Sensory choices as logistic classification

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Logistic classification is a simple way to make choices based on a set of factors: give each factor a weight, sum them, and use the result to set the log odds of a random draw. This operation is known to describe human and animal choices based on value (economic decisions). There is increasing evidence that it also describes choices based on sensory inputs (perceptual decisions). In fact, data from multiple studies in multiple species shows that logistic classification can describe a variety of choices. These include sensory choices influenced by stimuli of other modalities (multisensory integration) or by non-sensory factors such as expected value and recent choices. Logistic classification is the optimal strategy if factors are independent of each other, and a useful heuristic in other conditions. Using it to describe sensory choices can characterize not only normal brain function but also the effects of brain inactivations.

Many situations require choosing between two or more options based on a set of factors. For instance, in a choice between walking and driving, the factors may include distance, traffic, weather, cost, and parking[1]. In a choice between picking a berry vs. moving on, the factors may include ripeness, hunger, and ease of reach. How does the brain combine these diverse factors to make a choice?

A large body of research indicates that the brain makes these choices by logistic classification: perform a weighted sum of the factors, use the result to set the (log) odds of a coin, and toss that coin (Figure 1**a**). This approach also works if there are more than two options (the coin is replaced by a die). Logistic classification was invented by multiple statisticians in the secrecy surrounding WWII[2]. In the subsequent three decades, it was linked to the theory of choice from mathematical psychology and to economics[1,3,4]. Since then, it has become a workhorse of statistics and machine learning[5]. It characterizes value-based decisions by humans and animals[6-9] and the corresponding brain activity[7], suggesting that it was discovered first by evolution.

There is increasing evidence that logistic classification describes not only choices based on considerations of value (economic decisions) but also choices based on sensory input[2,10,11] (perceptual decisions) and on additional factors, alone or in combination. These factors include trial history and prior probability[12-22], disparities in value[7-9], brain manipulations such as local inactivations[23-25], and signals from additional sensory modalities[26] (multisensory integration).

Here I will briefly review this evidence, and I will argue that logistic classification is an effective description of results that had been analyzed with a different framework (Signal Detection Theory, Appendix 1). I will show that it is an optimal strategy in many conditions, and a useful heuristic in others, perhaps explaining why it is widely implemented by the brains of multiple species.

Sensory choices between two alternatives

When a choice involves only two alternatives, logistic classification has a particularly simple description (Figure 1**a**). First, give each of the factors $x_1, x_2, \dots, x_n$ a weight $w_1, w_2, \dots, w_n$. Second, sum them to obtain a *decision variable*

$$z = w_1 x_1 + w_2 x_2 + \cdots + b \qquad \text{Eq. 1}$$

Third, use that decision variable to bias a coin, i.e., to set the probability p that it will return Heads. Specifically, use it as the *log odds* of drawing Heads:

$$\log\left(\frac{p}{1-p}\right) = z \qquad \text{Eq. 2}$$

Fourth, flip the coin.

If a coin is not available, one can add a random variable to z and threshold the result (Appendix 1), or use z as the drift in a random walk between bounds (Appendix 2).

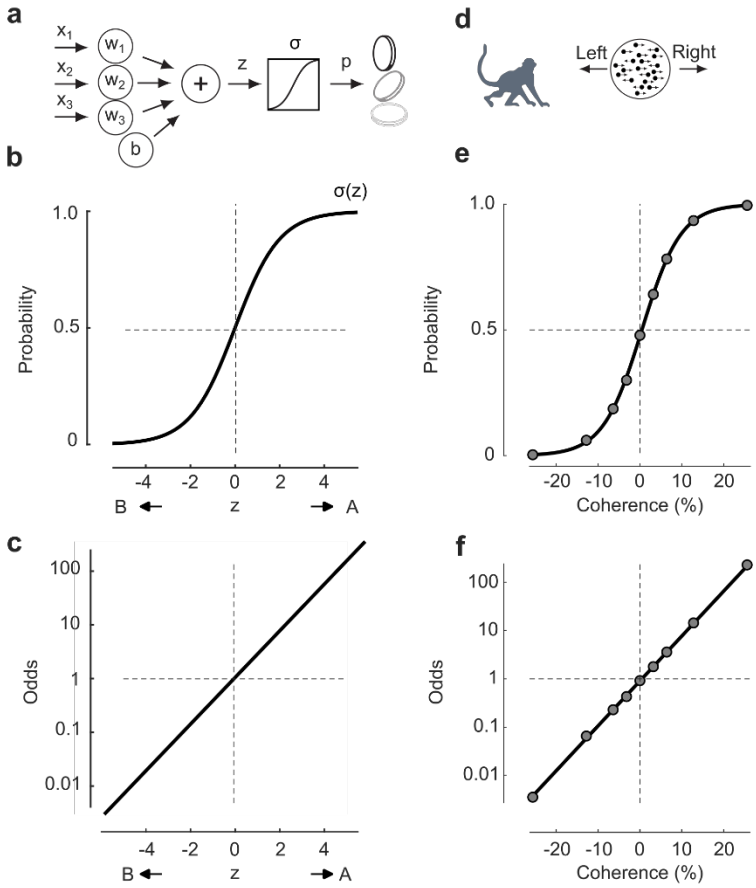

Figure 1. ***Logistic classification describes sensory choices between two alternatives in monkeys****.* ***a*** *Diagram of logistic classification, in the case of 3 factors x_1, x_2, and x_3.* ***b****. The logistic sigmoid, plotting probability of a choice vs. decision variable.* ***c.*** *The logistic sigmoid becomes a line when plotting the odds (in logarithmic scale) vs. the decision variable.* ***d*** *A monkey performing the random dots task, indicating whether most dots move Left or Right.* ***e****. Performance of a monkey performing the task, showing probability of Right choices as a function of coherence (negative for leftward motion, positive for rightward motion). Data were taken from Ref.[11] using a data grabber (grabit.m). Curve shows fit of the logistic classification model.* ***f*** *Same data and fit, in log odds.*

This process can be written as a single equation (Figure 1**a**):

$$p = \sigma(w_1 x_1 + w_2 x_2 + \cdots + b) \qquad \text{Eq. 3}$$

where σ is the *logistic sigmoid* (Figure 1**b**)

$$\sigma(z) = \frac{1}{1 + \exp(-z)} \qquad \text{Eq. 4}$$

In statistics, these equations are often used for "logistic regression", i.e. to find the weights $w_1, w_2, \ldots$ and bias b that best relate the factors $x_1, x_2, \ldots$ to some observed outcomes[3,5]. We are here interested in the reverse: using the weights as given, to classify a new observation of the factors and thus make a choice. This is best called "logistic classification"[5].

Though it is simple, logistic classification can do an excellent job at summarizing perceptual decisions, for example those in a classic motion discrimination task. In this task, a monkey views moving dots and estimates whether most of them move Left or Right (Figure 1**d**). The task difficulty depends on the coherence x of the dots, defined as positive if most dots move to the Right and negative otherwise. The *psychometric curve*, i.e., the probability of Right choices as a function of stimulus strength can then be fit with a logistic classification model[10,11]:

$$\mathrm{z} = Wx + B \qquad \text{Eq. 5}$$

With two free parameters (W and B) the model describes how nine values of coherence x determine the probability of choosing Right (Figure 1**e**). Indeed,

the logarithms of the odds fall neatly on a line (Figure 1**f**).

In this example, the measure of stimulus strength x that we placed in Eq. 5 is the same measure that is used in the laboratory: the coherence of the moving dots[10,11]. In other cases, however, it may be necessary to allow a nonlinear deformation[12,23,24]. For instance, one could raise the stimulus strength to an exponent q, which is fit to the data[24]. For simplicity, in the following we will write this as x^q, but the proper expression is $sign(x)|x|^q$, which maintains the sign of x.

Sensory choices influenced by priors

One reason why logistic classification is advantageous is that it accords with Bayes' rule for combining sensory information with prior probabilities. To see this, consider a task where a stimulus is on the Left or the Right (L or R) with probabilities $P(L)$ and $P(R)$. The observer receives sensory input s about the position of the stimulus, and aims to say that the stimulus is on the Right with probability $p = P(R|s)$, the probability that the stimulus s is indeed on the Right (this is called "probability matching" and will be discussed later). By Bayes' rule, the odds that the observer chooses Right are the product of two terms: one that depends on the sensory stimulus (posterior odds) and one that does not (prior odds):

$$\frac{p}{1-p} = \frac{P(R|s)}{P(L|s)} = \frac{P(s|R)}{P(s|L)}\,\frac{P(R)}{P(L)}$$

Taking the logarithm yields a sum of two terms:

$$z = \log\left(\frac{p}{1-p}\right) = \log\frac{P(s|R)}{P(s|L)} + \log\frac{P(R)}{P(L)} \qquad \text{Eq. 6}$$

In other words, the decision variable is simply the sum of a function of the stimulus and a constant bias,

$$z = f(s) + B \qquad \text{Eq. 7}$$

where $f(s)$ is a (possibly nonlinear) function of the stimulus, and the bias equals the log prior odds: $B = \log(P(R)/P(L))$. If the rewards for the two sides are equal, this strategy maximizes the overall reward (see Appendix 3 for proof).

These considerations lead to a prediction: an observer should adjust its bias B (and only the bias) in accordance with the prior probability of the stimuli. We don't expect the observer to set the bias to the ideal level (they may not be able to estimate true prior probabilities), but they should at least move it in the right direction.

This prediction is verified in humans performing a biased motion discrimination task: if the odds of a stimulus going rightward $p(R)/p(L)$ are 80:20 instead of 50:50 (Figure 2**a**), the observers make more Right choices[27] especially at zero coherence, when the stimulus is uninformative (Figure 2**b**). This shift is captured by the logistic classification model (Eq. 5) with the same weight W but a larger bias B (Figure 2**b**). The log odds of the choices fall on a line that is parallel but displaced from the 50:50 case (Figure 2**c**).

Analogous results are seen in mice that perform a biased position discrimination task[22] (Figure 2**d**). In this experiment, stimuli are divided in blocks having higher probability on the Left (80:20) or on the Right (20:80). As expected, the psychometric curves measured in the two blocks are displaced (Figure 1**e,f**), such that at zero contrast (no visual stimulus) Right choices are more likely in 20:80 blocks and Left choices more likely in 80:20 blocks. The model (Eq. 5) captures this difference with a bias B that is positive in the 20:80 block and negative in the 80:20 block, with no changes in sensory weight W.

