Breaking down hierarchies of decision-making in primates

Alexandre Hyafil*, Rubén Moreno-Bote1,2

1CBC, DTIC, Universitat Pompeu Fabra, Barcelona, Spain; 2Serra Húnter Fellow Programme, Universitat Pompeu Fabra, Barcelona, Spain

Abstract Possible options in a decision often organize as a hierarchy of subdecisions. A recent study concluded that perceptual processes in primates mimic this hierarchical structure and perform subdecisions in parallel. We argue that a flat model that directly selects between final choices accounts more parsimoniously for the reported behavioral and neural data. Critically, a flat model is characterized by decision signals integrating evidence at different hierarchical levels, in agreement with neural recordings showing this integration in localized neural populations. Our results point to the role of experience for building integrated perceptual categories where sensory evidence is merged prior to decision.

DOI: 10.7554/eLife.16650.001

Introduction

Coffee with Jules (if so, which cafe?) or cinema with Jim (if so, what movie?)? A recent study by Lorteije and colleagues investigated how perceptual mechanisms implement such hierarchically-structured decisions that fill up our daily lives (Lorteije et al., 2015). Monkeys performed saccades to one of 4 possible targets based on the information provided at the primary branching and at secondary branching points (the ‘correct’ and ‘incorrect’ branching points) leading to the targets (Figure 1A). Patterns of responses convincingly indicated that monkeys can integrate information from all branching points in parallel. But does the decision space mimic the hierarchical organization, with parallel decisions going on (about Jules/Jim, coffee place, movie) (Figure 1B), or does it directly compare final options (with Jules at Moe’s vs. Sicario with Jim vs. etc.) (Figure 1C)? Lorteije and colleagues report two behavioral and two neural effects that they argue speak unanimously in favor of the former hierarchical model against the latter non-hierarchical ‘flat model’ of decision-making. We show in contrast that all four effects can equally (and more parsimoniously) be explained by the flat model of decision-making, which is also perfectly compatible with the new effects from the same dataset described in the companion paper by Zylberberg and colleagues (Zylberberg et al., 2017).

Results

First, stimulus difficulty at the primary branch (L1) was shown to have no influence on the performance at the secondary branch (L2), a result that was replicated by a race-model implementation of hierarchical decision-making, but not of the flat decision-making. However, this result seems a particular feature of their specific choice of implementation of the race model (Vickers, 1979; Drugowitsch et al., 2014), which included neither inhibition between option representations, nor activation rectification (i.e. enforcing non-negative unit activation), two classical ingredients of race models (Usher and McClelland, 2001; Tsetsos et al., 2012; Churchland and Ditterich, 2012). Inhibition between option representations and rectification may underlie the well-known reduction of choice-related neural activity when more choice alternatives are provided (Churchland and Ditterich, 2012). We simulated a race model implementation of the flat model with both rectified
activation, cross-inhibition and self-excitation, whereby each of the four options competed during accumulation of evidence (Figure 1D, see Material and methods). Self-excitation models the instability present at the initial point of the race in attractor models of decision-making (Roxin and Ledberg, 2008) and can be at the heart of well-known urgency signals to speed up decisions (Drugowitsch et al., 2012). Noise in the model did not scale with stimulus intensity, in line with recent results suggesting that noise in perceptual accumulation tasks is associated with the accumulation rather than with the sensory process (Drugowitsch et al., 2016), and as it is typically assumed in drift-diffusion models of decision making (Gold and Shadlen, 2007). We used a non-absorbing decision threshold (i.e. activity after the decision as not bounded), but found the same results for simulations with an absorbing bound. Parameters were tuned to reproduce qualitatively the proportion for each of the four possible response types, as well as the impact of each sample in the stream and the psychometric curve for both L1 and L2 decision (Figure 2—figure supplement 2A–D). The impact of L1 difficulty onto L2 for the flat model indeed disappeared when we used this common implementation of the race model (Figure 2—figure supplement 2E).

