Decision making
Part 2

Jean-Pierre Nadal
CNRS & EHESS
Laboratoire de Physique de l’ENS
(LPENS, UMR 8023 CNRS - ENS – SU – Univ. De Paris)
Ecole Normale Supérieure (ENS)

and

Centre d’Analyse et de Mathématique Sociales
(CAMS, UMR CNRS - EHESS)
Ecole des Hautes Etudes en Sciences Sociales (EHESS)

http://www.phys.ens.fr/~nadal/Cours/MVA
jean-pierre.nadal@phys.ens.fr
Dynamics, Reaction times
neural correlates?
Reaction times
psychophysics

Random dots experiments
Shadlen & Kiani, 2013

A typical response time distribution
Ratcliff & Rouder 1998

« ba »/ « pa »
Pisoni & Tash, 1974
Reaction times neural correlates accumulation of evidence

Experimental support to diffusion models in LIP: Kim & Shadlen, 1999; Shadlen & Newsome, 2001; Heekeren et al., 2004; Huk & Shadlen, 2005...

Average response of LIP neurons during decision formation, for three levels of difficulty:

(Left) Responses during decision formation, aligned to onset of random-dot motion.

(Right) The LIP neural responses aligned to the eye movement.
(solid/dash curves: toward/away preferred direction).

(Bottom, shaded insert) Average responses from MT direction-selective neurons to motion in the preferred and anti-preferred directions. After a transient, MT responds at a nearly constant rate.
Models

- Accumulation of evidence

- Continuous modelling: diffusion
  - Drift-Diffusion to bound (DDM)
    Ratcliff 1978, Luce 1986
  - Race models
    (competing accumulators)
    Vickers 1979, Luce 1986
  - Correlated accumulators
    interpolates between DDM and race
    Moreno-Bote 2010
  - Other variants - accumulators with inhibition...
  - Fixed bounds vs. time dependent bounds
    Drugowitsch et al 2012, Zhang et al 2014

- Discrete modelling: random walk (RW) models

- Attractor neural network models

- Decision from transient dynamics
  Laurent 1996 (olfactory system); Mastrogiuseppe & Ostojic, 2018
Neyman-Pearson (1933): for a given set of n iid observations, r1, ..., rn: accept H0 (resp. H1) if  \( Y_n < K \) (resp. \( \geq K \)), where \( K \leftrightarrow \) desired accuracy level. \( \rightarrow \) optimal procedure, this if the data size n is fixed, given in advance. « interrogation paradigm »

Sequential Probability Ratio Test (SPRT)
A. Wald (1945, 1947), G. Bernard (1946): accumulation of log-likelihood ratios (at each step, independent sampling)

\[
Y_n = \sum_j \log \frac{p(r_j \mid H_1)}{p(r_j \mid H_0)}
\]

until \( Y_n \) hits for the first time one of two given bounds \( (A_0 \leq Y_n \leq A_1) \). « free response paradigm »

Optimality:
SPRT minimizes the expected number of steps needed to reach a decision (at any given value of the error probabilities)
Wald’s (1945) *sequential probability ratio test* (SPRT) in statistics: accumulation of log-likelihood ratios (at each step, independent sampling)

**Alan Turing**: use of SPRT to break the German *Enigma* code during World War II.

**Multiple options decision-making in biological systems**

Seeley, Vissher & Passino, «Group decision making in honey bees swarms», American Scientist 2006


Siggia & Vergassola, «Decisions on the fly in cellular sensory systems», PNAS 2013

Desponds et al, «Hunchback promoters can readout morphogenetic positional information in less than a minute”, eLife 2020 *(fly embryo development: gene expression → head or tail)*
Wald’s *sequential probability ratio test* (SPRT) in statistics: accumulation of log-likelihood ratios (at each step, independent sampling)

\[ Y_n = \sum_j \log \frac{p(r_j | H1)}{p(r_j | H0)} \]

*Relative judgment theory*, Link and Heath (1975)

\[ Y_n = \sum_{j=1}^n r_j \]

For Gaussian distribution, one can recover the optimality of Wald’s SPRT.

