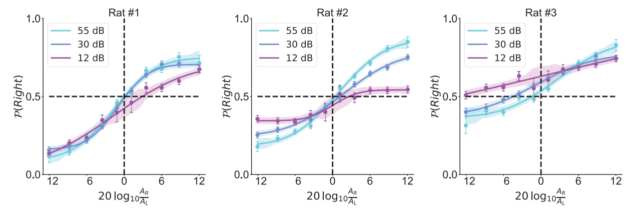

Figure 5: Modulation of the psychometric curves as function of the intensity levels. The lines show separate cumulative Gaussian fits with two lapse rates in each intensity conditions, colors representing the different intensity levels. X axis: the ratio of the amplitudes on the two sides. A_L stands for amplitude from the left while A_R represents the amplitude from the right speakers. Y axis: probability of right response. These descriptive fits only represent the results of the experimental manipulation without assuming an underlying computation model. The shaded areas show the 95% confidence intervals around the maximum likelihood fits.

$((A_R + A_L)/2)$ of the noise stimuli. Based on recent findings (Pardo-Vazquez, Castineiras, Valente, Costa, & Renart, 2018), we reasoned that the intensity of the stimulus, similar to the level of contrast in vision, influences the uncertainty in perception independently of the task relevant stimulus feature. Pardo-Vazquez et al. (2019) found that the intensity level does not modulate the accuracy if the stimulus is available until the response is made indicating a Weber's law in amplitude discrimination task. To observe the decrease in accuracy due to the decrease in intensity we fixed the duration of the stimulus at the range where the Weber's law breaks down.

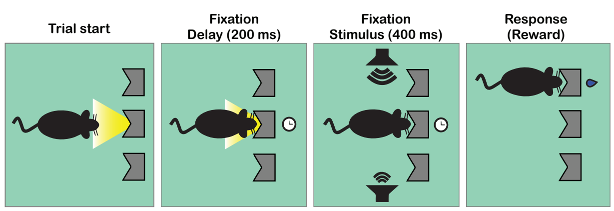

Figure 4: 2-AFC, fixed-duration, interaural amplitude discrimination task.

Results

The accuracy of the rats was modulated by the maximum intensity level of the sounds in the amplitude discrimination task (see the lines with different colors in Fig.5). Furthermore, the performance of the rats decreased significantly less on the preferred reward side than on the other, 'anti-preferred 'reward side due to the decrease in intensity (comparing the effect of the intensity on the regression weights at the two response sides: Rat1, $Z = 31.6$, $P < 0.01$; Rat2, $Z = 41.9$, $P < 0.01$; Rat3, $Z = 31.9$, $P < 0.01$; Fig.5). This asymmetric performance modulation on the two sides due to the changing intensity level suggests a post-decision bias. However, an alternative interpretation of these results assuming that the maximum intensity level and the left-right amplitude ratio modulates the performance through a multiplicative interaction could also produce asymmetric performance modulation as the intensity level changes. To compare the model assuming multiplicative interaction with the model assuming post-decision bias, we fitted the accuracy data with both models. We found that the model assuming post-decision bias provides much better fits to the data than the model assuming multiplicative interaction in all rats (Rat1: ΔAIC=67.6, ΔBIC=73.8, $log_{10}BF = 25.0$; Rat2: ΔAIC=18.4, ΔBIC=24.4, $log_{10}BF = 0.9$, Rat3: δAIC=57.6, ΔBIC=63.6, $log_{10}BF = 15.8$, where the Bayes factors of the models were estimated by the likelihood evaluated at the maximal likelihood parameter set divided by the square root of the log-determinant of its local Hessian; Fig. 4).

Discussion

We found that the decrease in the overall intensity level of the noise stimuli asymmetrically modulated the performance of rodents at the two reward sides during our interaural amplitude discrimination task. More specifically, as stimulus intensity dropped, the performance only minimally decreased at the preferred reward side while it decreased substantially on the reward side that the rats did not prefer. These results were best captured by the model that assumed a post-decisional origin for the fixed bias (Fig.1). This suggests that rats' fixed, history-independent choice biases might be related to post-decisional processes rather than to classical decisional processes that evaluate sensory evidence. Distinguishing between different types of choice biases based on accuracy data of 2-AFC tasks is a rather challenging problem (Linares, Aguilar-Lleyda, & Lopez-Moliner, 2019). Nevertheless, our method demonstrates that post-decisional biases can be distinguished from lapses and other biases even in simple 2-AFC tasks by modulating additional stimulus attributes that influence the uncertainty (or noise) during perception. It is worth noticing that according to our results, Weber's law broke down only at 400 ms stimulus duration with the range of intensity level varying between 12-55 dB. In a similar interaural amplitude discrimination task by Pardo-Vazquez et al. (2019) using the intensity range of 20-60 dB, Weber's

