Flexible control of representational dynamics in a disinhibition-based model of decision making

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# Abstract

Inhibition is crucial for brain function, regulating network activity by balancing excitation and implementing gain control. Recent evidence suggests that beyond simply inhibiting excitatory activity, inhibitory neurons can also shape circuit function through disinhibition. While disinhibitory circuit motifs have been implicated in cognitive processes including learning, attentional selection, and input gating, the role of disinhibition is largely unexplored in the study of decision-making. Here, we show that disinhibition provides a simple circuit motif for fast, dynamic control of network state and function. This dynamic control allows a novel disinhibition-based decision model to reproduce both value normalization and winner-take-all dynamics, the two central features of neurobiological decision-making captured in separate existing models with distinct circuit motifs. In addition, the disinhibition model exhibits flexible attractor dynamics consistent with different forms of persistent activity seen in working memory. Fitting the model to empirical data shows it captures well both neurophysiological dynamics of value coding and psychometric choice behavior. Furthermore, the biological basis of disinhibition provides a simple mechanism for flexible top-down control of network states, enabling the circuit to capture diverse task-dependent neural dynamics. These results suggest a new biologically plausible mechanism for decision-making and emphasize the importance of local disinhibition in neural processing.

# Introduction

Inhibition is an essential component in neural network models of decision-making. In standard decision models, pools of option-selective excitatory neurons compete in a winner-take-all selection process via feedback inhibition (Roach et al., 2023; X.-J. Wang, 2002; Wong & Wang, 2006). Generally, such inhibition is thought to be homogenous and non-selective, with a single pool of inhibitory neurons receiving broad excitation, and in turn inhibiting excitatory neurons. However, more recent empirical findings suggest that inhibitory neurons interact with the decision circuit in a more structured manner. Inhibitory neurons active in decision-making exhibit choice-selective activity on par with excitatory neurons in frontal cortex (Allen et al., 2017), parietal cortex (Allen et al., 2017; Najafi et al., 2020), and striatum (Gage et al., 2010), i .At an anatomic level, inhibitory interneurons also exhibit a remarkable diversity in morphology, connectivity, and physiological functions (Kepecs & Fishell, 2014; Markram et al., 2004; Tremblay et al., 2016). A prominent circuit motif observed in these anatomical studies is local disinhibition, in which vasoactive intestinal peptide (VIP)-expressing interneurons inhibit the neighboring interneurons expressing somatostatin (SST) or parvalbumin (PV) that inhibit dendritic or perisomatic areas in pyramidal neurons, so that locally disinhibit the activities of the pyramidal neurons in the neighboring area (Chiu et al., 2013; Fino & Yuste, 2011; Fu et al., 2014; Karnani et al., 2014, 2016; S. Lee et al., 2013; Letzkus et al., 2011; Pfeffer et al., 2013; Pi et al., 2013; Urban-Ciecko & Barth, 2016). Here we explore the computational implications of that motif in decision-making.

While disinhibitory circuit motifs have been implicated in cognitive processes including learning, attentional selection, and input gating (Fu et al., 2014; Letzkus et al., 2011; X.-J. Wang & Yang, 2018), how disinhibition functions in decision-making circuits is unknown. Local circuit inputs to the VIP neurons suggest that disinhibition may be a key mechanism for generating the mutual competition necessary for option selection in decision-making. In addition, given the existence of long-range inputs (Kepecs & Fishell, 2014; S. Lee et al., 2013; Pfeffer et al., 2013; Pi et al., 2013; Schuman et al., 2021) and neuromodulatory inputs (Alitto & Dan, 2013; Fu et al., 2014; Pfeffer et al., 2013; Prönneke et al., 2020; Rudy et al., 2011; Tremblay et al., 2016) to the VIP neurons, local disinhibition has been proposed to play a particular role in dynamic gating of circuit activity; such gating may be essential in decision circuits underlying flexible behavior, mediating top-down control of network function (Fu et al., 2014; Kamigaki, 2019; S. Lee et al., 2013; Letzkus et al., 2011; Pi et al., 2013; Schuman et al., 2021; S. Zhang et al., 2014). Here, we hypothesize that disinhibition controls a transition between information processing states, allowing a single decision-making circuit to both represent the values of alternatives and select a single best option amongst those alternatives.

Value representation is prominent in the early stage of a decision. Integrated decision variables combine outcome information such as expected gain and probability of realization. Neural firing rates in numerous decision-related brain areas vary with the integrated option values, including the frontal (Kiani et al., 2014; J.-N. Kim & Shadlen, 1999; Padoa-Schioppa, 2013; Padoa-Schioppa & Conen, 2017; Pastor-Bernier & Cisek, 2011; Roesch & Olson, 2003; Thura & Cisek, 2014, 2016; Yamada et al., 2018) and parietal (Andersen & Buneo, 2002; Churchland et al., 2008; Dorris & Glimcher, 2004; Hanks et al., 2014; Kiani et al., 2008, 2014; Louie & Glimcher, 2010; Platt & Glimcher, 1999; Roitman & Shadlen, 2002; Rorie et al., 2010; Shadlen & Newsome, 2001; Sugrue et al., 2004) cortices and basal ganglia (Ding & Gold, 2010, 2012, 2013; Thura & Cisek, 2017). Recent research shows more specifically that neural value coding is contextual in nature, with the value of a given option represented relative to the value of available alternatives (Churchland et al., 2008; Kira et al., 2015; Louie et al., 2011, 2013, 2014; Pastor-Bernier & Cisek, 2011; Rorie et al., 2010; Strait et al., 2014; Yamada et al., 2018). Furthermore, this relative value coding employs a divisive normalization-like representation (Hunt et al., 2012; Louie et al., 2011, 2015; Yamada et al., 2018), a canonical computation prevalent in sensory processing and thought to implement efficient coding principles (Carandini et al., 1999; Carandini & Heeger, 1994, 2012; Heeger, 1992, 1993; Schwartz & Simoncelli, 2001; Silver, 2010) and temporal adaptation (Chau et al., 2020; Heeger, 1992; Louie et al., 2013, 2015; Steverson et al., 2019; Webb et al., 2014).