In the companion paper (Zylberberg et al., 2017), Zylberberg and colleagues question the generality of this finding, arguing that it may not be compatible with the pattern of short reaction times they provide in a new analysis for the same monkey dataset. However, our mathematical analysis (Appendix 1) shows that a clear influence of L1 difficulty onto L2 performance emerges principally when L1 difficulty strongly modulates reaction times, and thus the time of integration of L2 evidence. Short reaction times with low modulation by task difficulty as described in the companion article are thus perfectly compatible with lack of influence of L1 difficulty onto L2 performance. This result was
indeed reproduced in a simulation where the threshold was lowered to produce shorter reaction times, and the boundary was eliminated for the first 10 samples (Figure 2A–F). This choice of the threshold implements a form of time-dependent, collapsing bound (Churchland and Ditterich, 2012; Drugowitsch et al., 2012) and it is consistent with the minimum viewing time imposed on monkeys (Figure 2). Without such time-dependent bound, the model can produce either a large proportion of premature responses or very large mean reaction times. The discrepancy between results from these simulations with those performed in the companion paper (who do find dependency of L2 performance on L1 difficulty with short reaction times) may emerge from early responses (<500 ms) in easy trials that are present in their simulations, but prohibited in our simulations by the absence of decision boundary for the first 10 samples.

The second interesting observation from monkey behavior reported by Lorteije and colleagues was that L1 decisions were biased towards the branch that leads to the easier L2 decision. The effect

---

Figure 1. Hierarchical vs. flat models of perceptual decision during a hierarchically-structured visual task. (A) Structure of the task. At each trial monkeys must detect the correct option out of four possible responses based on the visual information provided at the primary branching point L1 and at two secondary branching points L2 and L2'. Visual information consists of segments of flickering luminosity at the start of each branch (color segments in our depiction; visual samples changing every 50 ms for a total period of 1000 ms). Animals must make a saccade towards the final point that passes through branches of maximal luminosity; that is, must decide based on information scattered across the visual field. Each of the four responses is categorized as TT, TD, DT or DD depending on whether it corresponds to a target T (correct branch) or distractor D (incorrect branch) at first and second branching points. Detailed description of the task can be found in [Lorteije et al., 2015]. (B) Hierarchical decision model of perception. In the hierarchical model, parallel decision processes run at each branching point (L1, L2 and L2) and are integrated into a motor response at a later stage. It can be implemented as a race model composed of three races, each with two possible sub-choices. (C) Flat decision model of perception. In the flat model, the decision space is composed of the four possible final responses, so for each response the animal must sum the information provided at the corresponding primary and secondary branches (here depicted by the sum of the two luminosity signals). (D) Implementation of the flat decision model. (Left panel) Four units coding for the four possible responses integrate information from both L1 and L2 branches leading to that response, as represented by the pattern of connections from sensory units (coding for instantaneous sensory value). Connectivity include self-excitation as well as homogeneous cross-inhibition between all units. Black and red arrows indicate respectively excitatory and inhibitory connections. (Right panel) Simulation for one trial, depicting the activity of each unit across time during perceptual integration. Activity is bounded to positive values (rectification). When activity of one unit reaches the decision threshold, the related response is selected.

DOI: 10.7554/eLife.16650.003
could only be explained in the hierarchical model by invoking an extra modulatory signal passed on from L2 to L1 that must be carefully tuned (and was not implemented in the race model of [Lorteije et al., 2015]). By contrast, such effect is readily accounted for by the flat model, as a strong signal at a secondary branch will boost the chances of selecting the corresponding final option, and
thus bias towards selecting the L1 path leading to this option. Indeed, the effect was reproduced in
the simulations (Figure 2G). This relates to one important advantage of the flat model over the hier-
archical one: the flat model, by integrating the strength of evidence from each level, takes optimally
into account uncertainty in each of the decisions, leading to more accurate responses. By contrast,
the hierarchical model integrates decisions at each level independently of the level of evidence in
support of each decision. This can only be amended by ad hoc mechanisms such as that proposed
by Lorteije and colleagues, that probably do not scale up adequately when more than two options
are available at each level.