**Models**

- Discrete modelling: random walks
  - SPRT → Biased random walk between absorbing walls
  - For Gaussian distributions → Gaussian random walk
  - Continuous limit → Drift Diffusion models (Laming 1968)
Reaction times

Drift Diffusion Models (DDM)

\[ dy = \mu dt + \sigma dW \]

\( y(t = 0) = y_0 \)  
(initial bias/prior)

thresholds: \( \pm A \)

Results: assume \( \mu > 0 \).
hit rate = probability of reaching the \( +A \) bound. One gets:

\[
\text{hit rate} = \frac{1}{1 + e^{-\frac{2A\mu}{\sigma^2}}} \quad \text{error rate} = \frac{1}{1 + e^{\frac{2A\mu}{\sigma^2}}}
\]

Mean reaction time:

\[
\bar{\tau}_{RT} = \frac{\text{threshold}}{\text{drift}} \tanh \left( \frac{\text{threshold} \times \text{drift}}{\text{variance}} \right) = \frac{A}{\mu} \tanh \left( \frac{A\mu}{\sigma^2} \right)
\]

Remark: not intuitive: mean RT on success trials = mean RT on error trials
Reaction times

**Drift Diffusion Models (DDM)**

\[ dy = \mu dt + \sigma dW \]

\[ y(t = 0) = y_0 \text{ (initial bias/prior)} \]

Thresholds: \( \pm A \)

Mean reaction time, case \( y_0 = 0 \):

\[
\tau_{RT} = \frac{\text{threshold}}{\text{drift}} \tanh \left( \frac{\text{threshold} \times \text{drift}}{\text{variance}} \right) = \frac{A}{\mu} \tanh \left( \frac{A \mu}{\sigma^2} \right)
\]

**Case \( y_0 \neq 0 \)**

\[
\tau_{RT} = \frac{A}{\mu} \tanh \left( \frac{A \mu}{\sigma^2} \right) + \frac{A}{\mu} \left\{ \frac{1 - e^{-2y_0 \mu / \sigma^2}}{\sinh(\frac{2A \mu}{\sigma^2})} - \frac{y_0}{A} \right\}
\]

Error rate:

\[
\frac{1}{1 + e^{\frac{2A \mu}{\sigma^2}}} - \left\{ \frac{1 - e^{-2y_0 \mu / \sigma^2}}{2 \sinh(\frac{2A \mu}{\sigma^2})} \right\}
\]
Accumulation of evidence

\[ dy = \mu dt + \sigma dW \]

\[ y(t = 0) = y_0 \]
(initial bias/prior)

thresholds: \( \pm A \)

RT Distribution:
**Wald distribution** (Inverse Gaussian distribution)

\[
P(A, t) = \frac{A}{\sqrt{2\pi}\sigma^2 t^3} \exp\left(\frac{(A - \mu t)^2}{2\sigma^2 t}\right)
\]
**Wald distribution** (or « inverse Gaussian distribution »)

Let \( u \) be the first time that a Brownian motion with positive drift hits a fixed, positive value. This defines a random variable for which the distribution is the Wald distribution.

In Brownian motion, the distribution of the random position at a fixed time has a normal (Gaussian) distribution; the Wald distribution is for a random time at a fixed position \( \rightarrow \) it is also called the inverse Gaussian distribution.