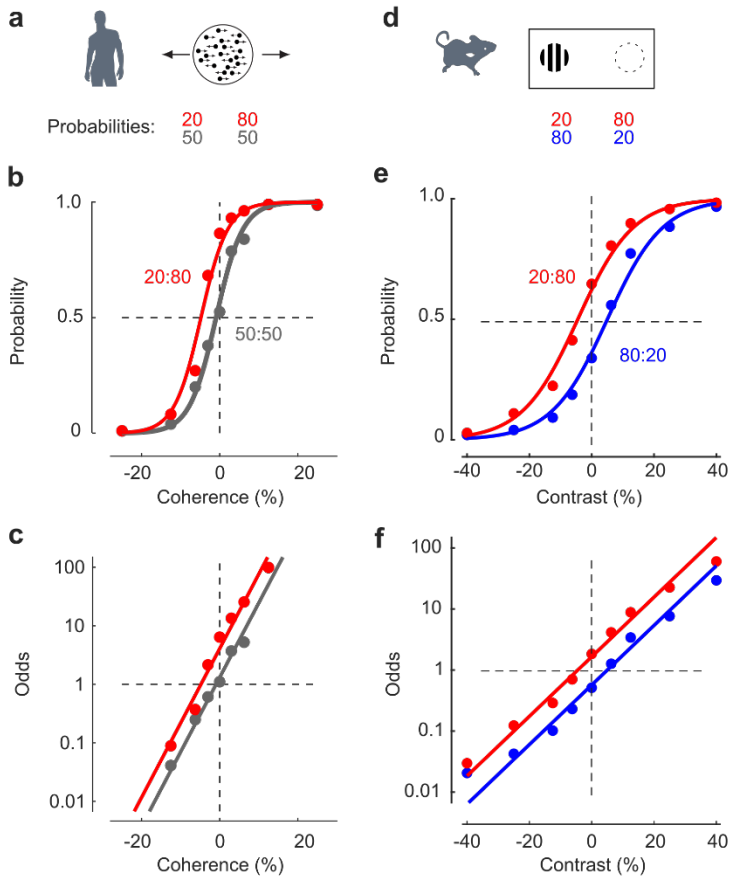

Figure 2. ***Logistic classification describes choices based on stimulus attributes and probability in monkeys and mice****.* ***a.*** *A random dots task where a human is told that rightward motion is more likely than leftward motion (blue) or that they are equally likely (gray).* ***b****. Data from an observer showing that probability of choosing Right depends not only on stimulus coherence (abscissa) but also on prior probability (blue vs. gray). Data grabbed from Ref.[27]. Curves show fit of the logistic classification model with same weight w but two different values for the bias b.* ***c.*** *The same data and curves plotted as odds of choosing Right vs. Left, in logarithmic scale.* ***d-f.*** *Same, for a mouse indicating whether a visual stimulus appears on the Left or the Right, presented in alternating blocks where Left was more likely (red) or less likely (blue) than Right. Data grabbed from Ref.[22].*

Sensory choices without evidence

In the absence of sensory evidence, these data exhibit a phenomenon that is widely observed in non-sensory tasks[8,9,28-35], called "probability matching": the probabilities of the observer's choices tend to match the probabilities of those choices being correct. For instance, at zero coherence the human in the 20:80 motion task chose Right with probability ~0.8 (Figure 2**b**). At zero contrast the mouse in the position task showed a similar tendency though (as is common[9,36]) not as pronounced (Figure 2**e**).

This phenomenon is puzzling because it is suboptimal[29,32]. Indeed, in the absence of evidence, one would obtain more rewards by always guessing Right if $P(R) > P(L)$ and always guessing Left otherwise.

The observer, however, does not know that some trials have no evidence. It may thus apply logistic classification (Eq. 6) to all trials. This strategy produces probability matching. Indeed, if the evidence s is uninformative, then $f(s) = \log(\,P(s|R)/P(s|L)\,) = 0$, yielding

$$p = \sigma\left(\log\frac{P(R)}{P(L)}\right) = \sigma\big(\sigma^{-1}\big(P(R)\big)\big) = P(R)$$

Perhaps participants use Eq. 6 as a heuristic, acting as if there were a correct answer that can be inferred from evidence (present stimuli, past stimuli, actions, outcomes, etc.) even when this evidence is irrelevant. This leads to probability matching.

Indeed, humans stop performing probability matching if they understand that they are gambling, i.e. guessing an independent random variable. In that

case, they become optimal: they choose the option that is more likely to be rewarded[32], perhaps because they stop using logistic classification to make their choices.

Sensory choices influenced by value

Logistic classification is also the ideal method to combine sensory inputs with considerations of value. In the experiments examined up to here, the rewards for correct Left and Right choices were equal. In that case, if the probabilities of the Left and Right stimuli are also equal, the strategy that maximizes reward is to set the bias B in Eq. 5 to close to zero. In general, however, the rewards, V_L and V_R, could differ. In that case, one can prove (Appendix 3) that the ideal bias B is the logarithm of their ratio:

$$z = Wx + \log\frac{V_R}{V_L} \qquad \text{Eq. 8}$$

In the absence of sensory stimuli, therefore, an optimal logistic classifier should engage in "value matching": its fraction of Right choices should match the ratio of Right rewards to total rewards. Indeed, if $x = 0$ the probabilities of Right choices should be $p_0 = \sigma(\log(V_R/V_L)) = V_R/(V_R + V_L)$.

There is ample evidence that the brain follows this strategy when making purely economic decisions[7], even though it would obtain more reward by sticking to the option with higher value. Once again, logistic classification could explain this behavior: the brain may assume that there is relevant evidence x to guide the choice even when there isn't any, so it may obey Eq. 8 even when not optimal.

In fact, the optimal logistic classifier (Eq. 8) captures how observers combine sensory signals with considerations of value. For example, when humans perform a position discrimination task (Figure 3**a**), they make more Left or more Right choices depending on which of these choices yields the larger reward[37]. The data are well fit by logistic classification (Eq. 5) with a single sensory gain W and different biases B in the two reward conditions (Figure 3**b**). Once again, the effects are easiest to judge in terms of log odds (Figure 3**c**): changing the stimulus moves the log odds along a line, and changing the reward ratio moves the log odds to a parallel line. Similar results are seen in monkeys doing the random dot motion task (Figure 3**d-f**)[38], and in mice performing the position discrimination task (Figure 3**g-i**)[39]. In all these cases the changes in bias were at least as large as predicted by optimality (Eq. 8). In fact, they were generally larger than optimal[40], perhaps because of a nonlinear utility scale that disproportionally favors large rewards[7,41].

More generally, logistic classification indicates how one should combine sensory signals and relative reward with relative probability. In the experiments considered above (Figure 3), the values of Left and Right stimuli were unequal but their probabilities, p_L and p_R, remained equal. If these probabilities differ, then the optimal strategy (Appendix 3) is to choose a bias $B = \log(p_R/p_L) + \log(V_R/V_L)$. This expression shows how the logarithm of the odds provides a "natural currency for trading off sensory information, prior probability and expected value"[10].

Logistic classification can also capture the effects of changing other task variables. For instance, in an experiment measuring rate discrimination in rats, changes in the ratio of rewards were yoked to changes in the total available reward[25]. Logistic classification fits those data (Supp Figure 1) but reveals changes not only in bias B, but also in sensory weight W. The changes in bias are expected given the changes in ratio of rewards (Eq. 8). The changes in sensory weight, instead, might result from the changes in total available reward, which might affect task engagement[12] or sensory attention[42]. Fluctuations in these and other factors may explain why the parameters of logistic classification often fluctuate over time[43,44].

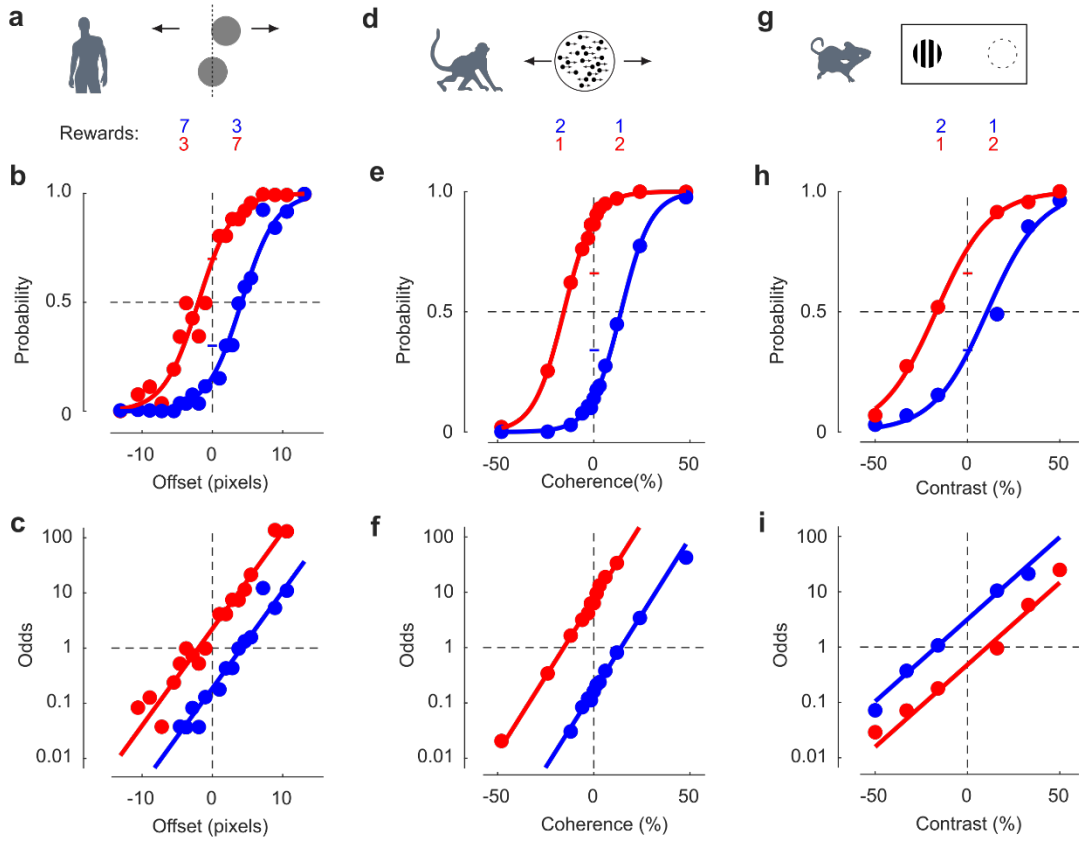

Figure 3. ***Logistic classification describes choices based on stimulus attributes and value in humans, monkeys, and mice. a****. A position discrimination task where the observer indicates whether the top stimulus is to the Right of the bottom one, in conditions where correct Left responses were rewarded less (red) or more (blue) than correct Right responses.* ***b****. Data from an observer showing that probability of choosing Right depends not only on stimulus offset (abscissa) but also on reward condition (blue vs. red). Data grabbed from Ref.[37]. Curves show fit of the logistic classification model with same weight W but two different values for the bias B. The red and blue ticks in the central axis indicate the intercepts predicted by the optimal strategy.* ***c****. The same data and curves plotted as odds of choosing Right vs. Left, in logarithmic scale.* ***d-f****. Same, for a monkey performing a random dots task where stimuli are presented in alternating blocks where correct Left choices were rewarded less (red) or more (blue) than correct Right choices. Data grabbed from Ref.[38].* ***g-i.*** *Same, for a mouse indicating whether a visual stimulus appears on the Left or the Right, presented in alternating blocks where correct Left choices were rewarded less (red) or more (blue) than correct Right choices. Data grabbed from Ref.[39].*

Sensory choices across modalities

Logistic classification can describe not only sensory choices based on a single modality but also those based on multiple modalities (multisensory integration). As shown in Eq. 1, logistic classification naturally accommodates multiple factors as input (Figure 1**a**). If those factors are statistically independent, Bayes' rule predicts that an observer should perform logistic classification based on their sum[26]. To see this, consider the case where there are two sensory stimuli s_1, s_2 of different modalities, e.g., vision and audition. In that case, using both Bayes rule and the definition of independence, $P(s_1, s_2|R) = P(s_1|R)P(s_2|R)$, one obtains

$$\frac{p}{1-p} = \frac{P(R|s_1, s_2)}{P(L|s_1, s_2)} = \frac{P(s_1|R)}{P(s_1|L)} \frac{P(s_2|R)}{P(s_2|L)} \frac{P(R)}{P(L)}$$

In other words,

$$z = \log\left(\frac{p}{1-p}\right) = f_1(s_1) + f_2(s_2) + B \qquad \text{Eq. 9}$$

This expression is exceedingly simple, and yet it describes multisensory choices in a variety of species, tasks, and combinations of modalities.