Option selection and categorical choice occurs when the decision process progresses beyond simple representation. A common and powerful neural mechanism for this categorical choice is winner-take-all (WTA) competition (Wickens et al., 2007; Wilson, 2007). WTA dynamics are widely observed in multiple brain regions: the neural firing rate representing the chosen option or action target increases in concert with selection (often reaching an activity threshold at choice), while firing rates representing the other unchosen option are suppressed (Churchland et al., 2008; Gold & Shadlen, 2007; Hanes & Schall, 1996; Hanks et al., 2014; Lo et al., 2015; Lo & Wang, 2006; Roitman & Shadlen, 2002; Rorie et al., 2010; Shadlen & Newsome, 2001; X.-J. Wang, 2002; Wong & Wang, 2006). The wide prevalence of WTA dynamics in decision-related neural activities suggests that it is a general feature of biological choice.

Existing models have identified core circuit motifs that produce either normalized value representation or WTA selection (**Fig. 1**). For normalized value representation, dynamic circuit-based models emphasize a crucial role for both lateral and feedback inhibition (LoFaro et al., 2014; Louie et al., 2014). In the dynamic normalization model (DNM), paired excitatory and inhibitory neurons represent each choice option (**Fig. 1A**); feedforward excitation gathers value inputs, lateral connectivity mediates contextual interactions, and feedback inhibition drives divisive scaling. This simple differential equation model emphasizes a crucial role of lateral connectivity and feedback inhibition in driving empirically-observed divisive scaling and contextual interactions (**Fig. 1B**).

For WTA selection, the predominant class of decision models (recurrent network models, hereafter RNM) propose a central role for recurrent connectivity (Houck & Person, 2014; Ito, 2002, 2006, 2008; Llinás, 1975; Sathyanesan et al., 2019; Sillitoe & Joyner, 2007) and non-selective feedback inhibition (Wickens et al., 2007; Wilson, 2007) (**Fig. 1C**). RNMs capture psychophysical and neurophysiological results in perceptual (Furman & Wang, 2008; X.-J. Wang, 2002; Wong et al., 2007; Wong & Wang, 2006) and economic (Hunt et al., 2012; Jocham et al., 2012; Rustichini & Padoa-Schioppa, 2015; Soltani, 2006) choices, recapitulating much of the complex nonlinear dynamics of empirical neurons (**Fig. 1D**). The competitive nature of the RNM generates attractor states which maintain continued activity even in the absence of stimuli, consistent with persistent spiking activity associated with working memory during delay intervals (Brunel & Wang, 2001; Compte, 2000; Constantinidis et al., 2018; Furman & Wang, 2008; Hart & Huk, 2020; Lo & Wang, 2006; Macoveanu et al., 2006; Murray et al., 2017; Tegnér et al., 2002; M. Wang et al., 2013, p. 201; X.-J. Wang, 1999, 2002; Wong & Wang, 2006).

[Insert **Figure 1** about here]

sequential sequentially many of values Iation(Ding & Gold, 2012; J.-N. Kim & Shadlen, 1999; Roesch & Olson, 2003)

Despite electrophysiological evidence for sequentially coexisting relative value coding and WTA signals in prominent decision-related circuits, no current model integrates both properties within a single circuit. The DNM cannot capture late-stage choice dynamics because it lacks a mechanism for WTA competition. Similarly, RNMs typically neither exhibit contextual value coding nor predict contextual choice patterns (X.-J. Wang, 2012), due to the lack of structured lateral inhibition. Here we propose that disinhibition is a biological plausible solution to unify these key features of decision-making into a single circuit. We develop and characterize a novel biological circuit consisting of three neuronal types which critically include a form of local disinhibition. This model hybridizes the architectural features of divisive gain control and recurrent self-excitation used in existing models, but utilizes disinhibition, rather than the commonly-assumed pooled inhibition, to implement competition. We find that the disinhibition-based model unifies multiple characteristics of decision activity including normalized value coding, WTA choice, and working memory. A top-down gating signal operating via this disinhibition enables the model to switch between the states of value representation and WTA selection, and to reproduce decision activity in a range of experimental paradigms with diverse task timing and activity dynamics. These findings suggest that local disinhibition provides a robust, biologically plausible integration of normalization and WTA selection in a single circuit architecture.

# Results

#### Local disinhibition decision model (LDDM)

To develop an integrated circuit model of decision making, we systematically tested a series of models incorporating disinhibitory motifs and the core elements of existing models, namely divisive gain control, recurrent excitation, and mutual competition (**Fig. 2-figure supplement 1**; see **Methods** *Motifs tested and compared for normalized coding and winner-take-all choice* for the analysis details). This analysis identified *local disinhibition* as the crucial component that can integrate mutual competition and value normalization within the existing circuit architecture of DNM. In the rest of this paper, outside of the methods and supplementary figures, we focus on this novel local disinhibition decision model (hereafter LDDM) that emerged from our detailed examination of potential models.