Figure from [http://www.vosesoftware.com/ModelRiskHelp/index.htm#Distributions/Continuous_distributions/Inverse_Gaussian_distribution.htm](http://www.vosesoftware.com/ModelRiskHelp/index.htm#Distributions/Continuous_distributions/Inverse_Gaussian_distribution.htm)
**Wald distribution** (or « inverse Gaussian distribution »)

Let $u$ be the first time that a Brownian motion with positive drift hits a fixed, positive value. This defines a random variable for which the distribution is the Wald distribution.

\[
E(U) = 1 \quad \text{var}(U) = \frac{1}{\lambda}
\]

Pdf: \( g(u) = \sqrt{\frac{\lambda}{2\pi u^3}} \exp -\frac{\lambda}{2u} (u - 1)^2 \)

Brownian motion with drift $\nu$ and std $\sigma$:
\[dX = \nu \, dt + \sigma \, dW\]
Then the distribution of the first passage time at a given level $\theta > 0$ starting at $X = 0$, is given by the general Wald distribution of mean \( \mu = \frac{\theta}{\nu} \) and shape \( \lambda = \frac{\theta^2}{\sigma^2} \)

\[\text{var}(X) = \frac{\mu^3}{\lambda}\]
Accumulation of evidence

\[ dy = \mu dt + \sigma dW \]

\[ y(t = 0) = y_0 \]
(initial bias/prior)

thresholds: ±A

M. Stone, 1960

Roger Ratcliff, 1978

F. Gregory Ashby 1983

Speed accuracy trade-off

RT Distribution:
**Wald distribution** (Inverse Gaussian distribution)

\[ P(A, t) = \frac{A}{\sqrt{2\pi \sigma^2 t^3}} \exp \left(-\frac{(A - \mu t)^2}{2\sigma^2 t}\right) \]

Fig. 5. Response time distributions for 3 subjects from Experiment 1. For each subject, two sample distributions from each of the speed and accuracy conditions are shown, one distribution for responses with relatively high probability ("Prob") and one for responses with intermediate probability. In each panel, the curve represents the theoretical predictions.

Ratcliff & Rouder 1998
Alternative: Attrator Networks

Attractor Networks


Random dot experiments paradigm

Excitatory cells, 3 sub-populations:
1 - specific to left movement direction
2 - specific to right movement direction
3 – non specific
Inhibitory cells (interneurons)

Recurrent network of LIF neurons

External input: fraction of dots moving in the left/right direction
→ Input strength onto the left/right
+ external noise (from other brain areas)

Wong & Wang 2006
Attractor Networks

Wong & Wang 2006: Reduced two variables model

\[
\frac{dS_1}{dt} = -\frac{S_1}{\tau_S} + (1 - S_1) \gamma r_1
\]

\[
\frac{dS_2}{dt} = -\frac{S_2}{\tau_S} + (1 - S_2) \gamma r_2
\]

\[r_1 = H(x_1) \quad r_2 = H(x_2)\]

\[x_1 = J_{11} S_1 - J_{12} S_2 + I_{\text{input } 1}\]

\[x_2 = J_{22} S_2 - J_{21} S_1 + I_{\text{input } 2}\]

\[H(x) \equiv \frac{x - \theta}{1 - \exp[-\beta(x - \theta)]}\]

Abbott & Chance, 2005
Attractor Networks

Wong & Wang 2006: Reduced two variables model

Random dots experiments

External input:

c = fraction of dots moving in the left/right direction

$\rightarrow$ input strength onto the left/right direction specific cells

\[
l_i = J_{ext} (1 \pm c)
\]

total input:

\[
l_{input,i} = l_i + l_0 + l_{\text{noise},i} \quad i = 1, 2
\]

non specific input

external noise (from other brain areas)
\[ i \in \{L, R\}, \quad r_i(t) = f\left(g_i(t)\right), \quad f(l) = \frac{a l - b}{1 - \exp\left[-\beta (a l - b)\right]} \]

\[ l_{L, \text{tot}}(t) = J_{LL} S_L(t) - J_{L,R} S_R(t) + I_{\text{stim},L}(t) + I_{\text{noise},L}(t) \]
\[ l_{R, \text{tot}}(t) = J_{RR} S_R(t) - J_{R,L} S_L(t) + I_{\text{stim},R}(t) + I_{\text{noise},R}(t) \]

\[ i \in \{L, R\}, \quad \frac{dS_i}{dt} = -\frac{S_i}{\tau_S} + (1 - S_i) f\left(g_i(t)\right) \]

\[ I_{\text{stim},L} = J_{\text{ext}} (1 \pm c) \quad I_{\text{stim},R} = J_{\text{ext}} (1 \mp c) \]

\[ i \in \{L, R\}, \quad \tau_{\text{noise}} \frac{dl_{\text{noise},i}}{dt} = -\left(l_{\text{noise},i}(t) - l_0\right) + \sqrt{\tau_{\text{noise}}} \sigma_{\text{noise}} \eta_i(t) \]

Decision threshold \( \theta \)
Phase-plane plot for the two selective neural populations. Colored regions = basins of attraction (dynamics in the absence of noise).