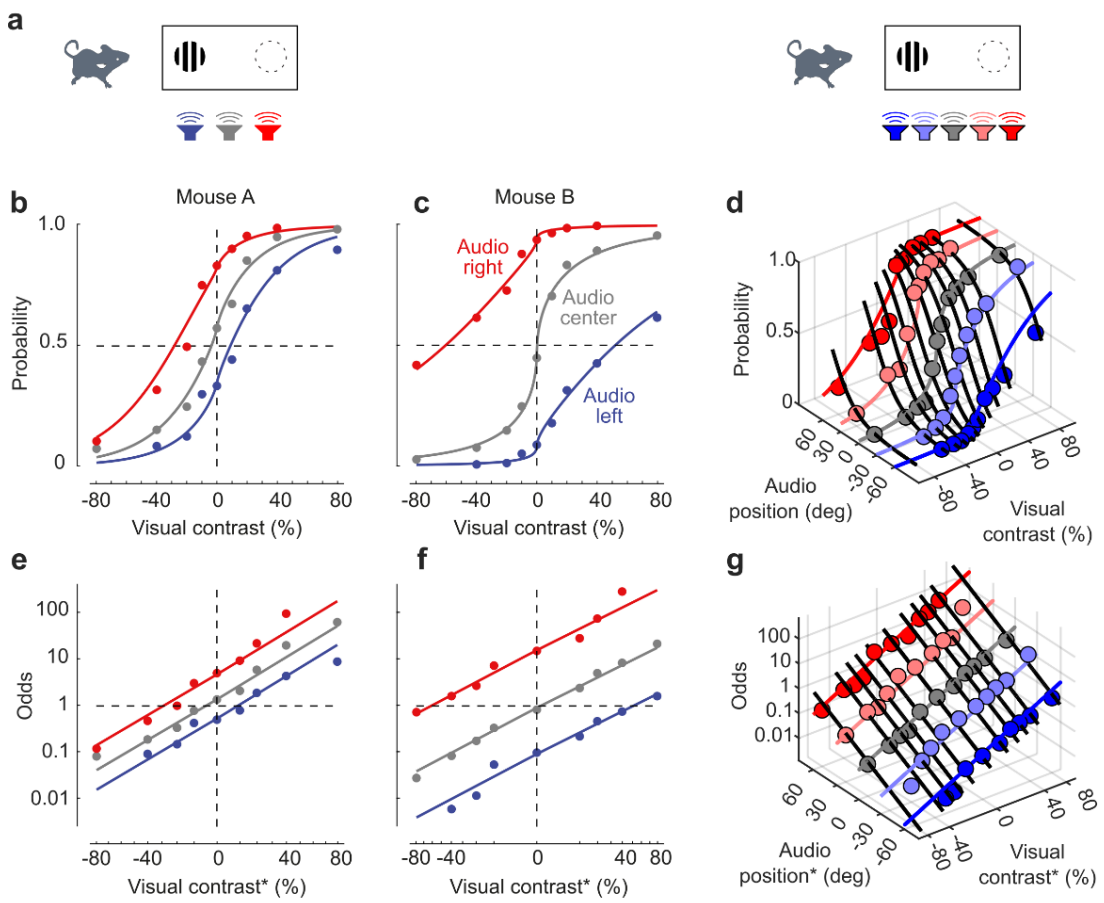

Figure 4. ***Logistic classification describes audiovisual position choices in mice****.* ***a****. The audiovisual task: images appear on the Left or right, and sounds are emitted at one of 3-5 positions.* ***b****. Probability that a mouse chooses Right based on the contrast of the visual stimulus (abscissa, negative for stimuli on the Left) and on the position of the auditory stimulus (colors as in a).* ***c****. Same, for a mouse with higher auditory sensitivity.* ***d****. Results in a task with 5 auditory positions.* ***e-g****. The data in b-d, replotted as odds of Right vs. Left choices, in logarithmic scale. The quantities on the abscissa (horizontal plane in g) are compressed (raised to an exponent q<1). Data from Ref.[26]. Therefore, the probability of choosing R is a logistic function $p = \sigma(z)$ with three terms: one that depends on vision, one that depends on audition, and a constant.*

For instance, Eq. 9 describes the choices of mice performing an audiovisual detection task[26]. In this task, a visual pattern appears on the Left or on the Right and a sound is played in one of 3 or 5 positions (Figure 4**a**). If the sound is in the middle, it is uninformative, and the task becomes purely visual (Figure 4**b,** *gray*). If it is on the Left or Right, the mouse is more likely to make those choices (Figure 4**b,** *blue* and *red*).

Logistic classification (Eq. 9) describes this behavior accurately, via a simple summation:

$$z = F_1 s_1^q + F_2 s_2^r + B \qquad \text{Eq. 10}$$

Here, the variables s_1 and s_2 are visual and auditory attributes, raised to exponents q, r (if necessary). The remaining parameters are the visual gain F_1, the auditory gain F_2, and the bias B. The first term describes the responses when the task is purely visual (Figure 4**b,** *gray*), and the second describes the responses when the task is purely auditory (Figure 4**b,** where abscissa is zero). The model provides excellent fits (Figure 4**b**, *curves*), correctly describing the choices not only when the two modalities agree, but also when they contradict each other[26]. Similar results are seen in a mouse with better hearing (higher performance at zero contrast, Figure 4**c**), and in a mouse tested with more auditory positions (Figure 4**d**).

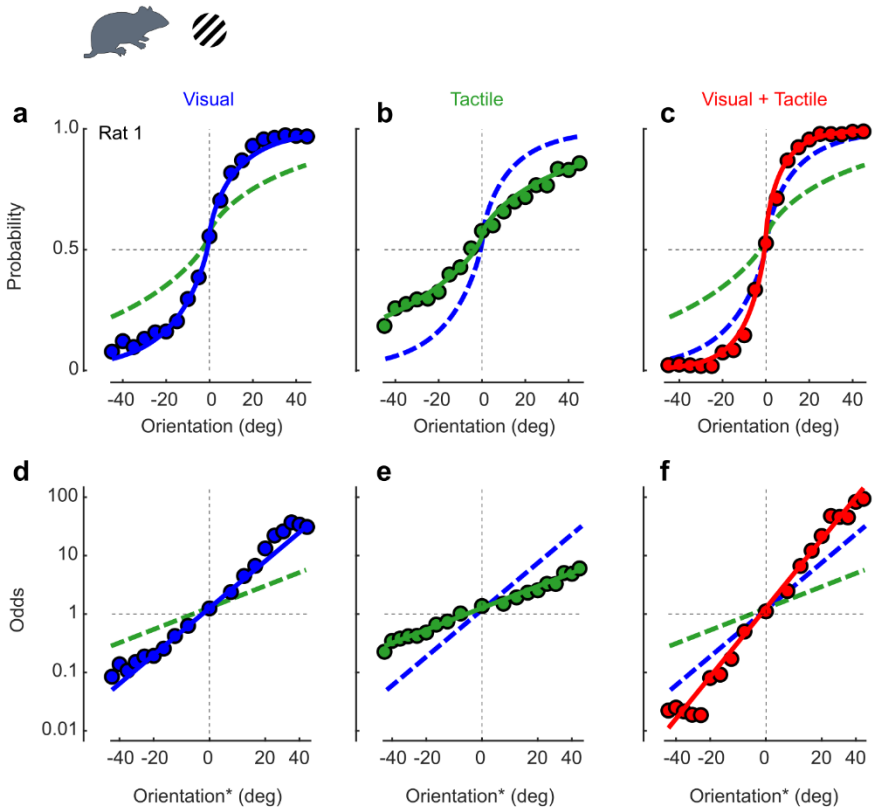

Figure 5. ***Logistic classification describes visuotactile orientation choices in rats.*** ***a****. Probability of Right choices for a rat performing the orientation discrimination task based on visual cues.* ***b****. Same, based on tactile cues.* ***c.*** *Same, based on stimuli that are both visual and tactile.* ***d-e****. Same data, plotted as odds of Right vs. Left in logarithmic scale. The quantity on the abscissa is compressed orientation (raised to an exponent q <1). Curves are from the logistic classification model. Data are from Rat 1 in Ref.[45].*

As usual, these results are easiest to understand in terms of log odds (Figure 4**e-g**). In this representation, and with a slightly different abscissa (s_1^q and s_2^r instead of s_1 and s_2) the results fall on parallel lines: changing visual contrast moves the points along the lines, and changing the auditory position shifts them to a different line.

For such high-dimensional data, one way to judge the performance of the model[46,47] is to plot the probability of all points as a function of the predicted decision variable z (Eq. 1) and see if they fall near the logistic curve $\sigma(z)$ (Eq. 4). Here they do (Supp. Figure 2).

Indeed, logistic classification describes multisensory choices in other species and across other modalities. Studies of multisensory integration indicate that observers are approximately Bayesian[25,26,45,48-54], at least when all stimuli are presented for the same duration[55]. These studies typically analyzed the responses with Signal Detection Theory (Appendix 1), which requires that observers combine two numbers for each modality: an estimate of mean and one of variance[48,49]. Below I examine three of these studies, which tested various combinations of sensory modalities in various species, and I show that logistic classification captures their entire psychometric curve. This success indicates that the observers can be Bayesian by summing a single number per modality: the log odds of the choice based on that modality.

In a study that measured visuo-tactile integration[45], rats indicated whether the orientation of a stimulus was closer to horizontal or vertical by choosing between Left or Right response ports. The stimulus could be purely visual or purely tactile (Figure 5**a,b**) or a combination of the two (Figure 5**c**). I applied the logistic classification model to those data with 4 free parameters: visual gain F_1, tactile gain F_2, their common exponent q (there was no need for different exponents), and bias B. The model provided good fits (Figure 5**a-c**), and would have done fairly well even with just two free parameters (setting $q = 1$ and $B =$

0, not shown). The model's performance is easy to evaluate if the data are plotted as log odds (Figure 5**d-f**). An additional check verifies that the predicted decision variables for all these measured data describe a single logistic curve (Supp. Figure 2).

Sensory choices for multimodal features

In the multisensory experiments described up to now, the features in the two modalities could only be equal (Figure 4 and Figure 5) or opposite (Figure 4). Other experiments tested multisensory integration in a richer way, by varying both the amplitudes and the features of two modalities, with multiple offsets between those features.

To discuss these experiments, it helps to define stimulus "feature" vs. "amplitude". The feature ϕ is the attribute on which the choice is based; it can be positive or negative, and is zero at the boundary between the two choices. The amplitude α, instead, is positive and is zero if the stimulus is absent. For instance, in the motion task (Figure 1**d-f** and Figure 2**a-c**), ϕ is direction (±1) and α is coherence (between 0 and 1). Similarly, in the position task (Figure 2**d-f**), ϕ is position and α is contrast. For both visual and tactile stimuli in the visuotactile task (Figure 5), instead, ϕ is orientation (between -45 and 45 deg) and α indicates presence (0 or 1).

If a stimulus s can have multiple combinations of amplitude and feature, we must define how those combinations affect the stimulus representation $f(s)$. A simple working hypothesis is that the stimulus representation is separable, i.e., the product of a function of amplitude and one of feature: $f(\phi, a) = g(\phi)h(\alpha)$. In the visual system, for example, this hypothesis would be appropriate for orientation and contrast[56] (but perhaps not for temporal frequency and contrast[57]).

Under this hypothesis, when there are two sensory modalities and thus two amplitudes α_1, α_2 and two features ϕ_1, ϕ_2, the model (Eq. 9) becomes

$$z = g_1(\phi_1)h_1(\alpha_1) + g_2(\phi_2)h_2(\alpha_2) + B \quad \text{Eq. 11}$$

As we will see next, this model successfully describes data obtained in two laboratories, which tested multisensory integration with different tasks, across different modalities (visual, auditory, and vestibular), in different species (rats, monkeys, and humans).