In the LDDM (**Fig. 2A**), as in the DNM, option-specific excitatory *R* units receive value inputs and interact via widespread lateral inhibition. However, the LDDM also includes an option-specific disinhibitory *D* unit that receives input from its associated excitatory *R* unit and locally inhibits the inhibitory *G* unit in the local circuit. In this way, disinhibition biased by different value inputs can serve to selectively release local circuit gain control, generating an unbalanced gain control between local and opponent circuits and leading to a WTA competition. In this model, the network thus shifts from value coding to WTA competition regimes in response to an onset of disinhibition (controlled by the coupling strength between *R* and *D*).With zero or weak *R-D* coupling, the circuit preserves normalized value coding consistent with the DNM; with strong *R-D* coupling, the circuit switches to a state of WTA selection (**Fig. 2B**). Inhibitory units, as a result, dynamically switch from a non-selective response pattern to a selective response pattern (*G* and *D* units in **Fig. 2B**) driven by local disinhibition. This flexible onset of disinhibition is modeled after biological findings, which show that activation of disinhibition in cortical circuits arises from exogenous, long-distance projections (Fu et al., 2014; Kamigaki, 2019; S. Lee et al., 2013; Pi et al., 2013; S. Zhang et al., 2014) (**Fig. 2C**). This form of top-down control allows for flexibility in the relative timing of the valuation and selection processes, consistent with neural and behavioral data in different task paradigms (see below *Gated disinhibition provides top-down control of choice dynamics*).

Activity dynamics of the LDDM are described by a set of differential equations:

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| --- | --- | --- |
|  |  | (1) |
|  |  | (2) |
|  |  | (3) |

where *i* = 1, …, *N* designates choice alternatives, each of which is represented by an R unit receiving selective input and non-selective baseline input *BR*. , , and are the time constants for the *R*, *G*, and *D* units. The weights represent the coupling strength between excitatory units and inhibitory (gain control) units , with each *G* unit driven by a weighted sum of excitatory inputs from all *R* units and a non-selective baseline input and inhibited by its local ; the parameter reflects the strength of recurrent self-excitation on *R* units. Finally, weights the coupling strength between the excitatory and the disinhibitory units and is presumed to be under external (task-triggered) control.

[Insert **Figure 2** about here]

[Insert **Figure 2-figure supplement 1** about here]

#### Dynamic divisive normalization preserved in the LDDM

We first examine whether the LDDM retains the dynamics of divisively normalized value coding seen empirically and in the DNM (LoFaro et al., 2014; Louie et al., 2014). As discussed above, during initial option evaluation the disinhibitory units are silent () and the sole difference between the LDDM and the DNM is recurrent excitation (controlled by ). Example activity traces in **Fig. 3B** show that the LDDM preserves characteristic early-stage dynamics and contextual modulation seen in both empirical data (**Fig. 3C**) and the original DNM (LoFaro et al., 2014; Louie et al., 2011, 2014). Immediately after stimulus onset, *R1* activities replicate the transient peak observed in a wealth of studies (Andersen & Buneo, 2002; Churchland et al., 2008; Gnadt & Andersen, 1988; Louie et al., 2011, 2014; Platt & Glimcher, 1999; Rorie et al., 2010; Sugrue et al., 2004). Further, the network settles to equilibrium displaying *relative* value coding: *R1* activity increases with *V1* and decreases with *V2* (**Fig. 3B,** *R1* activityacross *V1* inputs (upper panels) and *V2* inputs (bottom panels)), reflecting a contextual representation of value (see Methods for details of parameters used in visualization).

Taking advantage of its simplified mathematical form, we analytically evaluated the LDDM by conducting phase plane analyses and found that it represents each set of input values () as one unique and stable equilibrium point in its output space () when. Specifically, we solved for the equilibrium state of each *R* unit by setting each differential equation (Eqs. 1-3) to zero, which defines the nullcline of each *R* unit as a function of the activity of the complementary *R* unit, visualized in **Fig. 3D**. The nullclines of *R1* (solid) and *R2* (dashed) intersect at a unique equilibrium point, regardless of whether input values are equal or unequal (see different panels for examples of different inputs). This point indicates that the dynamical system, when receiving any positive inputs, can maintain a unique equilibrium where every unit maintains a steady level of activity. Linearization analysis around this point suggests that this point is attractive: given any initial values to the system, the activities of the units will converge into the unique equilibrium point for the network (see **Methods** *Equilibria and stability analysis of the LDDM* formathematical proof). The steady state of neural activity at equilibrium (noted as ) reflects divisive normalization (Eq. 4), as in the original DNM (LoFaro et al., 2014; Louie et al., 2014). The only difference between the LDDM and the DNM at equilibrium is the introduction of a constant in the denominator () introduced by baseline gain control and recurrent excitation; this change rescales the activity magnitudes but preserves normalized value coding.

|  |  |  |
| --- | --- | --- |
|  |  | (4) |

We next verified that the normalized value coding produced by the LDDM cannot be implemented by standard recurrent RNM models. **Fig. 4A** compares the activity of as a function of both value inputs (*V1* and *V2*) in the LDDM (left panel), the original DNM (middle panel), and the RNM (right panel). Both the LDDM and the DNM exhibit activities (indicated by color) that monotonically increase with input but decrease with , with a slightly steeper dependence in the LDDM versus the DNM model depending on the rescaling of . In contrast, strong WTA dynamics in the RNM implement categorical (choice) coding rather than relative value representation, with high or low coding of input values (right panel).

[Insert **Figure 3** about here]

To quantitatively test value normalization, we fit the models to observed firing rates of monkey lateral intraparietal (LIP) neurons under varying reward conditions (Louie et al., 2011). In the empirical data (**Fig. 4B**, dots), LIP activity increases with the reward (juice quantity) associated with the target inside the neuronal response field (*Vin*) and decreases with the summed rewards of targets outside the response field (*Vout*). The fitting results show that the DNM captures the rescaled firing rates very well with only two free parameters (baseline input *B­R* = 70.92, and an arbitrary scaling parameter ; see **Methods**; middle panel in **Fig. 4B**, *R2* = .9640). The LDDM with an additional parameter related to self-excitation () and baseline gain control () fitted slightly better than the DNM (*BR* = 71.53, ; see **Methods**; left panel in **Fig. 4B**,*R2* = .9646; parameter recovery analysis shows that the LDDM is highly robust in the data fitting, **Fig. 4-figure supplement 1**). Note that fitting to the current dataset is not able to differentiate the contributions of and to the neural dynamics (see proof in **Methods**); thus more empirical data will be needed to draw conclusions about the role of recurrent self-excitation in value coding. However, we do show below that self-excitation is critical for generating persistent activities (see section *Disinhibition controls point versus line attractor dynamics in persistent activity*).