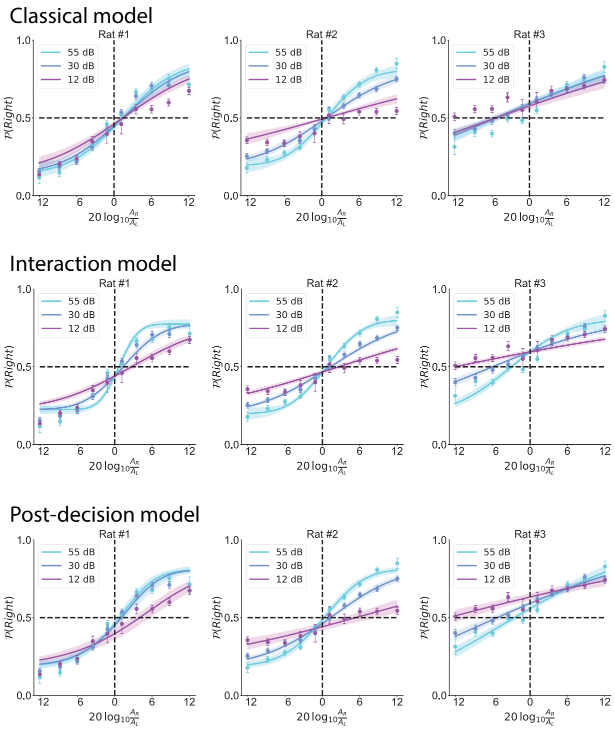

Figure 6: Model fits. Top: The classical model formalized in *Eq.*2. Middle: The multiplicative interaction model formalized as *Eq.*2 where an interaction between the amplitude ratio of the left-right sounds and the maximum intensity level is assumed in the $F(S)$ function. Bottom: the post-decision bias model formalized in Fig.1. The colored shaded areas show the 95$\%$ confidence intervals around the maximum likelihood fits. We used the 'profile likelihood' method to compute the confidence regions. Note that although the prediction for intensity conditions are shown separately (the colored lines) all intensity conditions were fitted together in the models.

law already started to break down around 250 ms stimulus duration. This co-variation between duration, intensity and Webers law provides additional support for a causal and proportional link between the two characteristics of the stimulus and perception. A recent study linked lapse rates to explorations suggesting that as uncertainty increases across decisions, rats' behavior becomes more explorative and hence lapse rates increase (Pisupati, Chartarifsky-Lynn, Khanal, & Churchland, 2019). Expanding this proposal that lapse rates indicate exploration with the idea that rats' exploration graded by the level of uncertainty at a given side, one could interpret our results in a model that assume asymmetrical modulation of lapse rates as a function of the intensity level instead of assuming a post-decision bias. While in principle, this alternative can capture our results, it has a couple of shortcomings in terms of parsimony. First, this interpretation should predict a symmetric change on the two reward sides since uncertainty on the two sides was modulated equally with the intensity level of the sounds. Any extra assumption about asymmetric uncertainty would require further justification. Second, while our proposed model is exceedingly simple since it assumes only one additional bias parameter outside the decisional process (formalized using the classical frameworks), the alternative model would require a number of extra parameters in the model as the function of sides and levels of uncertainty. Until now, researchers treated fixed biases as a nuisance parameter that they eliminated by modulating the statistics of the reward and stimuli during the task. While this practice is effective in terms of balancing the measurable parameters, it hides away factors of the decision process and leave the effects of the forced counterbalancing uncontrolled. An alternative approach is to understand the complex structure of the task that the overtrained animals learn and gain a fuller description of their acquired internal model that determine their behavior. Here we provide an important first step along this path by showing that the fixed biases in behavior of rodents is related to post-decisional processes.

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References

Brunton, B. W., Botvinick, M. M., & Brody, C. D. (2013). Rats and humans can optimally accumulate evidence for decision-making. *Science*, *340*, 9598.

Erlich, J. C., Brunton, B. W., Duan, C. A., Hanks, T. D., & Brody, C. D. (2015). Distinct effects of prefrontal and parietal cortex inactivations on an accumulation of evidence task in the rat. *eLife*.

Fritsche, M., Mostert, P., & de Lange, F. P. (2017). Opposite effects of recent history on perception and decision. *Current Biology*, *27*, 590595.

Linares, D., Aguilar-Lleyda, D., & Lopez-Moliner, J. (2019). Decoupling sensory from decisional choice biases in perceptual decision making. *eLife*, *8*, 43994.

Palmer, J., Huk, A. C., & Shadlen, M. N. (2005). The effect of stimulus strength on the speed and accuracy of a perceptual decision. *Journal of Vision*, *5*, 376404.

Pardo-Vazquez, J. L., Castineiras, J., Valente, M., Costa, T., & Renart, A. (2018). Webers law is the result of exact temporal accumulation of evidence. *bioRxiv*.

Piet, A. T., Hady, A. E., & Brody, C. D. (2018). Rats adopt the optimal timescale for evidence integration in a dynamic environment. *Nature Communications*, *9*, 4265.

Pisupati, S., Chartarifsky-Lynn, L., Khanal, A., & Churchland, A. (2019). Lapses in perceptual judgments reflect exploration. *bioRxiv*.

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. fitting, sampling, and goodness of fit. *Perception and Psychophysics*, *63*, 12931313.