In one of these multisensory tasks, humans received noisy sequences of visual and auditory stimuli, and judged whether their rate was above a criterion[53,54]. As expected, when stimuli were purely auditory or purely visual, the observers did well if the stimulus had high amplitude ("Easy"), and poorly if it had low amplitude ("Hard", Figure 6**a**,**b**). When the easy auditory stimulus was combined with the hard visual stimulus, it largely determined the observer's choices: if the two stimuli disagreed, the observer responded in a manner consistent with the auditory stimulus (Figure 6**c**). Similar results were obtained by combining the hard auditory stimulus with the easy visual stimulus (Figure 6**d**). In both cases the choices were largely determined by the easier stimulus, as expected from a Bayesian observer[48,49]. The original study analyzed these data with Signal Detection Theory (Appendix 1) and found the data broadly consistent the observer being Bayesian[54]. A later study found that the psychometric curves of rats in this task were well fit by logistic curves[25]. It is thus conceivable that these observers may be performing logistic classification.

The choices measured in this task agree with logistic classification, with amplitudes and features combined under the separable approximation (Eq. 11). To fit the data, I chose simple linear expressions for the functions: $h_i(\alpha_i) = \alpha_i$, and $g_i(\phi_i) = F_i\phi_i + B_i$ (with $i = 1,2$ denoting visual and auditory modalities). The result is a simple equation:

$$z = \alpha_1(F_1\phi_1 + B_1) + \alpha_2(F_2\phi_2 + B_2) + B \quad \text{Eq. 12}$$

With just 5 free parameters (visual gain F_1, visual bias B_1, auditory gain F_2, auditory bias B_2, and overall bias B) this function provided good fits to 10 psychometric curves comprising 114 measurements (Figure 6**a-d**, *curves*).

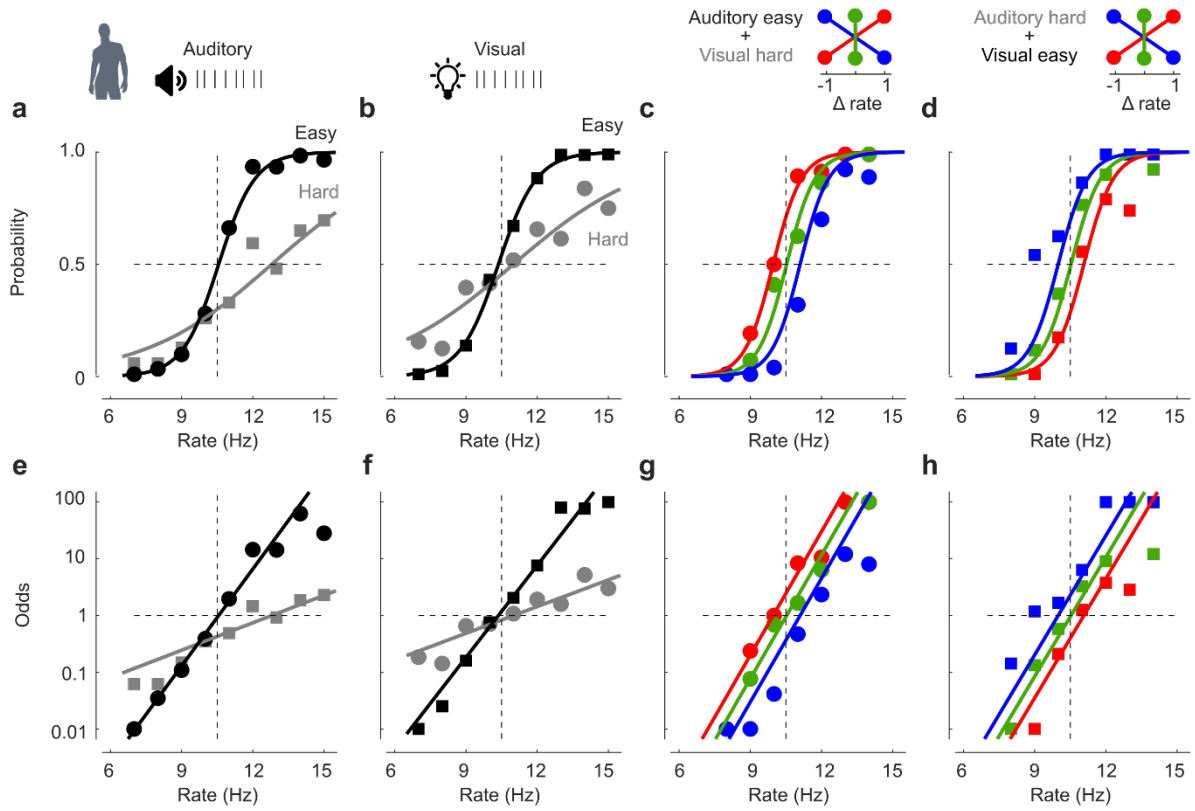

Figure 6. ***Logistic classification describes audiovisual rate choices in humans****.* ***a*** *Average choices of a human performing a rate discrimination task based on auditory sequences. The ordinate plots the probability that the observer judges the rate of the sequence to be higher than a reference (10.5 Hz) when stimuli have low amplitude (Hard) or high amplitude (Easy). Curves in this panel and subsequent ones are fits of the logistic classification model.* ***b****. Same, for visual stimuli.* ***c****. Same, for stimuli obtained by summing an easy auditory stimulus to a hard visual stimulus, with the rate of the former being lower (blue), equal (green), or higher (red) than the rate of the latter. The abscissa plots the average rate of the visual and auditory stimuli.* ***d****. Same, for stimuli obtained by summing a hard auditory stimulus to an easy visual stimulus.* ***e-h:*** *The same data as a-d, plotted in terms of odds, in logarithmic scale. Data are from Human 1 in Ref.[54].*

As usual, model and data are easiest to inspect in terms of log odds. In this scale, the unisensory responses are lines, which are steeper for Easy stimuli than for Hard stimuli (Figure 6**e**,**f**). When the steep line is summed to a shallow line in the multisensory responses, its slope and intercept determine the slope and intercept of the resulting line (Figure 6**g**,**h**).

In another multisensory task, monkeys judged whether their heading was Left or Right based on visual and vestibular cues[52]. The animals performed well when presented with purely vestibular stimuli (Figure 7**a**) and with purely visual stimuli with high coherence (Figure 7**b**). When the vestibular stimulus was combined with the hardest visual stimulus (lowest coherence), the former largely determined the observer's choices (Figure 7**c**). Conversely, when the vestibular stimulus was combined with the easy visual stimulus, the latter largely determined the choices (Figure 7**d**). In other words, the choices were largely determined by the modality that was easier, suggesting that the observers were Bayesian[52].

These data were well fit by the logistic classification model with the same equation as the previous data (Eq. 12). Here, ϕ_1 indicates the visual heading and ϕ_2 indicates the vestibular heading, both of them raised to an exponent q to capture increased sensitivity around the heading of 0. This function provided good fits to the psychometric curves (Figure 7**a**-**d**), and as usual, the reasons for its success are easiest to see in terms of log odds (Figure 7**e**-**h**).

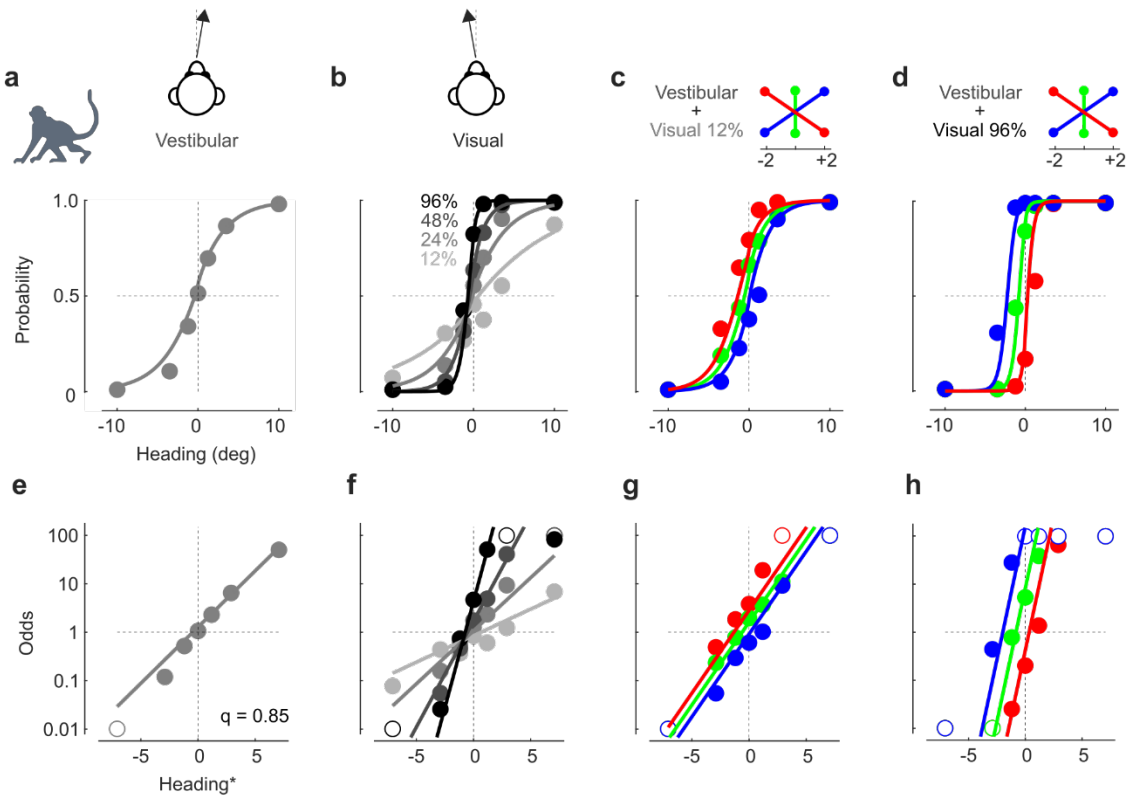

Figure 7. ***Logistic classification describes vestibulo-visual heading choices in monkeys****.* ***a*** *Average choices of a monkey performing a heading discrimination task based on unisensory vestibular stimulation. The ordinate plots the probability that the observer judges the heading to be Right. Curves are predictions of the logistic classification model.* ***b****. Same, for unisensory visual stimuli varying in coherence from 12% (hardest) to 96% (easiest).* ***c****. Same, for multisensory stimuli obtained by summing the vestibular stimulus to a hard visual stimulus, with the former having a heading left of (blue), same as (green), or right of (red) the latter. The abscissa plots the average heading of the vestibular and visual stimuli.* ***d****. Same, for stimuli obtained by summing the vestibular stimulus to an easy visual stimulus.* ***e-h:*** *The same data as a-d, plotted in terms of odds, in logarithmic scale. Open symbols indicate values where the probability is close to 0 or 1, where the odds would require a high precision, and are thus likely to lie outside the range of the ordinate. Data were grabbed from Ref.*[52]*.*

It is striking that logistic classification describes multisensory choices in so many species, tasks, and modalities, especially considering that the tasks do not perfectly conform to the conditions where logistic classification is optimal. Indeed, in deriving logistic classification (Eq. 9) we assumed the modalities to be independent, but in the tasks that we considered the two modalities had positive correlations. For instance, in the audiovisual position task (Figure 4) the modalities agreed more often than they disagreed[26]. More strikingly, in the visuotactile task (Figure 5) the two modalities had a correlation of 1 when both present, because they always had the same orientation. Strong correlations between modalities were present also in the other two tasks (Figure 6 and Figure 7). In these conditions, the additivity at the core of logistic classification may no longer be optimal, but the brain seems to adopt it nonetheless as a useful heuristic[58].

Sensory choices influenced by history

A key challenge in making a choice is to weigh only the factors that are relevant: giving weight to irrelevant factors decreases the chance of correct answers. And yet, superstitious behavior is widespread. For instance, in sensory tasks where the sequence of stimuli is random, humans[14-18,21,59,60] and animals[12,13,19,20,22,41,61-66] typically act as if it followed some order ("serial dependence").