We found that fitting the standard RNM with its standard four parameters (see **Methods**) cannot capture the pattern of neural activity as well as the LDDM and DNM (right panel in **Fig. 4B**) (*R*2 = .8920). This small but clear difference in performance between model classes arises from the difference between divisive (DNM, LDDM) and subtractive (RNM) types of inhibition, with subtractive inhibition failing to capture the concave contextual effects predicted by divisive models. Furthermore, fitting the RNM to the data results in a parameter regime that can no longer generate WTA competition; instead, the model predicts mean firing rates in a low-activity regime with maximum value ~ 3.5 Hz (**Fig. 4-figure supplement 2**). These results suggest that RNM models cannot simultaneously support both normalized value coding and WTA selection regimes.

[Insert **Figure 4** about here]

[Insert **Figure 4-figure supplement 1** about here]

#### Local disinhibition drives winner-take-all competition

A key question is whether the LDDM can also produce WTA competition. Given the architecture of the LDDM, local disinhibition is hypothesized to break the symmetry between option-specific *R*-*G* sub-circuits, enabling a competitive interaction between sub-circuits. To examine whether this competition produces WTA selection, we simulated model activity in a reaction-time version of a motion discrimination task, a standard perceptual decision-making paradigm in non-human primates (Churchland et al., 2008; Roitman & Shadlen, 2002). The task contains two stages of processing: the pre-motion stage with only the choice targets presented and the motion stage presenting a random-dot motion stimulus simultaneously with a go signal. Animals are allowed to select an option, indicating their perception of the main direction of motion, at any time following motion stimulus/go signal onset (see timeline, **Fig. 5A**). During the pre-motion stage, we simulated equal value inputs, given the equal prior probability of either target being correct in the standard task. The simulated dynamics replicate the characteristic transient peak observed in both perceptual and economic decision-making tasks (Andersen & Buneo, 2002; Churchland et al., 2008; Louie et al., 2011; Rorie et al., 2010). At motion stimulus onset, inputs to the two *R* units are changed according to the task design; disinhibition (i.e., value) is switched on at the go signal, simultaneously with motion inputs.

We find that the LDDM replicates neural and behavioral aspects of WTA competition. In **Fig. 5A**, we show example model activity for five input strengths corresponding to different motion coherence levels. Consistent with electrophysiological recordings in posterior parietal cortex (Churchland et al., 2008; Roitman & Shadlen, 2002; Shadlen & Newsome, 2001), model *R* unit activities bifurcate based on the input strengths, with the unit receiving stronger input ramping-up to an (arbitrary) decision threshold while the activity of the opponent unit is suppressed. The speed of bifurcation depends on the contrast between the inputs, a variable equivalent to motion coherence in the experimental literature (Roitman & Shadlen, 2002; Shadlen & Newsome, 2001). Furthermore, the LDDM predicts the dynamics of the two types of interneurons *G* and *D* governing excitatory neuron computation (**Fig. 5B**). Prior to the go signal, the two *G* units share the same activity, but after the go signal, the activity levels bifurcate because of disinhibition. In contrast to *R* units, the *G* unit in the sub-circuit receiving stronger input shows lower activity, indicating a stronger disinhibition of the associated *R* unit. Thus, the LDDM exhibits mutual competition that generates WTA selection in excitatory neurons, as in the existing RNM; this competition is mediated by a novel disinhibitory control input achieved through the use of biologically identified different interneuron subtypes.

What features of the LDDM are essential to generate WTA competition? We examined the dynamical properties of the system under disinhibition by conducting phase plane analyses. As shown in **Fig. 5C**, the network in the choice regime ( in this example) shows a different configuration of nullcline intersections than the network in the value representation regime (; **Fig. 3D**). Given equal (value) inputs, the nullclines of *R1* and *R2* intersect at three equilibrium points (left panel in **Fig. 5C**), with the central point unstable and the two peripheral points stable. Thus, given an initial configuration of *R1*-*R2* activities (with the presence of noise), the system will converge to the closer peripheral attractor (see example activity traces in blue and red thin lines) and implement WTA competition. Given moderately unequal inputs, the basin of attraction is biased towards the side with higher input, resulting in a higher probability falling into the side with higher input (middle panel in **Fig. 5C**). When inputs are extremely unequal, the stable equilibrium in the middle of the basin and the unstable equilibrium point associated with weaker input no longer exist, leaving only the attractor associated with stronger input (**Fig. 5C**, right). Thus, across varying degrees of input coherences, disinhibition drives the LDDM towards a selection of one of the potential choices. This can be seen in **Fig. 5D** by viewing the output ratio () of the preferred attractor as a function of input ratio (): under active disinhibition () we observe categorical coding (green line), in contrast to under inactive disinhibition () where the output ratio faithfully preserves the original ratio of inputs (dark line) (other parameters used in simulations: , , , , , and ).

To understand the operating regimes of the LDDM, we quantified model behavior across the full parameter space defined by recurrent excitation weight () and local disinhibition weight (), both of which are critical in determining the properties of the system (see **Methods** *Equilibria and stability analysis of the LDDM* for mathematical proof). Decisions with equivalent inputs are a critical test of WTA behavior, since WTA systems should select an option (stochastically) even in these symmetric scenarios (Furman & Wang, 2008; Lo & Wang, 2006; X.-J. Wang, 2002; Wong & Wang, 2006); we therefore analyzed system behavior under equal value inputs. As shown in **Fig. 5E**, this analysis revealed two distinct territories corresponding to value representation and WTA operating regimes. The value representation regime generates a unique attractor for normalized value representation but no WTA attractors; in contrast, the WTA regime (induced by a change in ) generates no normalization attractor but instead *R1* and *R2* always diverge into high-contrast attractors (see **Figure 5-figure supplement 1** and **Methods** *Equilibria and stability analysis of the LDDM* for a full description of regime parcellation). The value in the WTA regime is always larger than zero even when it asymptotically approaches zero when recurrent excitation is extremely strong, suggesting that disinhibition is always required to generate WTA choices. Models with a wide range of recurrent excitation can shift from value representation to WTA choice with an increase in local disinhibition strength (for example, red arrow in **Fig. 5E**) or under more limited conditions with an increase in recurrent activation. These findings emphasize the impact of changes in local disinhibition to WTA choice, and highlight a particular role for a dynamic gating signal in controlling the transition from value coding to option selection.