At the physiological level, neural groups in visual cortex integrated information conveyed at the
primary and secondary branching points leading to the path in their receptive field. Selection signals
were shown to first differentiate options at the level of secondary branches irrespective of whether
the branch is the correct or incorrect one (L2 or L2' branching), and subsequently grow larger for the
L2 than for L2’ branching. In the hierarchical model, this can only be explained by referring to a mod-
ulating signal once decision is reached in L1 that differentially modulates the L2 race signals corre-
sponding to the selected and non-selected L1 branches. In the flat model, such dynamics emerges
naturally with activation rectification, because activation corresponding to the two incorrect options
in the incorrect L1 branch vanish as L1 signals favor the two alternative options, and so their differ-
ence is also reduced (Figure 3A). Indeed, activation rectification plays a role in the dynamics of
recorded neural responses, that reach a floor value (0) in the final part of the integration period in
non-selected branches (Figure 4 of [Lorteije et al., 2015]). Finally, an interaction between L2 and L2’
selection signals was reported: clear evidence in favor of one of the two options in L2 reduced the
selection signal in L2’, and vice versa. In the hierarchical model, this would require complex modula-
tory signals passing on from L2 to L1 to L2’. By contrast, both effects are observed in the flat model
(Figure 3B): strong evidence for one option will decrease the activation of all other three options
through inhibition, increase their chance of collapsing at the zero boundary, and thus reduce the
selection signal in the opposite secondary branch.

Overall we show that all four observations that were taken as evidence in favor of the hierarchical
model could be accounted for with a standard race-model implementation of the flat model. These
observations were robust and did not rely on fine tuning of the parameters. Table 1 summarizes
how each of these observed properties depend on the features of the model. Note that all these
features are classical constituents of race models and not ad hoc mechanisms. Overall the flat model
provides a more parsimonious explanation of the data, as it does not require appending modulatory
signals between parallel decisions as the hierarchical model does.

These behavioral and neural effects reported in the original study provide however no univocal
evidence in favor of either model. One fundamental difference between the two is indeed that selec-
tion signals in the flat model mix evidence from both L1 and L2 branches, while the hierarchical
model predicts unmixed selection signals (the influence across branches can only occur posterior to
decision). [At this point, an important distinction has to be made in the flat model between localized
activations, which indeed mix evidence from both branches, and selection signals at L2, extracted by
looking at the difference between two units in the same L1 branch, and which as shown above are
largely insensitive to L1 signals]. In the companion paper, Zylberberg et al. now provide data show-
ing that selection signals in at least 3 out of 4 L2 branches mixes evidence from both L1 and L2
branches (their Figure 4). We believe this observation is most compatible with the flat model and by
itself rules out the hierarchical model that relies on complete neural segregation of integration of L1
and L2 evidence (although the possibility remains that these level-mixing integrative neural signals
are completely non-causal in monkey decisions). Our simulations reproduce these effects: signals in
TT is larger for stronger L1 evidence, while signals in DT and DD are weaker (p<10^{-9}, Figure 3C;
see Also Appendix 2). As pointed out by Zylberberg and colleagues, our simulations also display a
positive modulation in TD signals, unlike the null effect found in monkey data. However, despite a
single source of inhibition, the modulation was not equally strong in all four branches: indeed, it was
by far the weakest precisely in the TD branch (Figure 3C). This weaker effect may have explained
the lack of significance in monkey data. Moreover, modulation in TD could be reduced or abolished
if the flat model implied stronger inhibition between options related to the same L1 branch (TT-TD
and DT-DD) than between options related to distinct L1 branches (e.g. TT-DT, TT-DD). Stronger inhi-
bition between local circuits is indeed a general pattern of cortical connectivity (Douglas and Mar-
tin, 2004; Lund et al., 2003).
Zylberberg and colleagues produced a last analysis of the original dataset, showing that in the flat model errors in L1 are associated with higher sensitivity at L2, whereas monkeys display no such effect. While we acknowledge that this result challenges the current implementation of the flat model, it is at this point equally unknown whether the hierarchical model proposed by the authors could avoid this feature (the reward maximization introduced in the hierarchical model to account for the influence of L2 bias onto L1 choice may produce the same interaction).

**Discussion**

It is unclear whether selection signals recorded in visual cortex are generated locally or reflect feedback process from higher regions where integration of evidence takes place. The flat model is arguably more consistent with the latter hypothesis, as it implies integration from and inhibition across distant locations in visual field, which are more typically associated with higher cortical regions (Wimmer et al., 2015). In any case, these selection signals certainly represent neural markers for a specific integration process along one subbranch.