- **(Left)** In the absence of stimulation three attractors coexist (white circles):
  - a spontaneous state (when both $r_A$ and $r_B$ are low),
  - and two persistent activity states (with a high $r_A$ and a low $r_B$ or vice versa).

- **(Middle and Right)** Upon the presentation of a stimulus, the spontaneous steady state disappears. The system is forced to evolve toward one of the two active states = perceptual decisions (A or B). Blue and red: network’s trajectory in two individual trials.

- After the offset of the stimulus, the system’s configuration reverts back to that in the left panel. Because a persistently active state is self-sustained, the perceptual choice (A or B) can be stored in working memory for later use.

- Before a new trial: reset to the neutral state is needed. Taking into account the corollary discharge (non specific inhibitory input received after decision is made) $\rightarrow$ relaxation towards the neutral state (K. Berlemont & JPN 2018).
<table>
<thead>
<tr>
<th>Experimental findings</th>
<th>Drift-Diffusion/RW models</th>
<th>Attractor network models</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Long tail of reaction time distributions (but not always true? - Ditterich 2006)</td>
<td>• OK</td>
<td>• No</td>
</tr>
<tr>
<td>· Longer response times in error trials than in correct trials</td>
<td>• OK but only with additional features: fluctuations in drift and diffusion coeff. values from trial to trial (Ratcliff 1978, Ratcliff &amp; Smith 2004)</td>
<td>• OK</td>
</tr>
<tr>
<td>· Performance saturation</td>
<td>• Not necessarily. Performance can be made as good as one wants by increasing the bound (the decision threshold).</td>
<td>• OK</td>
</tr>
<tr>
<td>· Influence of newly arriving inputs decreases over time</td>
<td>• No difference, or even opposite effect</td>
<td>• OK</td>
</tr>
<tr>
<td>· Sequential effects, post error adjustments</td>
<td>• Partly. Needs fitting separately trials of different conditions</td>
<td>• OK ↔ nonlinear dynamics</td>
</tr>
<tr>
<td>Modeling:</td>
<td>• Easy interpretations; analytical computations; (partly) optimal inference framework</td>
<td>• Nonlinear network dynamics: closer to biophysics but harder to analyze</td>
</tr>
</tbody>
</table>
Multiple choices ($n > 2$ stimuli)
Multiple choices ($n > 2$ stimuli)

- Observation: Hick’s law (1952) (or Hick-Hyman law)

average reaction time (RT) for a correct identification among $n$ possibilities:

$$<\text{RT}> = a + b \log n$$

If processing time is controlled (decision asked to be made at a given time $T$),
extracted Shannon information $= k \ T$
Multiple choices \((n > 2 \text{ stimuli})\)

- Analysis based on competing accumulators (stochastic race model)

  *Usher, Olami, McClelland, 2002*

\[
dx_i = \mu_i dt + \sigma dW_i \quad i = 1, \ldots, n
\]

\[
\mu_1 = \mu \quad i \neq 1, \quad \mu_i = 0
\]

\[
g_\mu(\theta, t) = \frac{\theta}{\sqrt{2\pi\sigma^2t^3}} \exp\left(-\frac{(\theta - \mu t)^2}{2\sigma^2t}\right) \quad g_0(\theta, t) = \frac{\theta}{\sqrt{2\pi\sigma^2t^3}} \exp\left(-\frac{\theta^2}{2\sigma^2t}\right)
\]

Probability of correct choice \(P(n, \theta)\)?