[Insert **Figure 5** about here]

[Insert **Figure 5-figure supplement 1** about here]

#### The LDDM captures empirical choice behavior and neural activity

While the preceding analyses show that the LDDM can generate value normalization and WTA selection, a critical question is whether this circuit architecture accurately captures empirically observed behavioral and neural aspects of decision making. Here, we take advantage of the limited number of parameters in this differential equation-based LDDM (compared to more complicated conductance-based biophysical models (Tegnér et al., 2002; X.-J. Wang, 1999, 2002; Wong & Wang, 2006)), which allows model fitting to empirical data. Specifically, we fit LDDM parameters to nonhuman primate *behavior* from the reaction-time version of the motion discrimination task described above. These choice and RT data from monkeys align with a reduced form model of decision making (the drift diffusion model) (Ratcliff & McKoon, 2008), and the activity of posterior parietal neurons recorded during this task display characteristic decision-related features (motion-dependent ramping, a common decision threshold, and WTA activity).

To fit the LDDM to behaviorally observed RTs, we employed the standard quantile maximum likelihood method (QMLE) to the RT distributions across input coherence levels (0 – 51.2%), with correct and error trials dissociated (Hawkins et al., 2015; Heathcote et al., 2002; Ratcliff & Tuerlinckx, 2002). We set as 1 and the baseline input *BR* as zero. Baseline gain control () and self-excitation () are collinear mentioned above (see model fitting in **Fig. 4**) and this is also true in fitting WTA choice behavior (see **Fig. 6-figure supplement 3**). To address this we kept as a free parameter but set to zero (note that this limits the interpretability of fit values as simply the level of recurrence, a point we address below and in the supplementary materials). The model is then reduced to seven parameters: recurrent excitation weight , local disinhibition weight , noise parameter , input value scaling parameter *S*, and time constants , , and (see Methods for model-fitting details). Predictions of the best fitting model are shown in **Fig. 6A** (best fitting parameters: , , , *S* = 3251, , , and ). The optimization surfaces visualized across pairs of parameters (**Fig. 6-figure supplement 1**) were consistent with robust parameter fitting, and a parameter recovery analysis indicated that the parameters are recoverable and identifiable within the network (**Fig. 6-figure supplement 2**).

Model-predicted RT distributions (lines) closely follow the empirical distributions (bars) for both correct (blue) and error (red) trials across different levels of input coherence. The aggregated mean choice accuracy and RT data are shown in **Fig.** **6C**. Model choice accuracy (line) captures the average empirical psychometric function (crosses); model RT captures coherence-dependent changes in the chronometric function, including longer RTs in error trials (dashed line and empty dots) compared to correct trials (solid line and dots). Beyond mean RT data, the LDDM accurately captured aspects of the empirical RT distributions, as evident in the quantile probability plot (QPP) of RT quantiles as functions of chosen ratio (**Fig. 6B**). Given the mathematical collinearity issue between and , it is important to note that the fitted value of should not be interpreted as reflecting the exact level of recurrence in the circuit, and future empirical data will be needed to differentiate how recurrence and baseline inhibition contribute to LDDM WTA selection.

We compared the performance of the LDDM in fitting this classical dataset with the reduced form of the RNM (Wong & Wang, 2006) (**Fig. 6-figure supplement 4**), as well as another prominent computational decision model with a similar architecture of mutual inhibition – the leaky competing accumulator model (LCA; Usher & McClelland, 2001; see **Fig. 6-figure supplement 5**). The performances of the three models were close in predicting averaged RTs and choice accuracy. However, the LDDM captures the skewness and the shape of RT distributions better than the other two as reflected in goodness of fit (negative log likelihood) and AIC measures (nLLLDDM = 16546, nLLRNM = 16573, nLLLCA = 16948, AICLDDM = 33109, AICRNM = 33165, AICLCA = 33932).

Importantly, the LDDM – fit only to behavior – generates predictions about the underlying neural dynamics that can be compared to electrophysiological findings. We examined *R* unit activity in the best-fitting model, with predicted activity aggregated across trials and aligned to the onset of stimuli and the time of decision as in the original study (Roitman & Shadlen, 2002). Aligned to the onset of stimuli **(Fig. 6D**, left), neural responses are aggregated by coherence level and eventual choice, and truncated at median RT. These data show clear evidence of WTA competition: chosen (solid) and unchosen (dashed) activity traces diverge over time. Moreover, neural activity is stimulus-dependent: the dynamics of both chosen and unchosen units ramp at different, coherence-dependent speeds, consistent with empirical findings consistent with an accumulation process. More quantitatively, we examined the relationship between activity and coherence at the specific time point (arrow points **a** and **b**) reported in the original work (**Fig. 6E**). Model predictions align well with empirical observations: across the three alternative models, the deviation between empirical recordings and model-predicted activity is the smallest for LDDM (quantified by root-mean-square error (RMSE); RMSELDDM = 2.74, RMSERNM = 20.10 (**Fig. 6-figure supplement 4E**), RMSELCA = 3.92 (**Fig. 6-figure supplement 5E**)).