The logistic classification model can readily capture this serial dependence, by simply including history factors as regressors in addition to the sensory factors[12]. This approach[12] merged the logistic classification approaches that had been used for sensory decisions[10] and for history-based decisions[7-9].

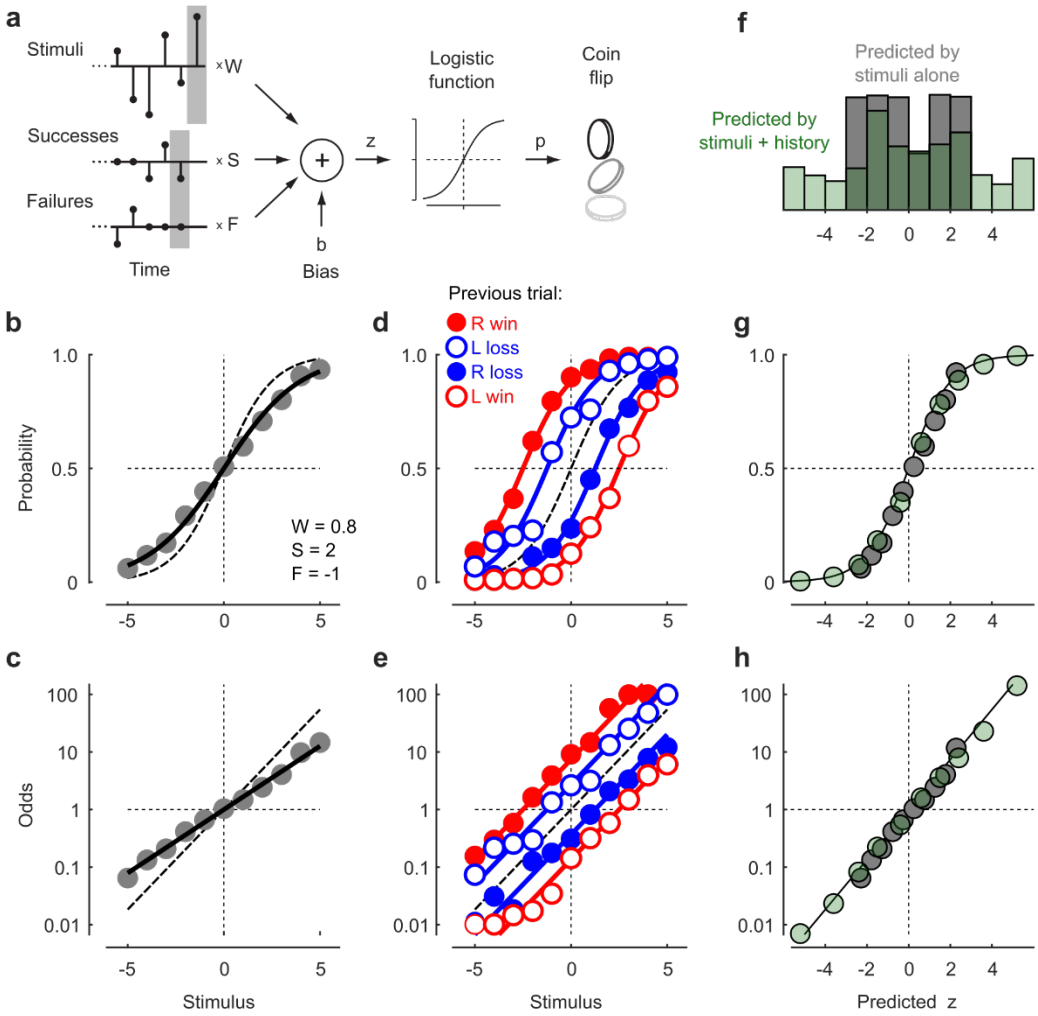

Figure 8. ***Logistic classification describes effects of history. a****. Model of logistic classification where choices are determined not only by a stimulus but also by prior wins or losses (Eq. 13). Adapted from Ref.[12]. The subsequent panels show results of simulations with W = 0.8, S = 2, F = -1, B = 0.* ***b****. Simulated data showing the probability of R choices as a function of contrast, compared to what would be observed based on the sensory factor alone (dashed).* ***c****. Same, plotted as the logarithm of the odds.* ***d-e****. Same as b-c, contingent on previous trial being a success or a failure (red vs. blue) on the L or R (open vs. closed). The dashed curve shows the result that would be observed based on the sensory factor alone.* ***f****. Distribution of values of the decision variable z, as predicted by the stimuli alone (gray) or by the stimuli plus the history terms (green).* ***g.*** *Binned values of the decision variables for the two models, on top of a logistic curve.* ***h.*** *Same, plotted as the logarithm of the odds.*

In this framework (Figure 8**a**), choices depend not only on the present sensory stimulus $x(t)$ as in Eq. 5, but also on whether the preceding choice was a success s or a failure f:

$$z(t) = Wx(t) + Ss(t-1) + Ff(t-1) + B \qquad \text{Eq. 13}$$

where $s(t) = sign\big(x(t)\big), f(t) = 0$ if trial t was a success, and $s(t) = 0, f(t) = -sign\big(x(t)\big)$ if it was a failure.

This equation describes just one of various possibilities, chosen for its simplicity. In the many studies that used this approach[12-22,66,67], the history regressors typically extended further in the past, or were expressed in different combinations, such as past choices (regardless of success) or past rewards (regardless of choice).

If serial dependence is present, ignoring it can make one underestimate stimulus sensitivity. Indeed, plotting the performance as a function of the present stimulus yields shallower psychometric curves (fewer correct answers) than would be observed based only on sensory sensitivity W (Figure 8**b**,**c**). A better estimate of sensitivity (and a measure of the effect of history) is obtained by plotting performance conditional

not only on the present stimulus but also on the choice and outcome of the previous trial (Figure 8**d**). If the effect is additive (as in Eq. 13), it will result in simple shifts of the lines representing the log odds of the choices, because the history factors sum with the fixed bias B to yield a variable overall bias (Figure 8**e**). One can confirm that these history factors are in play by comparing a model that ignores them (Eq. 5) to one that includes them[47] (Eq. 13). In our example, the model that includes history factors predicts larger (positive or negative) values for the decision variable z (Figure 8**f**), while providing good fits to the actual choices (Figure 8**g**,**h**).

The strength of the history terms varies across individuals and in time[12]. It can change with learning[43] and can be increased or decreased by appropriate design, but it cannot be entirely removed[16]. In humans, for instance, it correlates with education[16]: PhD candidates or graduates have strongly negative failure weights (lose-switch) but weak success weights, whereas the remaining observers have positive success weights (win-stay). This correlation is not necessarily causal and may reflect other unmeasured factors.

However, some effects of history are more complex than can be captured by a simple logistic classification model such as Eq. 13. For instance, past choices have a stronger effect if they were made with low confidence[64], a behavior that is more readily explained by models based on reinforcement learning[39]. Also, engagement in the trial typically fluctuates, and these fluctuations can be captured by allowing the weights to change across trials[43,44]. Variations in engagement will vary the fraction of successes, so observing data after a success vs. a failure may be a way to gauge the effect of engagement. This phenomenon may explain results observed in rats during rate discrimination[25], where past successes and failures affect not only the overall bias but also the sensory weight W, which was slightly higher after a success than after a failure (Supp Figure 1**g**-**l**). Given that successes tend to occur in an engaged state and failures in a disengaged state, the latter effect may be explained by a dependence of sensitivity on engagement.

Sensory choices during brain manipulations

Logistic classification is a good model not only for how the brain makes decisions, but also for how these decisions are modified by brain manipulations such as local inactivations[23-26]. If the effects of inactivating a brain region can be summarized by changes in a few weights, one can surmise that the region is necessary for processing the corresponding factors.

For example, in mice performing the audiovisual localization task (same as Figure 4), inactivation of the right visual cortex decreases the contralateral visual weight, but no other weights. As a result, it impairs the detection of visual stimuli on the left side, but does not affect visual detection on the right side or auditory detection on either side (Figure 9**a**). This effect is particularly easy to see in terms of log odds (Figure 9**b**).

To describe these asymmetric effects, it helps to extend Eq. 10 to allow for different weights for stimuli on the left vs. right[26], whether visual (F_{1L} and F_{1R}) or auditory (F_{2L} and F_{2R}):

$$z = F_{1,L}s_{1,L}^{q} + F_{1,R}s_{1,R}^{q} + F_{2,L}s_{2,L} + F_{2,R}s_{2,R} + B \qquad \text{Eq. 14}$$

In principle, the parameters (weights, exponent, and bias) might all vary in the control vs. manipulation condition (see Methods). In practice, however, the model is parsimonious, because the control condition is typically described by fewer parameters (e.g., the weights on the left and right are the same), and because only a few parameters change during brain manipulations[23-26]. For instance, the effects of inactivating right visual cortex are described by a single parameter: a smaller weight applied to visual stimuli on the left, F_{1L}, and this simple change describes the data faithfully (Figure 9**a**,**b**). This result indicates that right visual cortex is necessary for processing visual on the left, and not for processing visual stimuli on the right or auditory stimuli[26].

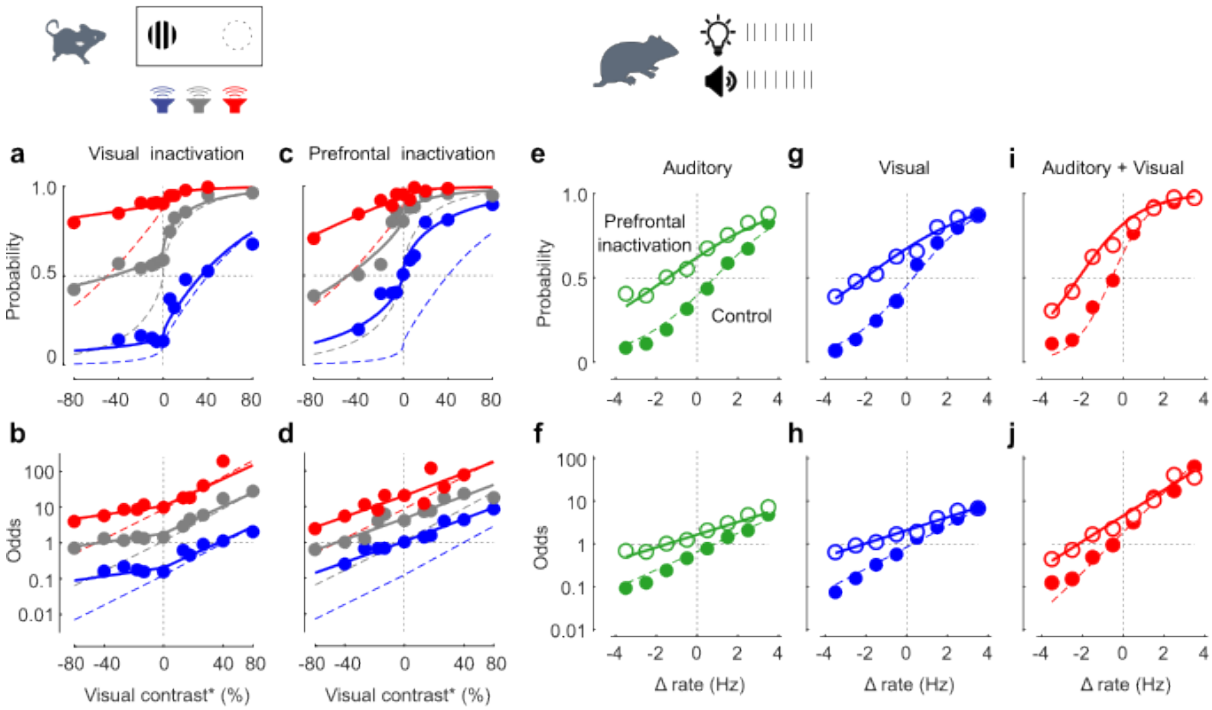

Figure 9. ***Logistic classification describes effects of brain manipulations. a****.Effects of inactivating right visual cortex in mice that perform an audiovisual localization task[26]. Showing the probability of Right choices as a function of visual contrast (abscissa) in the presence of sounds from the Left (blue), center (gray), and Right (red), in control conditions (dashed) and during inactivation (data and continuous curves). The curves are predictions of the model (Eq. 14) allowing only one parameter to change with inactivation: the weight applied to visual stimuli on the left, F_{1L}.* ***b****. Same data, plotted as log odds.* ***c,d****. Same format, showing the effects of inactivation of the right prefrontal cortex. The model captured them via changes not only in the contralateral visual weight but also in the contralateral auditory weight and in the overall bias. From[26].* ***e****. Effects of prefrontal inactivation in a rat performing auditory rate discrimination, showing the probability of choosing "Right" (for high rates) as a function of rate (expressed relative to the reference).* ***f****. Same data, in log odds.* ***g-h****. Same, for visual rate discrimination.* ***i-j*** *Same, for combined auditory and visual stimuli. From Ref.[25].*

By contrast, inactivating right prefrontal cortex reduces both visual weights and auditory weights (regardless of side), and increases bias B thus increasing the proportion of Right choices (Figure 9**c**,**d**). This result indicates that prefrontal cortex processes bilateral visual and auditory signals and promotes contralateral choices[26].