Computation \(\rightarrow\) if decision efficiency kept constant, \(\theta(n)\) affine in \(\log n\) and \(<\text{reaction time}> \sim \theta(n)\) 

Hence, Hick’s law
Multiple choices \((n > 2 \text{ stimuli})\)

\[ \mu_1 = \mu \quad i \neq 1, \quad \mu_i = 0 \]

If decision taken at a given time \(T\).

Extracted information after a given time \(T\)?

Simple hypothesis:

• equiprobable stimuli

• if error, \(\text{proba( decide } i > 1) = 1/(n-1)\)

\[ I(n, T) = \ln n + p(n, T) \ln p(n, T) + (1 - p(n, T)) \ln \frac{1 - p(n, T)}{n - 1} \]

\[ p(n, T) \quad = \text{proba correct response at time } T \]

\(T=0\): in the absence of any information, \(p(n,0)=1/n\)

At short times, \(p(n,T) = (1/n) \left( 1 + \varepsilon \right) \rightarrow I(n,T) \text{ of order } \varepsilon^2\)

Race model \(\rightarrow \varepsilon \text{ of order } \sqrt{T} \rightarrow I(n,T) \text{ is of order } T\)

which one of the Hick’s observations.
Decision making:
on (some of the many) topics not discussed in this course
Decision making: on (some of the many) topics not discussed in this course

- Decision making in socio-economic context

**Behavioral economics, behavioral game theory, neuroeconomics**
Herbert Simon *bounded rationality*
Daniel Kahneman, Amos Tversky
Colin Camerer
Ernest Fehr, Simon Gächter

**Social psychology**
Stanley Milgram
Solomon E. Asch (*Opinion and social pressure*, 1955)
Serge Moscovici

Roles of expected reward/punishment, emotion, trust, social pressure...

- Intertemporal choices
Moreira et al 2016, Neurobiological bases of intertemporal choices: A comprehensive review
Ortega & Tishby, 2016 Memory shapes time perception and intertemporal choices
  (role of coding efficiency of sensorimotor representation, information theoretic approach)

- Executive control
  *Cogmaster Course ‘Action, décision, volition’ (E. Koechlin)*
Social conformity

- Conformity, Social norms – peer group pressure; conforming to the prevailing conventions; tradition, culture transmission

- Social psychology: Asch conformity experiment (1951, 1955)

When individual judgment conflicts with a group, the individual will often conform his judgment to that of the group.
Social conformity

• Conformity, Social norms – peer group pressure; conforming to the prevailing conventions; tradition, culture transmission

Social psychology: Asch conformity experiment (1951, 1955)

When individual judgment conflicts with a group, the individual will often conform his judgment to that of the group

Neurobiological correlates of social conformity (Berns et al 2005)

http://www.ccnl.emory.edu/greg/

- brain regions classically associated with perception can be altered by social influences

- independence (non conformity) is found to be associated with subcortical activity changes indicative of emotional salience (amygdala activation ↔ emotional load associated with standing up for one’s belief)
Neurobiological correlates

**Figure 1.** Participants were presented with pairs of three-dimensional objects on a computer screen during a mental rotation period, and they had to decide whether the objects were the “same” (can be rotated to match) or “different” (no rotation can make them match). To induce social conformity, each trial began with the objects being shown first to a group of peers (Group; top panel). In actuality, the group was composed of actors, and their responses were predetermined. After a variable-duration decision phase, the collective response of the group was displayed to the participant. This ensured that the participant would see the group’s response. After 3 sec, the same pair of objects was displayed to the participant. In the example shown, the objects are different, but the group has unanimously said they are the same (the participant has not responded yet). The participant responded with a button press, indicating whether the objects were the same or different. Trial types were randomized across three conditions: group correct, group incorrect (as shown), and baseline (responses blinded to participant with an “X”; bottom panel). One run of 48 trials was performed with the group, and another run of the same 48 trials was performed with the group replaced by computers (bottom panel), in which the faces of the group were substituted with computer icons. The order of group and computer runs was counterbalanced across participants and gender.
Neurobiological correlates

Conformity was defined as agreeing with the exogenous source of information, either peers or computers, when the information was wrong. Conformity was measured behaviorally by the change in error rates of the participants between their baseline performance and the conditions in which exogenous information was presented.