Aligned to the onset of decision (**Fig. 6D,** right), model *R* unit activity near the time of choice shows further evidence of the WTA competition observed in real neurons: the initial divergence between chosen and unchosen activity traces extends into a categorical coding of choice. The relationship between activity and coherence quantitatively replicates the empirical pattern immediately preceding the decision time (Roitman & Shadlen, 2002): chosen activity (indicated by arrow **c** in **Fig. 6D** and plotted in **Fig. 6E**) no longer shows much difference across coherence conditions, while unchosen activity (indicated by **d** in **Fig. 6D** and plotted in **Fig. 6E**) retains a decrease. Quantification shows that LDDM again best predicted empirical neural activity with data aligned to choice onset (RMSELDDM = 6.77 (**Fig. 6E**); RMSERNM = 9.35 (**Fig. 6-figure supplement 4E**); RMSELCA = 7.51 (**Fig. 6-figure supplement 5E**)). Thus, *R* unit activity – in a model with parameters fit only to behavior – replicates the recorded activity of parietal neurons during both initial decision processing and eventual choice selection.

Unlike the RNM and LCA models, the LDDM predicts different dynamics in different subtypes of interneurons (**Fig. 6F-I**). The inhibitory (*G*) units selectively code input values and choice but exhibit complex dynamics due to the interplay of feedforward excitation, lateral inputs, and disinhibition. Early on (dynamics sorted to the left in **Fig. 6F** and upper panel in **Fig. 6G**), the *G* activities initially increase due to excitatory drive from *R* units. Later on, when the inhibition from *D* units increases (**Fig. 6H**), the *G* activities start to decrease. Near the time of choice (dynamics sorted to the right in **Fig. 6F** and the lower panel in **Fig. 6G**), the chosen *G* units show lower activities than the unchosen side because of stronger inhibition from *D* as an outcome of WTA competition. The dynamics of *D* units rapidly increase in the early stage, driven by excitatory *R* unit activity(dynamics sorted to the left in **Fig. 6H**). Dynamics in the late stage (dynamics sorted to the right in **Fig. 6H**) show higher activity on the chosen side than the unchosen side as an outcome of WTA competition. Both types of interneurons show different time-dependent patterns of coherence-dependence that likely reflect the complex dynamics of the system and RT-based data aggregation methods (**Fig. 6G**, **H**). While the activity of different interneuron subtypes have not been widely recorded in decision tasks, these new LDDM predictions provide a testbed for future empirical and theoretical investigations.

[Insert **Figure 6** about here]

[Insert **Figure 6-figure supplement 1** about here]

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[Insert **Figure 6-figure supplement 5** about here]

#### The LDDM integrates normalized value coding and WTA choices

While the LDDM separately replicates normalized value coding and WTA dynamics shown in different empirical studies, a key distinguishing feature of the LDDM is that it can capture both phenomena within a single experimental context. Numerous studies using the random-dot motion paradigm show two stages of dynamics: target (action) representation during the pre-motion stage and WTA selection after the go cue following motion stimuli (Churchland et al., 2008; Rorie et al., 2010). Neural activity in the pre-motion stage shows a characteristic phasic-sustained dynamic response to the presentation of visual cues; rather than purely sensory information, activity during this stage reflects the magnitude and probability of reward associated with the visual cues (Rorie et al., 2010). After the go cue, WTA dynamics reflect an integration of motion information and implements a transition from initial value coding to a categorical coding of choice in the late stage of decision (Churchland et al., 2008; Ding & Gold, 2010; Kiani et al., 2008; Roitman & Shadlen, 2002; Rorie et al., 2010; Shadlen & Newsome, 2001). Studies of economic choice show a similar set of dynamics, a context dependent valuation followed, after a go-cue, by a shift to WTA (Louie et al., 2011, 2014; Louie & Glimcher, 2010; Pastor-Bernier & Cisek, 2011; Sugrue et al., 2004).

Neural dynamics are also observed to be influenced by the number of options, a feature captured by the LDDM. Specifically, the number of alternatives offered to a non-human primate has been empirically observed to affect the neural dynamics during both representation and choice (Basso & Wurtz, 1997, 1998; Churchland et al., 2008). When the choice set is expanded from two options to four options, early representational activity is lower during pre-motion dynamics (**Fig. 7A**) and the speed of WTA dynamics slows after motion onset (**Fig. 7C**).

Here we show that the LDDM replicates the impact of the number of options on both early and late empirical neural dynamics during both the representation phases and the WTA phases observed in real neurons. Under four (versus two) alternatives, LDDM R unit activity during the representation stage decreases because of increased recurrent inhibition, driven by multiple contextual inputs (left side in **Fig. 7D**). Similarly, the ramping speed after motion onset and disinhibition decreases in the 4-option (versus the 2-option) condition, despite identical parameters (**Fig. 7E**). These results highlight the LDDM as a potential mechanism of integrating normalized value coding and WTA competition within a single circuit architecture.

[Insert **Figure 7** about here]

#### Disinhibition controls point versus line attractor dynamics in persistent activity

We next examine implications of the local disinhibition architecture for another characteristic of decision-related neural firing: persistent activity. In brain areas such as parietal (Kiani et al., 2008, 2014; Kiani & Shadlen, 2009; Roitman & Shadlen, 2002; Shadlen & Newsome, 2001), prefrontal (Funahashi et al., 1989; Fuster & Alexander, 1971; Goldman-Rakic, 1995; Rigotti et al., 2013), and premotor cortices (Pastor-Bernier & Cisek, 2011), neurons show elevated firing in the absence of stimulus-driven input over intervals of seconds; such persistent activity is thought to underlie working memory and enable decisions based on internally maintained information. In RNMs, recurrent excitation and feedback inhibition preserve categorical choice information after input withdrawal because of point-attractor dynamics (Furman & Wang, 2008; X.-J. Wang, 2002; Wong & Wang, 2006). Here, we answer two questions: does the LDDM generate persistent activity, and how does this persistent activity differ from that in standard RNMs?