Similar results are seen in rats performing the audiovisual rate discrimination task[25] (same as Figure 6): the control and inactivation conditions are well fit by logistic classification (Eq. 14), and inactivation reduces both auditory and visual weights (regardless of whether stimuli have low or high rate), and increases the bias (Figure 9**e**-**j**).

Sensory choices with multiple outcomes

In all the analyses above, we have assumed that the observer faces a binary choice. However, this is not a strict requirement: The logistic classifier is readily extended to the case when the choice involves n classes. First, one obtains a vector of decision variables $\boldsymbol{z} = z_1, z_2, \ldots, z_n$ for each of the possible choices:

$$\boldsymbol{z} = \boldsymbol{W}^T \boldsymbol{x} + \boldsymbol{B}$$

Then, one applies a smooth version of the argmax function, called *softmax*:

$$p_i = softmax(\boldsymbol{z})_i = \frac{\exp(z_i)}{\sum_j \exp(z_j)}$$

For example, if there are 3 possible choices, and we assume for simplicity that $z_3 = 0$, then the probability p_1 of the 1st choice is largest when $z_1 > 0$ and $z_1 > z_2$, dividing the space of probabilities in three regions where the three choices are more probable than the others (Figure 10**a**).

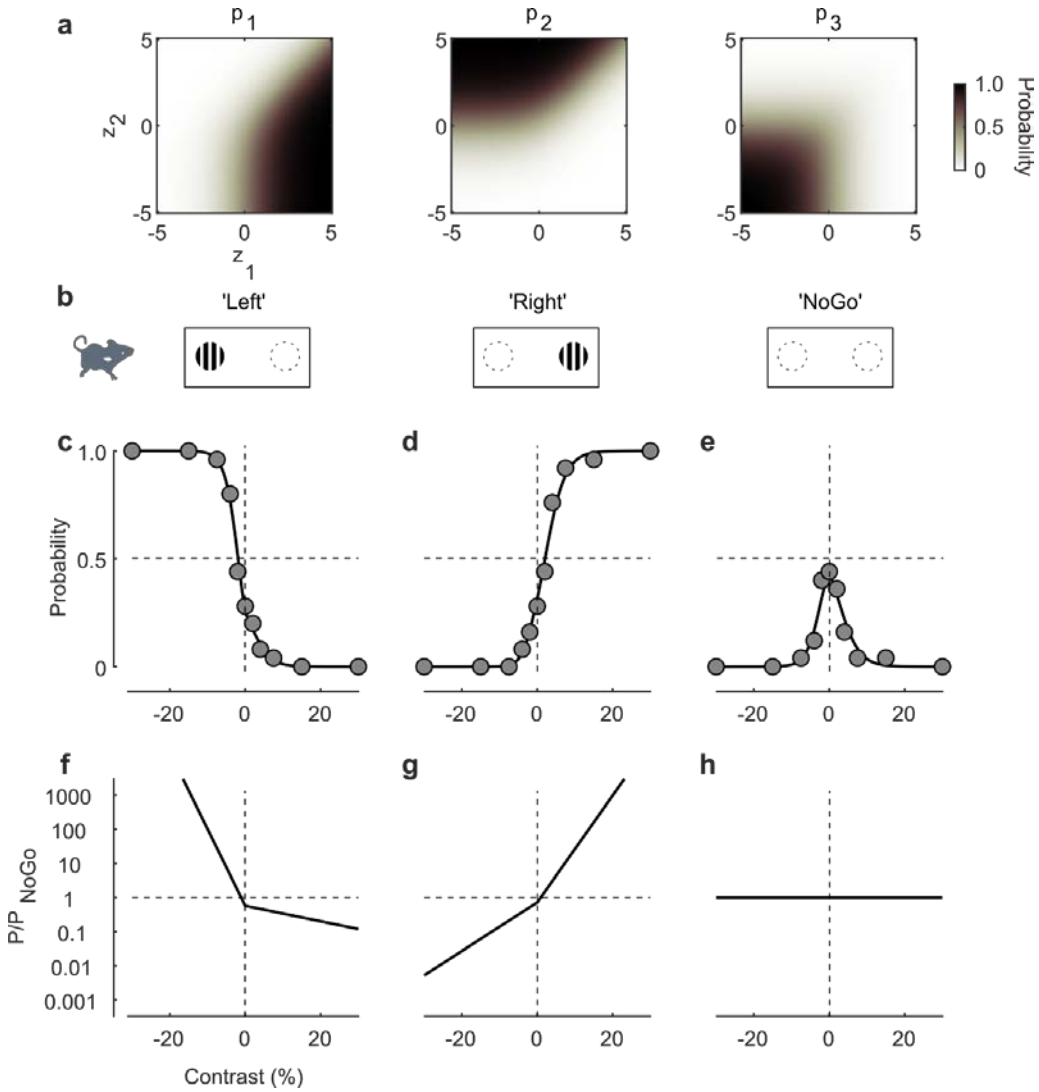

Figure 10. ***Logistic classification with more than two choices. a****. Multinomial logistic classification among 3 choices , showing probability of choices 1,2, and 3 (left to right) as a function of z1 (abscissa) and z2 (ordinate), when z3 = 0.* ***b****. The 3-choice version of the position detection task, where mice choose "Left" or "Right" to indicate stimulus position, and "NoGo" if the stimulus is absent.* ***c-e****. Probabilities of the three choices for a mouse in this task (Mouse I from Fig. 3 of Ref.[23]), as a function of stimulus contrast.* ***f-h****. The odds of the three choices relative to the third choice.*

Reassuringly, when there are only two outcomes the softmax function reduces to the familiar logistic sigmoid $p = \sigma(z)$ with decision variable $z = z_2 - z_1$:

$$p_1 = \frac{\exp(z_1)}{\exp(z_1) + \exp(z_2)} = \frac{1}{1 + \exp(z_2 - z_1)} = \sigma(z)$$

In a network, the softmax can be thought of as a competitive process among units that each receive one z_i as external input[5]. Because the outputs of softmax sum to 1, an increase in the input to one unit decreases the activity of others. When the difference between the largest z_i and the others is large, this process becomes a winner-take-all.

A logistic classifier with multiple outcomes can provide excellent fits to psychophysical data[23,24]. For example, consider a 3-choice version of the position detection task[23], where the mouse chooses the stimulus position as "Left" or "Right" if the stimulus is present, and chooses "NoGo" if it is absent (Figure 10**b**). This three-choice design was originally devised in the framework of signal detection theory[68,69] but it is particularly easy to analyze in terms of logistic classification, where it boils down to two equations[23]:

$$z_L = \log\left(\frac{p_L}{p_{NoGo}}\right) = w_{LL}c_L + w_{RL}c_R + B_L$$

$$z_R = \log\left(\frac{p_R}{p_{NoGo}}\right) = w_{LR}c_L + w_{RR}c_R + B_R$$

where c_L and c_R are the stimulus contrasts on the left and right. These equations provide good fits to the mouse choices (Figure 10**c**-**e**). As usual, the model is easiest to understand in terms of log odds, i.e., by plotting the values of z_L and z_R (Figure 10**f**-**h**).

Conclusions

A growing body of evidence indicates that the brain uses logistic classification to make choices based on a multitude of factors alone or in combination. These factors include relative value, relative probability, sensory inputs from one or more modalities, recent history, and brain manipulations. To illustrate this body of evidence, I have followed a hybrid approach, in most cases reviewing existing results and in others applying the logistic classification model to data that were previously analyzed with other approaches.

I have also shown that logistic classification is an optimal strategy in many conditions. For instance, it is the only procedure that accords to Bayes' rule for putting together sensory signals with estimates of prior probabilities or with sensory signals from a different modality, and it is the strategy that yields the highest overall reward when the options differ in value or prior probability.

As we have seen, these considerations of optimality provide a potential reason for the puzzling strategies of "probability matching" and "value matching". These strategies seem suboptimal: it would be better to always choose the option that is more likely or has higher value. However, they are fully expected from an optimal logistic classifier if that classifier is unaware that the stimulus is absent. This suggests a reason for probability matching and value matching: the observer does not know that the evidence is irrelevant or absent (i.e. that they are gambling). Rather, they act as if they were performing a task based on some evidence.

In fact, we have seen that logistic classification is also widely used in cases where it is not optimal, for instance when stimuli are absent (and choices exhibit probability matching or value matching) or stimuli of two modalities are not independent. This suggests that logistic classification is a heuristic that the brain implements in a variety of conditions even when it is not strictly optimal[58].

Finally, we have seen that logistic classification is a good model not only for how the brain makes decisions, but also for how these decisions are modified by manipulations such as local brain inactivations. Indeed, the effects of inactivating some key brain regions can often be summarized by changes in a few weights, suggesting that the inactivating regions are necessary for processing the corresponding factors.

Throughout the paper, I have described logistic classification as an addition of factors that each contribute to the log odds of a choice. However, we could have just as easily talked about multiplication of factors, each of which contributes to the odds, and we could have taken the logarithm only after the multiplication. Mathematically, the two are identical but numerically it is easier to deal with log odds that vary, say, between -5 and 5, than with the corresponding odds, which would vary between less than one hundredth and over a hundred (for a natural logarithm). Using firing rates, it seems easier to encode the former than the latter. Indeed, when decoding the activity of neurons in prefrontal cortex the activity seems more commensurate to log odds[13,26].

Going forward, one promising direction is to develop the temporal aspect of logistic classification in ways that go beyond the well-established drift diffusion model (Appendix 2), which is already quite flexible[70]. For instance, logistic classification can capture the effect of stimulus fluctuations, teasing apart the dynamics of complex cognitive computations[71,72]. At a longer time scale, it seems clear that the weights of the logistic classifier should not be considered to be constant, because they change with factors such as learning and brain state[43,44].

Another promising direction is to use neural data as a predictor. Ultimately, a model of choice should be based on neural data, and a way to start on this path is to add neural activity to task factors[67] such as those considered in this paper. Ultimately, the neural activity should be superior and make any other factor irrelevant[7,73], because it is the sole determinant of the brain's choices.

Acknowledgments

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Methods

Most of the data were taken from the original papers using a manual data grabber (the MATLAB function *grabit.m*). In a few cases (noted in the legends of the relevant figures), I accessed the original data.