One important limitation of flat models is they require to learn high-order representations of the environment that can appropriately integrate evidence from all relevant sensory sources, i.e. the structure of connectivity described in Figure 1D may take time to be acquired (Garrard et al., 2015).
Here, monkeys performed ~60,000 trials each, possibly long enough to learn appropriate global representations linking all visual cues relevant to each response. When such time is not afforded, the system may rely on less efficient strategies such as a hierarchical model. Indeed, the comparison of flat and hierarchical models in this visual task sheds new light to the ancient debate of whether information from distinct sources is integrated before or after the decision stage, analogous respectively to the flat and hierarchical strategies. In multimodal integration such as object localization or motion detection, different modalities provide complementary cues about common objects or features of the environment (object motion, phoneme identity, etc.), so over the lifetime the brain can learn the appropriate crossmodal representations and integrate bimodal information directly over those representations. Indeed, in such context both sources of information are merged prior to decision (Körding and Wolpert, 2004). By contrast, when subjects must detect the presence of either a visual or an auditory cue, requires to mapping arbitrarily two distinct unimodal signals into a single response, the relevant crossmodal representations are not formed, and therefore integration could by default only be formed following unimodal decisions, as it has been found experimentally (Otto and Mamassian, 2012). One important hypothesis we make is that the level of integration could strongly depend on experience, gradually switching from post-decision (i.e. hierarchical) to pre-decision (i.e. flat) integration.

Finally, an important distinction has to be made between the hierarchical vs. flat nature of the integration process, and the serial vs. parallel nature of the integration process. While the former has to deal with the level and the structure of the representations at which integration takes place before reaching a decision, the latter corresponds to whether evidence from different sources can be integrated at the same time in these representations. The flat model is perfectly compatible with serial integration of evidence, for example if attentional constraints limit the capacity to process evidence from distant visual locations, such as when subjects must integrate from three distinct levels (Zylberberg et al., 2012).

In summary, despite premature conclusions, we think that the experimental framework developed by Lorteije and colleagues opens a new promising venue for understanding the level at which evidence is accumulated and individual perceptual decisions are taken in ecological settings.

**Methods**

We present here the equations governing the flat race model of decision-making used for simulations. Our implementation of the flat model departs from the one in [Lorteije et al., 2015] in the following aspects, which are typically subsumed in many standard implementations: (1) added noise is constant instead of being proportional to signal strength, (2) there is a positive loop (i.e. negative leak) in the integration process and mutual inhibition between competitors and (3) activities cannot be negative (i.e. activation rectification). The variable $x_i^t$ represents the activity of the activation unit $i$ (from 1 to 4) at sample $t$, and evolves according to:

$$\Delta x_i^t = I_0 + \alpha x_{i-1}^t - \beta \sum_{j \neq i} x_j^{t-1} + I_i^t + N(0, \sigma)$$

where $I_0$ is the constant input, $\alpha$ is the auto-excitation term (negative if leaking, positive if positive loop providing bistability), $\beta$ is the inhibition strength, $I_i^t$ is the sensory evidence at sample $t$, and the last term represents white noise of variance $\sigma$. Inhibition is homogeneous and all-to-all between activations units, that is, each unit inhibits equally the other unit from the same branch and the two units

| Effect | Required model features |
|--------|-------------------------|
| Independence of L2 from L1 difficulty | Signal-independent noise, low dependence of RTs on L1 difficulty |
| Bias of L1 choice by L2 difficulty | None |
| Amplification of L2 signals by L1 choice | Activation rectification |
| Cross-talk between L2 and L2’ signals | Activation rectification |

Table 1. Each of reported behavioral and neural effects and the associated features from the flat decision model required to display such effects.
from the alternative branch. Sensory evidence integrates information from the primary and secondary branching points:

\[ I'_i = k_1a'_i + k_2b'_i \]

\( k_1 \) and \( k_2 \) represent the sensitivity to evidence at level 1 and 2 respectively, \( a'_i \) represents the information provided at level 1 in favor of the corresponding branch (i.e. the difference between instantaneous luminosity in that branch and luminosity in the alternative branch at sample \( t_i \)), and \( b'_i \) represents the information provided at level 2 in favor of the corresponding branch.