The baseline error rate was computed for each participant from the trials in which no group (or computer) information was given (mean 13.8%, SEM 2%).

The error rate increased to 41% (SEM 5%) when the group gave wrong information, which was significantly greater than when the computers gave wrong information (mean 32%, SEM 4%) [paired t (32) 3.55, p < .001].

*Figure 2.* Mean error rates as a function of the source (Computers or Group) and type (Correct or Incorrect) of information. The actual number of errors in the Computers and Group conditions are shown on the right-hand scale (the number of errors in the baseline condition must be multiplied by two, because there were twice as many trials in this condition). Repeated-measures analysis of variance revealed a large main effect of the type of information (Correct, Incorrect, or None) on error rates \(F(2,31) = 31.29, p < .0001\), and post hoc comparisons indicated that incorrect information resulted in significantly greater error rates (\(p < .0001\)) than both baseline (green) and correct information (which were not significantly different from each other, \(p = .348\)). The interaction of the source of information (Group or Computers) with the type of information (Correct, Incorrect, or None) was also significant \(F(2,31) = 6.53, p < .004\), and the post hoc comparison indicated that the error rate when the group gave wrong information (mean 41%, SEM 5%) was significantly greater than when the computers gave wrong information (mean 32%, SEM 4%) [***paired t(32) = 3.55, p < .001].
There were significant differences in RTs, and these differences depended on several factors (Figure 3). After adjusting for the effect of Same/Different stimuli, there was a significant lengthening of RT when external information was present \( F(2,579) = 20.27, p < .0001 \). But restricting the analysis to trials in which incorrect information was provided, there was no significant difference in RT between going with (i.e., Conformity) or against (i.e., Independence) the information \( F(1,190) = 2.65, p = .105 \), indicating that participants did not take longer for one behavior or the other. Notably for the subsequent image analysis, the source of the external information, either Group or Computers, also did not have a significant effect on RT \( F(1,576) = .554, p = .457 \).
Social conformity


- *Social Influence and Perceptual Decision Making: A Diffusion Model Analysis*
- *Social conformity is due to biased stimulus processing: electrophysiological and diffusion analyses*

Experiments: EEG

Analysis: diffusion model analysis of reaction time data to uncover the neurocognitive processes underlying social conformity in perceptual decision-making.
Social conformity

EEG experiments and
Drift diffusion model analysis of reaction time data

**Initial position**

- \( t_0 \): total non-decisional processing time

**drift rate**

**Example of a stimulus**

**Task:** dominant color?
(blue or orange)

**Trial sequence**

- Half stimuli: half/half pixels in blue/orange
- Half stimuli: dominant color well above chance level (performance 80%)
Social conformity

- Markus Germa et al, 2016

Social conformity is due to biased stimulus processing: electrophysiological and diffusion analyses

Experiment: EEG measuring stimulus evoked potentials (SEPs), lateralized readiness potentials (LRPs)

- Analysis of EEG signals: participants under social influence initially activated choices in line with the majority even when they finally chose against the majority.

- Analysis of reaction times: diffusion model analysis of reaction time data

  Conformity: correlated with a change in the drift rate, implying that participants predominantly accumulated stimulus information favoring the majority response

  → longer reaction times when decision against the majority.

→ the opinion of others can cause individuals to selectively process stimulus information supporting this opinion, thereby inducing social conformity.

→ this effect is present even when individuals do not blindly follow the majority but rather carefully process stimulus information.
Perceptual Decision making

Categorical perception

see slides
Supplementary informations
monkeys performing a direction discrimination task commit to a choice when the accumulated evidence reaches a threshold level (or bound), sometimes long before the end of stimulus.