I then fitted these data with the 2-choice logistic classification model using the MATLAB function *glmfit*. In the case of 3 choices, instead, I used the function *mnrfit*.

To describe sensory choices influenced by priors (Figure 2) I fit this equation:

$$p = \sigma(Vv + H(h - 0.5) + B) \qquad \text{Eq. 15}$$

where v is visual strength (coherence for the motion task, contrast for the position task), h is the probability of a Right stimulus (determined by the block), and V, H, B are parameters (visual gain, prior gain, and bias).

To describe sensory choices influenced by value in humans, monkeys, and mice (Figure 3) I fit this equation:

$$p = \sigma(Vv + Rr + B) \qquad \text{Eq. 16}$$

where v is visual strength (position, coherence, or contrast, depending on the experiment), r is the relative reward offered for Left vs. Right choices (determined by the block) and V, R, B are parameters (visual gain, reward gain, and bias).

To describe audiovisual position choices in mice (Figure 4) and visuotactile orientation choices in rats (Figure 5) I fit Eq. 10.

To describe audiovisual rate choices in humans (Figure 6) I fit Eq. 12.

To describe vestibulo-visual heading choices in monkeys (Figure 7) I fit the same equation but with an exponent q applied to both ϕ_1 and ϕ_2.

To illustrate the effects of stimulus history (Figure 8) I simulated the model in Eq. 13 using the parameters W = 0.8, S = 2, F = -1, B = 0.

To describe the effects of brain manipulations (Figure 9) I modified Eq. 14 to allow not only for different sensitivities on L vs R but also for possible effects of manipulations:

$$z = \sum_{i=1,2} \sum_{j \in \{L} (F_{ij} + \Delta_{ij}) s_{ij} \; + (B + \Delta_B) \qquad \text{Eq. 17}$$

where the variables s_{ij} are the stimuli, indexed by their modality ($i = 1$ for visual contrast raised to exponent q and $i = 2$ for auditory position), and by their position ($j = L$ or R). The parameters $F_{1L}, F_{2L}, F_{1R}, F_{2R}$ are the corresponding weights, and the five Δ parameters allow for the effects of the brain manipulation on the four weights F and on the bias B.

Appendix 1. Relation to Signal Detection Theory

In the description of logistic classification given in the main text, the processing of the factors is deterministic, and the choice is stochastic: it is made by flipping a coin (Figure 1**a**). There is, however, an alternative description where the processing of the factors is stochastic, and the choice is deterministic. In this description, the utilities L, R in favor of Left and Right choices are each the sum of a deterministic value x (determined by the factors) and a random variable ε (which varies across trials). The model subtracts the two and thresholds the result (Figure 11**a**). This description is mathematically equivalent to the one in the main text if the random variables are drawn from a Gumbel distribution (Figure 11**b**); in that case their difference is drawn from a logistic distribution (Figure 11**c**), and the model performs logistic classification[1,3] (Figure 11**d**).

This description makes it easier to compare logistic classification (for two alternatives) to Signal Detection Theory[74,75] (SDT), which is the dominant formalism used to describe perceptual decisions. In SDT, the deterministic part of L and R is the "signal", and the random variable is "noise", which is generally thought to be sensory and related to limitations of sensory systems. In SDT, the random variable is commonly taken to be Gaussian, resulting in a psychometric curve that is a cumulative Gaussian function (Figure 11**e**).

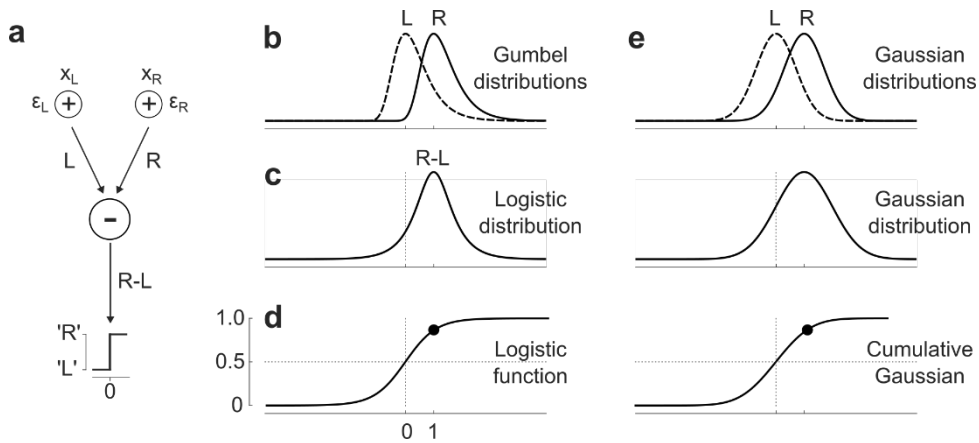


Figure 11. ***Logistic classification and Signal Detection Theory. a****. An alternative description of the choice model, where the utilities L, R in favor of Left and Right choices are each the sum of a deterministic value x and a random variable ε. The model subtracts the two and thresholds the result to obtain a choice.* ***b****. Probability distributions for the utilities L and R in the case where $x_L = 0$ and $x_R = 1$, and the random variables ε are distributed according to the Gumbel distribution.* ***c****. The distribution of the difference R-L is logistic.* ***d****. After thresholding, the probability of choosing 'R' as a function of $x_R - x_L$ is a point on the logistic function.* ***e****. The same quantities, if the random variables ε are drawn from a Gaussian distribution. In that case the difference is Gaussian, and the probability of 'R' choice is a point on a cumulative Gaussian function. This is the formalism typically used in Signal Detection Theory.*

When describing a psychometric curve determined by a single factor, the two frameworks (logistic and Gaussian) are hardly distinguishable[25,75-78]. For example, consider the probabilities of choosing 'R' in a two-alternative task (Figure 12**a**). These were generated by a logistic classification model $p = \sigma(Wx + B)$, where x is the stimulus and W, B are parameters (sensory weight and bias). The same probabilities can be fitted extremely well by the cumulative Gaussian $\Phi((x - \mu)/\sigma)$, where the two parameters σ, μ determine a "threshold" and a "bias" (Figure 12**b**).

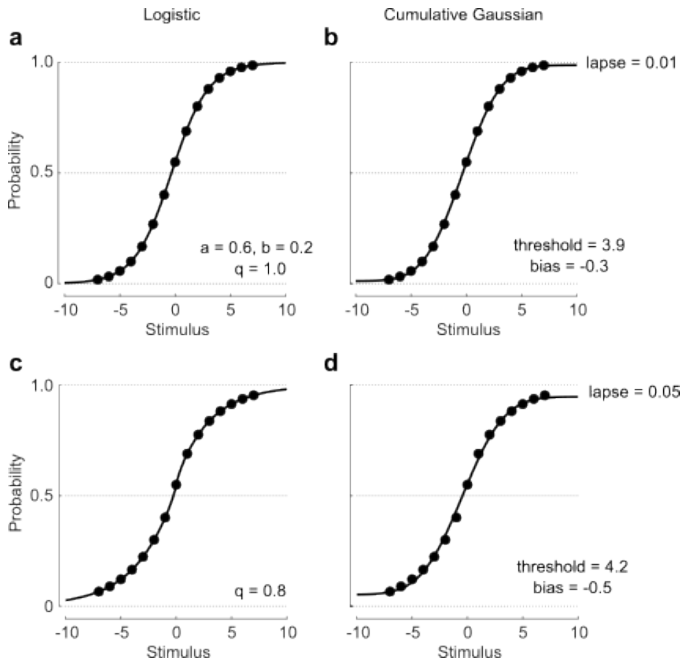


Figure 12. ***Logistic classification vs. fitting a cumulative gaussian. a****. Probabilities simulated by a two-alternative logistic classification model (data points and curve).* ***b****. The same data points, fitted by a cumulative Gaussian with a lapse rate (curve).* ***c****. Probabilities simulated by a logistic classification model with a slight compression of the stimulus axis (exponent q=0.8).* ***d.*** *The same data points, fitted with the cumulative Gaussian with a larger lapse rate (curve).*

When fitting actual data, however, the probabilities don't always reach zero or one, even for the easiest stimuli. To deal with this eventuality, when fitting a cumulative Gaussian one typically adds an extra parameter λ (or two) to account for a "lapse rate" λ (Figure 12**d**), to obtain

$$p = \lambda + (1 - \lambda)\Phi\left(\frac{x - \mu}{\sigma}\right)$$

With logistic classification, it is generally not necessary to add such a lapse rate. In many cases, one can use the logistic function as is, because it tends to zero or one more gradually than the cumulative Gaussian (the logistic distribution has long tails). The probabilities are then below 1 or above 0 simply because the observer does not give enough weight W to the sensory input x. In other cases, as shown in multiple occasions in the main text, the observer may process stimulus strength in a nonlinear fashion. For instance, the sensory input x may be given by the measure s of stimulus strength used in the laboratory, raised to the power $q < 1$ to obtain a compressive nonlinearity (Figure 12**c**). In other cases, one may need a nonlinearity that is even more compressive[12,23].

More generally, logistic classification outstrips Signal Detection Theory (SDT) when it comes to representing more general choice environments. For instance, as I have shown in the main text, logistic classification makes it trivial to add predictors, both sensory and non-sensory; it has a simple linear interpretation; it makes it easy to describe the effects of brain manipulations; and it is readily extended to an arbitrary number of alternatives. Moreover, logistic classification incorporates the Bayesian assumption, without having to postulate that an observer keeps track separately of stimulus estimate and confidence. SDT lacks these advantages. For instance, it makes it unwieldy to have more than one or two predictors or more than two choice alternatives. Logistic classification is thus often preferable to SDT to describe sensory choices.

Appendix 2: Relation to drift diffusion

By itself, logistic classification model says nothing about a decision's time course. The most established model for the time course is the drift diffusion model[2,46,79]. In the model the decision variable does a random walk, going up or down at each step in time depending on the evidence. When the decision variable hits one of the two boundaries, the corresponding decision is made.

If the random walk starts from the middle between the two bounds, then the probability that it will hit one of the bounds (say, the upper one) is given by the logistic function. For a full derivation, see Refs.[46,80]. Here I give a simpler derivation, which is based on a simplified analogy.

In the drift diffusion model, at any moment in time the decision variable can jump by an arbitrary amount based on a probability distribution. Let's consider a simpler system, where at each moment in time the decision variable can only go up or down by 1.

Define P as the probability that it will go up and define $r = P/(1-P)$. This is the well-known "gambler's ruin" problem, and it has a simple solution[81]: if the funds of players 1 and 2 are N_1 and N_2, then the probability that player 1 will win (i.e. that player 2 goes bankrupt) is

$$p = \frac{1 - r^{-N_1}}{1 - r^{-(N_1+N_2)}}$$

where we have assumed that $r \neq 1$ (the drift is preferentially in one direction). If the two players start with equal amount of money ($N_1 = N_2 = N$), then player 1 will win with probability

$$p = \frac{1}{1 + r^{-N}} = \frac{1}{1 + e^{-N\log(r)}} = \sigma(x)$$

where $x = N\log(r)$. In other words, the probability of hitting a boundary in this random walk is proportional to the logarithm of the odds of going up vs. down in each step.

There are many implementations of the drift diffusion model, and many ways to change it, e.g. by applying a constant bias at each step, or by starting by an unequal starting point, or giving more weight to one of the sensory options[82]. In some of those cases there may not be a closed form equation for the probability of hitting a boundary. In those cases, the psychometric functions must be simulated numerically[70].

Appendix 3: The optimal bias

Here I derive the ideal bias for an observer that performs logistic classification when the rewards for correct left vs. right choices V_L, V_R are unequal, and the prior probabilities of stimuli being on the left or right, p_L, p_R are unequal. My derivation is inspired by an analogous result obtained with signal detection theory using cumulative gaussians[37].