We found that the LDDM can generate two distinct forms of persistent activity, controlled by the state of disinhibition. **Fig. 8A** shows example dynamics of two *R* units before and after withdrawal of inputs while disinhibition is silent. Following input withdrawal, network activity decreases but still preserves elevated firing rates, governed by the self-excitation parameter (the network loses elevated activity when ). The persistent activity ratio between *R1* and *R2* preserves information about the ratio between the input values *V1* and *V2* during the memory interval, in contrast to RNMs which immediately lose all value information and only preserve categorical information about the largest value (see **Fig. 8-figure supplement 1** and **Methods** *Analysis for persistent activity* for mathematical proof). Phase plane analyses suggest that relative value coding in persistent activity arises from a line-attractor dynamic in the network during the inactivation of disinhibition, unlike the point-attractor dynamics in the RNM which shed value information immediately (**Fig. 8B**). Like other line-attractor models of persistent activity that store continuous-valued information (Burak & Fiete, 2009; Compte, 2000; Ganguli et al., 2008; Seung, 1996), an unbiased coding of the input ratio requires perfectly balanced gain control weights from *G* to *R*. Unbalanced weights will result in distorted coding of the input ratio and graded coding of the inputs will decay over time (**Figs. 8-figure supplement 1D** and **E**). For perfectly balanced weights, the line attractor state is vulnerable to noise perturbation. A small perturbation can easily drive the activity to drift on the line of attractors, with the summed value of *R1* and *R2* as a constant (). The preserved ratio between *R1* and *R2* drifts stochastically over time, similar to the prediction of other line-attractor circuits and consistent with behavioral and neural variability related to working memory (Seung, 1996; Wimmer et al., 2014).

However, a line attractor is not the only state that the LDDM predicts. If disinhibition is activated during the delay interval, the network switches to a point attractor dynamic similar to the one employed by the RNM (see **Figs. 8-figure supplement 2** and **Methods** *Analysis for persistent activity* for mathematical proof). **Fig. 8D** shows example dynamics of two *R* units before and after withdrawal of inputs. Disinhibition drives a competition between the two *R* units, resulting in a switch between graded coding of the input ratio to a categorical coding of the largest value ( in visualization). Interestingly, a transition of coded information from input values to categorical information has been widely observed in firing rates in decision-related regions, such as LIP and the superior colliculus, during the delay period of decision making (Rorie et al., 2010; Shadlen & Newsome, 2001; B. Zhang et al., 2021). The point attractor predicted by the circuit under disinhibition (**Fig. 8E**) is highly tolerant to perturbations compared to the line attractor, and choice performance over long delays may require a switch from the value coding to the categorical regimes to achieve this robustness. As a plausible biological mechanism for mediating top-down control, disinhibition may gate such a transition without imposing any distinct change on the network architecture.

The LDDM can be easily expanded to multiple alternatives. Here we show an example of a 5-alternative case, with 5 sets of option-specific *R*-*G*-*D* units. A line attractor network with silent disinhibition (**Fig. 8C**, right) is able to retain relative input value information for all 5 items simultaneously in the network. Due to normalization, the neural activity representing each alternative decreases with the total number of alternatives, with the summed value as a constant (), leading to a lower signal-to-noise ratio when coding more items; this set-size effect may be related to WM memory span constraints (Cowan, 2010, 2016; Engle, 2001, 2002; Oberauer et al., 2016). When disinhibition is active, the LDDM exhibits a point attractor (**Fig. 8F**, right), and the network only holds the information of the largest item as a categorical code during persistent activity.

[Insert **Figure 8** about here]

[Insert **Figure 8-figure supplement 1** about here]

[Insert **Figure 8-figure supplement 2** about here]

#### Gated disinhibition provides top-down control of choice dynamics

In addition to its crucial role in generating WTA competition, local disinhibition provides an intrinsic mechanism for top-down control of choice dynamics. Decision circuits show remarkable flexibility in timing, with similar neurophysiological evidence of this flexibility recorded in a variety of task paradigms. In addition to reaction-time tasks, in which subjects can choose at any time immediately after onset of stimulus, decision-rela­ted neural activity has been widely studied in fixed-duration and delayed-response tasks. In fixed-duration tasks, subjects are required to withhold selection of an action until an instruction signal. Neural activity prior to the instruction signal reflects value information, for example about reward characteristics (Dorris & Glimcher, 2004; Louie et al., 2011; Platt & Glimcher, 1999; Sugrue et al., 2004; Watanabe, 1996) or accumulating perceptual evidence (Kiani et al., 2008, 2014; Kiani & Shadlen, 2009; J.-N. Kim & Shadlen, 1999; Roitman & Shadlen, 2002; Rorie et al., 2010; Shadlen & Newsome, 2001); however, this activity never fully diverges or reaches the decision threshold until after the instruction cue, suggesting a gating of the competition process. In delayed-response (working memory) tasks, subjects must postpone selection for an interval that includes both stimulus presentation and an additional subsequent interval after the stimulus is withdrawn. As in fixed-duration tasks, neural activity in delayed-response tasks typically carries decision–related information (across both the stimulus and delay periods) but WTA selection – and behavioral choice – is withheld until the instruction cue is given (Kiani et al., 2008, 2014; Kiani & Shadlen, 2009; J.-N. Kim & Shadlen, 1999; Roitman & Shadlen, 2002; Shadlen & Newsome, 2001). Thus, biological decision circuits are able to evaluate choice options while selectively initiating the WTA selection process with variable context-dependent timing.