We enforce non-negative values for unit activity by using rectification:

\[ x'_i = \max(x'_{i-1} + \Delta x'_i, 0) \]

All units are initiated from the same starting point \( x'_0 = 0.5 \), and the decision is reached whenever any of the units reaches threshold \( K \) (Figure 1C). If no decision is reached after presentation of all samples, the response corresponding to the unit with highest final activity is selected. Parameters are: input strength at primary branching point \( k_1 = 0.016 \), at secondary branching points \( k_2 = 0.012 \), auto-excitation \( \alpha = 0.1 \), inhibition \( \beta = 0.07 \), constant input \( I_0 = 0.5 \), decision threshold = 50, initial values \( x'_0 = 0.5 \), white noise variance = 1. We chose parameters to reproduce qualitatively the monkey behavioral and neuronal data. We simulated 100,000 trials, which is the same order of magnitude as used in the original experiment. All analyses performed on simulated data strictly reproduced those realized in the original experiment. Results from these analyses are presented in Figure 2—figure supplement 2.

In the simulation set of Figure 2, designed to reproduce the pattern of reaction times described in the companion paper, we lowered the decision threshold to 30 to produce shorter reaction times. We introduced a minimum integration time of 10 samples (i.e. no boundary for the first 10 samples), consistent with the minimal time of 500 ms after stimulus onset monkeys had to wait before performing a responses saccade. We also changed inhibition to 0.05 and auto-excitation to 0.12. All other parameters were unchanged.

A matlab script for all simulations and analyses is available at http://bit.ly/hyafilmoreno2017.

Acknowledgements
The authors thank Jan Drugowitsch for his comments on the manuscript.

Additional information

Funding

| Funder                          | Grant reference number       | Author           |
|---------------------------------|------------------------------|------------------|
| European Commission             | Marie Curie IEF - CEMNET (agreement 629613) | Alexandre Hyafil |
| Ministerio de Economía y Competitividad | PSI2013-44811-P | Rubén Moreno-Bote |

The funders had no role in study design, data collection and interpretation, or the decision to submit the work for publication.

Author contributions

AH, Conceptualization, Software, Formal analysis, Funding acquisition, Investigation, Visualization, Methodology, Writing—original draft, Project administration, Writing—review and editing; RM-B, Supervision, Investigation, Writing—original draft, Project administration, Writing—review and editing

Author ORCIDs

Alexandre Hyafil, http://orcid.org/0000-0002-0566-651X
References

Brunton BW, Botvinick MM, Brody CD. 2013. Rats and humans can optimally accumulate evidence for decision-making. *Science* **340**:95–98. doi: 10.1126/science.1233912, PMID: 23559254

Churchland AK, Ditterich J. 2012. New advances in understanding decisions among multiple alternatives. *Current Opinion in Neurobiology* **22**:920–926. doi: 10.1016/j.conb.2012.04.009, PMID: 22554881

Douglas RJ, Martin KA. 2004. Neuronal circuits of the neocortex. *Annual Review of Neuroscience* **27**:419–451. doi: 10.1146/annurev.neuro.27.070203.144152, PMID: 15217339

Drugowitsch J, Moreno-Bote R, Churchland AK, Shadlen MN, Pouget A. 2012. The cost of accumulating evidence in perceptual decision making. *Journal of Neuroscience* **32**:3612–3628. doi: 10.1523/JNEUROSCI.4010-11.2012, PMID: 22423085

Drugowitsch J, Moreno-Bote R, Pouget A. 2014. Relation between belief and performance in perceptual decision making. *PLoS One* **9**:e96511. doi: 10.1371/journal.pone.0096511, PMID: 24816801

Drugowitsch J, Wyart V, Devauchelle AD, Koechlin E. 2016. Computational Precision of Mental Inference as Critical Source of Human Choice Suboptimality. *Neuron* **92**:1398–1411. doi: 10.1016/j.neuron.2016.11.005, PMID: 27916454