**A**, Probability of correct response as a function of stimulus duration for the five motion strengths. The trials are divided into 20 quantiles based on stimulus duration (n1024 trials per data point).

**B**, Behavioral discrimination thresholds deviate from perfect accumulation for longer viewing duration. The discrimination thresholds were estimated by fitting cumulative Weibull function to the 20 columns of points in **A**. The threshold is motion strength supporting 81.6% correct choices. The red line shows the expected change of threshold for perfect accumulation of evidence. Error bars represent SE

*Kiani, Hanks, Shadlen, The Journal of Neuroscience, 2008*
i ∈ {L, R}, \quad r_i(t) = f \left( l_{i,\text{tot}}(t) \right), \quad f(l) = \frac{a l - b}{1 - \exp[-\beta (a l - b)]}

\begin{align*}
    l_{L,\text{tot}}(t) &= J_{LL} S_L(t) - J_{L,R} S_R(t) + I_{\text{stim},L}(t) + I_{\text{noise},L}(t) \\
    l_{R,\text{tot}}(t) &= J_{RR} S_R(t) - J_{R,L} S_L(t) + I_{\text{stim},R}(t) + I_{\text{noise},R}(t)
\end{align*}

\begin{align*}
    i \in \{L, R\}, \quad \frac{dS_i}{dt} &= -\frac{S_i}{\tau_S} + \left( 1 - S_i \right) f \left( l_{i,\text{tot}} \right) \\
    I_{\text{stim},L} &= J_{\text{ext}} (1 \pm c) \quad \quad I_{\text{stim},R} = J_{\text{ext}} (1 \mp c)
\end{align*}

i \in \{L, R\}, \quad \tau_{\text{noise}} \frac{dl_{\text{noise},i}}{dt} = -(l_{\text{noise},i}(t) - l_0) + \sqrt{\tau_{\text{noise}} \sigma_{\text{noise}}} \eta_i(t)

Decision threshold \theta
Sequential effects
biases in favor of the decision made at the previous trial

Post-error adjustments
depending on the experimental conditions:

Post-Error Slowing (PES): longer reaction times after an error trial.

In some less frequent cases, reverse effect, Post-error quickening (PEQ): shorter reaction times after an error trial.

Post-error improvement in accuracy (PIA): better accuracy after an error trial.

The effects are observed even in the absence of feedback on the correctness of the decisions

Danielmeier and Ullsperger 2011
non specific inhibitory input delivered once a decision is made

\[ i \in \{L, R\}, \quad r_i(t) = f(l_{i, \text{tot}}(t)), \quad f(l) = \frac{a l - b}{1 - \exp[-\beta (a l - b)]} \]

\[ l_{L, \text{tot}}(t) = J_{LL} S_L(t) - J_{L,R} S_R(t) + I_{\text{stim}, L}(t) + I_{\text{noise}, L}(t) + I_{\text{CD}}(t) \]

\[ l_{R, \text{tot}}(t) = J_{RR} S_R(t) - J_{R,L} S_L(t) + I_{\text{stim}, R}(t) + I_{\text{noise}, R}(t) + I_{\text{CD}}(t) \]

\[ i \in \{L, R\}, \quad \frac{d S_i}{d t} = - \frac{S_i}{\tau S} + (1 - S_i) f(l_{i, \text{tot}}) \]

\[ I_{\text{stim}, L} = J_{\text{ext}} (1 \pm c) \quad I_{\text{stim}, R} = J_{\text{ext}} (1 \mp c) \]

\[ i \in \{L, R\}, \quad \tau_{\text{noise}} \frac{d I_{\text{noise}, i}}{d t} = -(I_{\text{noise}, i}(t) - I_0) + \sqrt{\tau_{\text{noise}} \sigma_{\text{noise}}} \eta_i(t) \]

\[ I_{\text{CD}}(t) = \begin{cases} 0 & \text{during stimulus presentation} \\ -I_{\text{CD, max}} \exp\left(-\frac{(t - t_D)}{\tau_{\text{CD}}}\right) & \text{after the decision time, } t_D \end{cases} \]
Post-Error Slowing/Post-Error Quickening  

A  

Corollary discharge (nA)  

Coherence level (%)  

B  

Post-error Improvement in Accuracy  

C  

Corollary discharge (nA)  

Coherence level (%)  

K Berlemont & JPN 2018
PES regime

Assuming previous decision = $R$, relaxation dynamics (dash curves), and next trial dynamics (full curves), for post-error and post-correct cases.