If an observer performs logistic classification based on evidence x with weight a, the probability that they will choose Right is $p = P('R'|x) = \sigma(ax + b)$. Here I show that the bias b that maximizes expected value is

$$b = \log\left(\frac{V_R}{V_L}\right) + \log\left(\frac{p_R}{p_L}\right) \qquad \text{Eq. 18}$$

The expected value of a choice is the product of the probabilities of each answer being correct times the corresponding reward:

$$V = V_L P('L' \,\&\, x < 0) + V_R P('R' \,\&\, x > 0)$$

The evidence x is a random variable with prior probability $p(x)$. We can thus write

$$V = V_L \int_{-\infty}^{0} P('L', x)\, dx + V_R \int_{0}^{\infty} P('R', x)\, dx =$$

$$= V_L \int_{-\infty}^{0} P('L'|x) p(x) dx + V_R \int_{0}^{\infty} P('R'|x) p(x) dx$$

We assume that the prior probability is different between Left and Right, but otherwise flat: $p(x) = p_L/T, x \in [-T, 0]$ and $p(x) = p_R/T, x \in [0, T]$. Later we will set $T \to \infty$. Using the fact that $P('R'|x) = \sigma(ax + b)$ and $P('L'|x) = 1 - \sigma(ax + b) = \sigma(-ax - b)$, we obtain:

$$V = \frac{p_L V_L}{T} \int_{-T}^{0} \sigma(-ax - b) dx + \frac{p_R V_R}{T} \int_{0}^{T} \sigma(ax + b) dx$$

To maximize V we need to find b that such that $dV/db = 0$. We can bring the derivative inside the integrals:

$$\frac{dV}{db} = \frac{p_L V_L}{T} \int_{-T}^{0} \frac{d}{db} \sigma(-ax - b) dx + \frac{p_R V_R}{T} \int_{0}^{T} \frac{d}{db} \sigma(ax + b) dx = 0$$

A nice property of the logistic function is that its derivative has a simple form: $d\sigma(x)/dx = \sigma(x)\sigma(-x)$. Using this property and rearranging the terms, we obtain:

$$\frac{p_R V_R}{p_L V_L} = \frac{\int_{-T}^{0} \sigma(ax + b)\sigma(-ax - b) dx}{\int_{0}^{T} \sigma(ax + b)\sigma(-ax - b) dx}$$

With a change of variable $z = ax + b$ the Eq. becomes

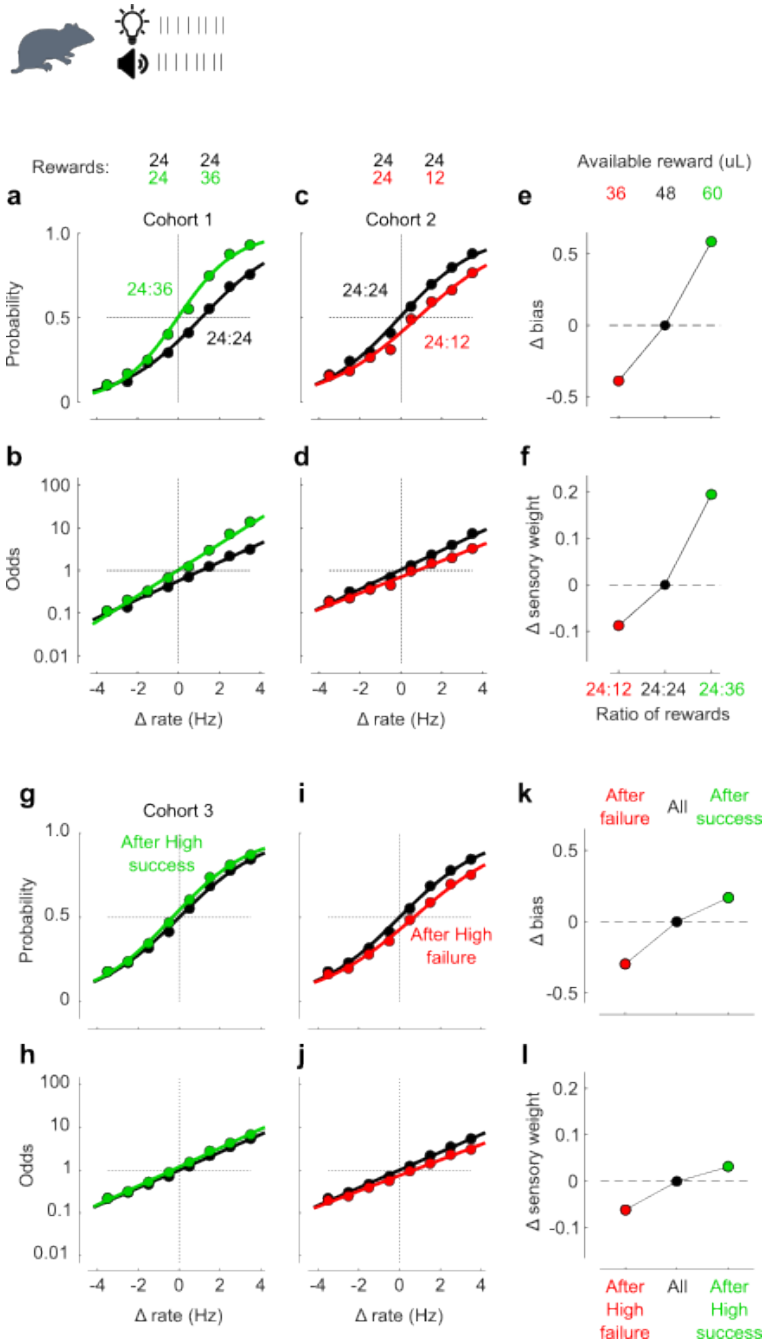
$$\frac{p_R V_R}{p_L V_L} = \frac{1/a \int_{-aT+b}^{b} \sigma(z)\sigma(-z) dz}{1/a \int_{b}^{aT+b} \sigma(z)\sigma(-z) dz} = \frac{\sigma(b) - \sigma(-aT + b)}{\sigma(aT + b) - \sigma(b)} \xrightarrow{T \to \infty} \frac{\sigma(b)}{1 - \sigma(b)}$$

Where in the second equality we have solved the integrals by using the expression for the derivative of σ in reverse, and in taking the limit we have used the fact that $\sigma(\infty) = 1$ and $\sigma(-\infty) = 0$. If we now take the logarithm of both sides, and recognize that $\sigma^{-1}(p) = \log\ p/(1-p)$, we obtain:

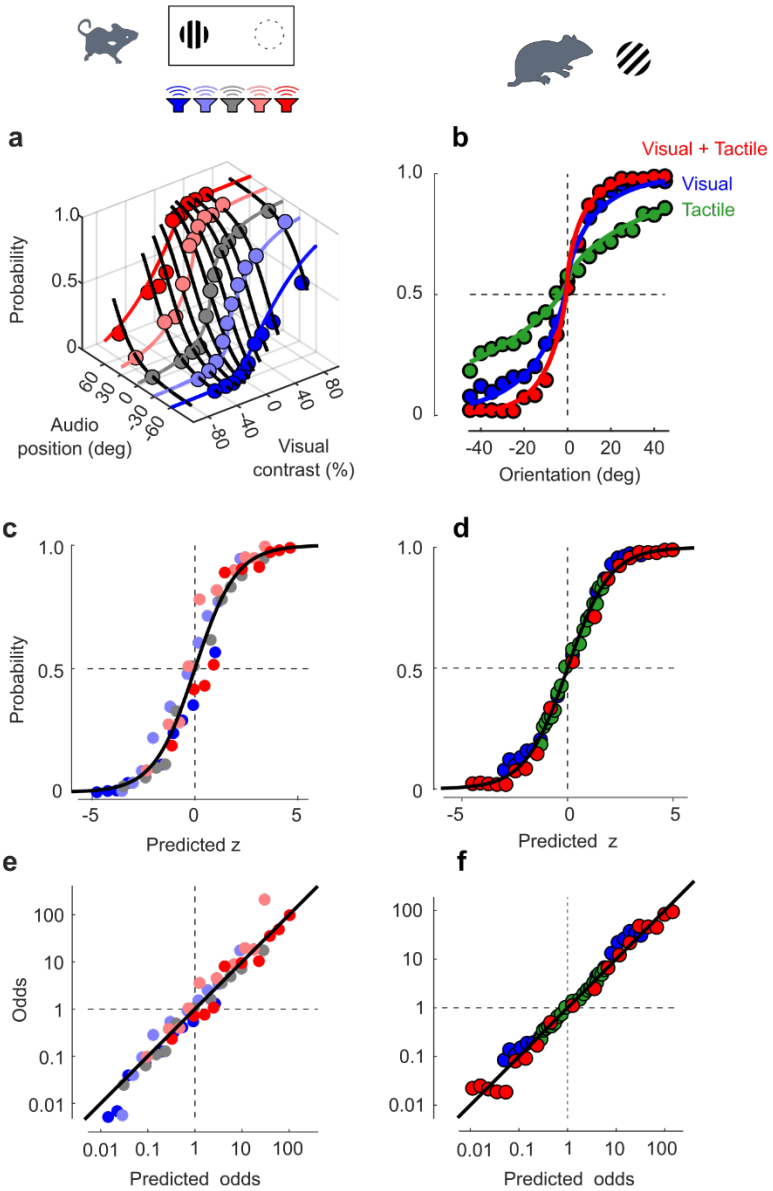
$$log\frac{p_R V_R}{p_L V_L} = log\frac{\sigma(b)}{1-\sigma(b)} = \sigma^{-1}\big(\sigma(b)\big) = b$$

which proves the result in Eq. 18.

Supplementary figures



Supp Figure 1. ***Logistic classification describes the effects of unequal rewards and of recent history***. ***a***. *Probability of choosing "high" in a task where rats judge the rate of audiovisual stimuli, in conditions where the rewards for correct "high" choices are the same as correct "low" choices (24 µL, black) or higher (36 µL, green). Curves show fits of the logistic classification model where both the sensory weight W and the bias B are allowed to change when the rewards are unequal.* ***b***. *Same data and curves, plotted in terms of the logarithmic odds of choosing "high".* ***c,d***. *Same, for a cohort of rats that were run in conditions where the rewards for correct "high" choices are the same as correct "low" choices (24 µL, black) or lower (12 µL, green).* ***e***. *As predicted by logistic classification under the hypothesis that observers seek to maximize reward, the bias parameter was affected in opposite directions by the two manipulations. The changes in bias predicted by the model (Eq. 8) would be log(12/24)=-0.69 and log(36/24)=0.41.* ***f***. *In addition, the sensory weight increased when the ratio of rewards increased, perhaps because the total available reward also increased (abscissa). This may have caused an increase in attention to the task variable.* ***g-j***. *Same as a-d for a cohort of rats that were run with equal rewards for "low" and "high" correct choices, distinguishing performance following a "high" choice that was correct (green) or incorrect (red).* ***k***. *The bias term followed the predictions of logistic classification with history terms (Eq. 13) in a win-stay lose-switch strategy.* ***l***. *The sensory weight was slightly higher after a success than after a failure, possibly because failures tended to occur during behavioral states where the rats were paying less attention to the stimulus. Data were obtained from Fig. 4 of Ref [25].*



Supp Figure 2. ***Summarizing multiple conditions on a single logistic curve***. ***a***. *Probabilities of Right choices in an audiovisual task (replotted from Figure 4).* ***b***. *Probabilities of Right choices in a visuotactile task (replotted from Figure 5). Curves in a,b show fits of the logistic classification model.* ***c-d***. *The same data as a-b, plotted as a function of the decision variable z predicted by the model, plotted on top of a standard logistic curve.* ***e-f***. *The same data, in log odds.*

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