Garrard P, Perry R, Hodges JR. 1997. Disorders of semantic memory. *Journal of Neurology, Neurosurgery & Psychiatry* **62**:431–435. doi: 10.1136/jnnp.62.5.431, PMID: 9153596

Gold JI, Shadlen MN. 2007. The neural basis of decision making. *Annual Review of Neuroscience* **30**:535–574. doi: 10.1146/annurev.neuro.29.051605.113038, PMID: 17600525

Körding KP, Wolpert DM. 2004. The loss function of sensorimotor learning. *PNAS* **101**:9839–9842. doi: 10.1073/pnas.0308394101, PMID: 15210973

Lorteije JA, Zylberberg A, Ouellette BG, De Zeeuw CI, Sigman M, Roelfsema PR. 2015. The formation of hierarchical decisions in the visual cortex. *Neuron* **87**:1344–1356. doi: 10.1016/j.neuron.2015.08.015, PMID: 26365766

Lund JS, Angelucci A, Bressloff PC. 2003. Anatomical substrates for functional columns in macaque monkey primary visual cortex. *Cerebral Cortex* **13**:15–24. doi: 10.1093/cercor/13.1.15, PMID: 12466211

McClelland JL, Rumelhart DE. 1985. Distributed memory and the representation of general and specific information. *Journal of Experimental Psychology: General* **114**:159–188. doi: 10.1037/0096-3445.114.2.159, PMID: 3159828

Otto TU, Mamassian P. 2012. Noise and correlations in parallel perceptual decision making. *Current Biology* **22**:1391–1396. doi: 10.1016/j.cub.2012.05.031, PMID: 22771043

Roxin A, Ledberg A. 2008. Neurobiological models of two-choice decision making can be reduced to a one-dimensional nonlinear diffusion equation. *PLoS Computational Biology* **4**:e1000046. doi: 10.1371/journal.pcbi.1000046, PMID: 18369436

Tsetsos K, Gao J, McClelland JL, Usher M. 2012. Using Time-Varying Evidence to Test Models of Decision Dynamics: Bounded Diffusion vs. the Leaky Competing Accumulator Model. *Frontiers in Neuroscience* **6**:79. doi: 10.3389/fnins.2012.00079, PMID: 22701399

Usher M, McClelland JL. 2001. *The time course of perceptual choice: the leaky, competing accumulator model*. *Psychological Review* **108**:550–592. doi: 10.1037/0033-295X.108.3.550, PMID: 11483378

Vickers D. 1979. *Decision Processes in Visual Perception*. Academic Press.

Wimmer K, Compte A, Roxin A, Peixoto D, Renault A, de la Rocha J. 2015. Sensory integration dynamics in a hierarchical network explains choice probabilities in cortical area MT. *Nature Communications* **6**:6177. doi: 10.1038/ncomms7177, PMID: 25649611

Zylberberg A, Lorteije JAM, Ouellette BG, De Zeeuw CI, Sigman M, Roelfsema P. 2017. Serial, parallel and hierarchical decisionmaking in primates. *eLife* **6**:e17331. doi: 10.7554/eLife.17331

Zylberberg A, Ouellette B, Sigman M, Roelfsema PR. 2012. Decision making during the psychological refractory period. *Current Biology* **22**:1795–1799. doi: 10.1016/j.cub.2012.07.043, PMID: 22921368
Appendix 1

Dependence of L2 performance on L1

Lorteije and colleagues defend that a flat model would necessarily yield a dependence of L2 performance on L1 difficulty. In the flat race model described above, the selection signals at branches L2 ($s_2^t = x_1^t - x_2^t$) and at L2' ($s_2^0 = x_3^t - x_4^t$) evolve according to:

$$
\Delta s_i^t = (\beta - \alpha) s_i^t + J_i^t + N\left(0, \sqrt{2}\right),
$$

with $J_i^t = I_i^1 - I_i^2 = 2k_2b_i^t$ and $J_i^0 = I_i^3 - I_i^4 = 2k_2b_i^0$.

The impact of each sample onto L2 selection signal can be directly derived as

$$
x_i^t = -2k_2 \sum_{u=1}^t (1 + \beta - \alpha)^{t-u} b_u^t + N(0, \gamma_t^t),
$$

where $\gamma_t^t = \sqrt{2(1 - (1 + \beta - \alpha)^t)}$.