Top plots: the new decision is identical to the previous one; Bottom plots: the new decision is the opposite of the previous one.

All trajectories are followed during the same duration, as if there was no threshold. Actual decision occurs at the crossing of the threshold (gray dashed lines).

Black dot: neutral attractor of the relaxation dynamics.

Green dashed and dashed-dotted lines: boundary between the basins of attraction of the attractors associated to the next stimulus.
Fig. 3.1: A. Schema of synaptic transmission. Upon arrival of a presynaptic spike, neurotransmitter spills into the synaptic cleft and is captured by postsynaptic receptors.

B. Schema of a postsynaptic AMPA receptor of an excitatory synapse. When glutamate is bound to the receptor, sodium and potassium ions can flow through the membrane.

Leaky Integrate-and-Fire (LIF) model

Membrane potential, $V(t)$
resting potential $V_L = -70mV$,
spiking threshold $V_{th} = -50mV$,
reset potential $V_{reset} = -55mV$.

Membrane leak conductance and membrane time constant: $g_L = 25nS$ and $\tau = 20ms$ for pyramidal cells (excitatory cells),
$20nS$ and $10ms$ for interneurons (inhibitory cells).

Simplest model: Below $V_{th}$, the membrane potential of the cell $V(t)$ is governed by

$$C_m \frac{dV(t)}{dt} = -g_L(V(t) - V_L) - I_{syn}(t)$$

(synaptic current < 0 for excitatory input)

When $V(t)$ reaches $V_{th}$, the cell generates an action potential in the form of a spike (a delta function).

After that, the cell stays in a short absolute refractory period (2ms for pyramidal cells and 1ms for interneurons), where the membrane potential is clamped at $V_{reset}$.

*Louis Lapicque, 1907*

*Brunel and Wang 2001*

*Wong & Wang 2006, Supplementary Information*

*Gerstner et al, book online, [https://neuronaldynamics.epfl.ch/online/Ch1.S3.html](https://neuronaldynamics.epfl.ch/online/Ch1.S3.html)*
Recurrent networks of Leaky Integrate-and-Fire (LIF) neurons

Figure 1. The cortical network model. Pyramidal cells (E cells) send connections to other pyramidal cells through AMPA and NMDA synapses. Interneurons (I cells) send GABAergic connections to pyramidal cells and other interneurons. Both receive excitatory connections from other cortical areas. Pyramidal cells can be functionally divided in several groups according to their selectivity properties. Group #1 is selective to object #1, etc. Cells within a group have relatively stronger connections (modulated by $w_+ > 1$), while connections between different groups are relatively weaker (modulated by $w_- < 1$). See Methods for more details.

Brunel and Wang 2001
Recurrent networks of
Leaky Integrate-and-Fire (LIF) model

Mean-field analysis (large number of cells)

\[
\tau_E \frac{dV(t)}{dt} = -(V(t) - V_L) + \mu_E + \sigma_E \sqrt{\tau_E} \eta(t)
\]

\[
\langle \eta(t) \rangle = 0
\]

\[
\langle \eta(t)\eta(t') \rangle = \frac{1}{\tau_{\text{AMPA}}} \exp \left( -\frac{|t - t'|}{\tau_{\text{AMPA}}} \right)
\]

Activity rate of the excitatory cells: self consistent equation

\[
\nu_E = \phi(\mu_E, \sigma_E)
\]

(and similar equation for the inhibitory activity rate).

Brunel and Wang 2001