In other words the selection signals at levels 2 are only influenced by information provided at level two branches $b_i^t$, and not by information provided at level 1 $a_i^t$. It is thus expected as a general result that L2 selection does not depend on L1 difficulty nor any other L1-related variable, contrary to the predictions of Lorteije and colleagues. We detail below four factors that could in principle go against this conclusion. We found however than in practice none induced a significant bias in our simulations:

i. the above formula is only valid when activation remain above the non-negative boundary. Nevertheless we observed in our simulations that the independence of L2 performance on L1 difficulty still held, even when the zero boundary played an active role (as is the case for the chosen parameter set).

ii. the decision boundary biases towards earlier choices when L1 task is easy compared to when L1 task is hard. In turn, this would mean lower average integration time for L2 choice and thus a decrement of L2 performance. This is exactly what is observed in the original simulation of the flat race model by Lorteije and colleagues. Evidence for a relatively small decision boundary was taken from the primacy effect, whereby earlier samples had larger impacts onto the decision than later samples in the trial (their Figure 2E). However, such primacy effect can alternatively emerge from inhibition, as soon as it outweighs leak: indeed, the weight of each sample $(1 + \beta - \alpha)^{t-u}$ decreases when sample position $u$ increases (Suppl. Figure 1A). We can thus replicate primacy effect and independence of L2 on L1 difficulty by implementing a relatively high decision threshold, consistent with findings from another fixed-duration perceptual accumulation task (Brunton et al., 2013). Indeed, very similar results were observed when we used an infinite threshold.

iii. whether L2 decision corresponds to selection signals at L2 or L2' depends ultimately on which unit finally wins the race. Thus, while both L2 decision are independent of L1, the observed L2 selection signal can be influenced by L1. In practice, we found this had no impact for the parameters reported above and in a large part of the parameter space.

iv. when additive noise in the units is stimulus-dependent, i.e. if it grows larger when the intensity of the stimulus is larger (our simulations used stimulus-independent noise). In such case, since easier L1 trials correspond to stronger L1 signals, then easier L1 trials also induce larger noise added to the integration process. This could thus deteriorate L2 selection process.
Dependence of selection signals on L1 evidence

When the zero bound for unit activity is hypothesized to play no role, activity for each of the 4 units (TT, TD, DT, DD) at each time step can be decomposed as the sum of a term relative to integration of L1 information, a term relative to integration of L2 information, and a noise term:

\[
x_{TT}^t = s_1^t + s_2^t + N(0, \gamma, \sigma) \\
x_{TD}^t = s_1^t - s_2^t + N(0, \gamma, \sigma) \\
x_{DT}^t = -s_1^t + s_2^t + N(0, \gamma, \sigma) \\
x_{DD}^t = -s_1^t - s_2^t + N(0, \gamma, \sigma)
\]

The first term in each equation induces a positive correlation between evidence at L1 and activity at TT and TD units, and a negative one between evidence at L1 and activity at DT and DD units. Furthermore, the design of the experiment with three different difficulty levels for trials creates correlations between evidence at the different levels, as each difficulty level \(d\) associated with a given mean \(\mu_d\) and standard deviation \(\zeta_d\) for the intensity of the individual samples. The correlation across trials between sensory evidence at two different levels (L1 and L2/L2') and at two different sample positions (t and t') is:

\[
\rho(a^t, b^{t'}) = \frac{\text{Var}(\mu_d)}{\text{Var}(\mu_d) + <\zeta_d>}
\]

where \(\text{Var}\) and \(<\cdot>\) represent the variance and mean over the different difficulty levels, respectively. Such correlation between samples increases the correlation between TT activity and L1 evidence, but decreases the correlation between TD and L1 evidence, hence the difference observed in Figure 3C (in the other branch, the amplitude of the negative correlation with L1 evidence is enhanced for DD units and decreased for DT units). The other source of heterogeneity of the impact of L1 evidence is the rectification, which impacts more the activity of DD, DT and TD units. Overall, the flat model predicts different levels of modulation of unit activity by evidence in L1 for the four different branches, and an especially low (positive) correlation for the case of the TD unit.