[Insert **Figure 9** about here]

Despite this evidence of top-down control, how neural circuits implement dynamic control of selection – and temporal separation of evaluation and WTA choice – is largely unaddressed in current decision models. In RNM models, neural activity is driven by fixed attractor dynamics; option evaluation and the selection process cannot be disambiguated, and WTA competition is essentially ballistic and not under top-down control. In this section, we examine how the timing of a dynamic top-down control signal – modulating the strength of disinhibition via long-range inputs and neuromodulation – allows the LDDM to capture neural activity in different task paradigms. In these simulations, disinhibition is activated when the instruction cue to choose is presented. **Fig. 9A** shows LDDM activity in a reaction-time task, a standard paradigm in perceptual decision-making (Churchland et al., 2008; Roitman & Shadlen, 2002). As in prior analyses (**Figs. 5** and **6**), LDDM *R* units show simultaneous evaluation (coherence-dependent ramping) and WTA selection (rise to threshold) processes, driven by an immediate activation of disinhibition at motion stimulus onset.

In a fixed-duration task (**Fig. 9B**), disinhibition is activated after a required interval of stimulus presentation as in the empirical data. Compared to the reaction-time task, LDDM activity here shows distinct, temporally separated patterns during stimuli viewing and option selection; this temporal segregation is driven by the activation of disinhibition (a step function on in this example), which promotes a transition between value representation and WTA choice.

A further demonstration of this temporal flexibility arises from considering delayed-response tasks (**Fig. 9C**), which include an interval between stimuli offset and onset of the instruction cue. Consistent with its ability to maintain persistent activity (**Fig. 8**), the LDDM shows value coding across the delay interval and delays WTA selection until after the instruction cue and the accompanying activation of disinhibition. These results show that the LDDM – via modulation in the timing of disinhibition activation - can temporally separate the value representation and selection processes (unlike the RNM), enabling it to capture the diversity of neural dynamics seen in reaction-time, fixed-duration, and delayed-response tasks.

#### Inhibitory potentiation distinguishes LDDM from earlier models

The architecture of disinhibition employed by the LDDM is more structured than the earlier non-selective inhibition used in most standard competition networks. This distinction gives rise to the novel prediction from LDDM that the influence of global changes in inhibitory tone are non-selective during representation, but switch to being input-selective after disinhibition is increased. This reflects a fundamentally novel prediction of this class of model. The LDDM contains two different types of inhibition and thus its reaction to inhibitory potentiation depends on both the state of the disinhibitory network and the intensity of potentiation. To highlight the importance of that prediction, we implemented different levels of inhibitory connection weights in both the LDDM and the standard RNM.

[Insert **Figure 10** about here]

At the neural level, the LDDM predicts a dissociable effect of potentiated inhibition on the primary (*R*) neuron’s activity (**Fig. 10A**). During option representation (cue interval in fixed duration trials), potentiated inhibition increases both recurrent and lateral inhibition, leading to decreased firing rates and a weaker modulation by value in the R neurons. During option selection (go/choice intervals in fixed duration trials), increases in local disinhibition increases WTA activity and simultaneously decreases the late-stage representation of value. As an outcome, these changes produce a speeding up of RTs but a decreased choice accuracy (**Fig. 10B**). The expected differences between the control condition and the inhibitory potentiation condition would be evident in chronometric and psychometric curves across different levels of inputs effectively implementing a speed-accuracy tradeoff (**Fig. 10C**). Note that the qualitative predictions for inhibitory potentiation effects on RT and accuracy are robust to specific LDDM parameterizations (**Fig. 10D**). In contrast, in more traditional networks like the RNM that employ non-selective inhibition, potentiated inhibition suppresses the excitatory neural activities during the WTA competition (**Fig. 10E**). The suppression in neural coding in these models slows down RTs but does not affect choice accuracy (**Figs. 10F**, **G**), thus failing to replicate the observed speed-accuracy tradeoff. We note that these novel predictions that differentiate models which rely on structured disinhibition could be readily tested using modern optogenetic techniques.

# Discussion

The prevalence of disinhibitory circuit motifs in the brain, and recent evidence for structured decision-related inhibitory activity, argue for a more structured implementation of inhibition in computational models of decision-making. Here, we show the disinhibition-based LDDM replicates three characteristic features of neurobiological decision-making – normalized value coding, WTA choice, and persistent activity – all within a single circuit architecture. Furthermore, the LDDM outperforms existing recurrent circuit and leaky accumulator decision models in fitting empirical choice data and replicating decision-related neural dynamics. Perhaps most importantly, the LDDM provides a novel mechanism for top-down control of decision dynamics. When controlling the timing of disinhibition, the LDDM effectively paces the decision process and replicates neural dynamics from a wide range of empirical choice tasks.

*Flexible control of dynamic regimes*

While normalized value coding and WTA selection have largely been modeled separately, the LDDM offers a biologically-plausible circuit architecture that integrates the two features via local disinhibition. Existing neurophysiological evidence show that WTA dynamics and normalized coding co-exist in the same brain regions. On the one hand, neural activities show relative value coding in the early stage of decision-making, reflecting a context-dependent modulation consistent with the canonical divisive normalization computation (Churchland et al., 2008; Kira et al., 2015; Louie et al., 2011; Pastor-Bernier & Cisek, 2011; Rorie et al., 2010; Strait et al., 2014; Yamada et al., 2018). On the other hand, WTA choice dynamics are widely observed during decision making across multiple brain regions of non-human primates (Andersen & Buneo, 2002; Churchland et al., 2008; Ding & Gold, 2010, 2012, 2013; Dorris & Glimcher, 2004; Hanks et al., 2014; Kiani et al., 2008, 2014; J.-N. Kim & Shadlen, 1999; Louie & Glimcher, 2010; Padoa-Schioppa, 2013; Padoa-Schioppa & Conen, 2017; Pastor-Bernier & Cisek, 2011; Platt & Glimcher, 1999; Roesch & Olson, 2003; Roitman & Shadlen, 2002; Rorie et al., 2010; Shadlen & Newsome, 2001; Sugrue et al., 2004; Thura & Cisek, 2014, 2016, 2017; Yamada et al., 2018), including many of the brain regions that show normalized value coding. In addition, neural firing rates shows a graded coding of perceptual evidence and reward during the early stage of decision-making and gradually transition to a categorical coding for choice in the late period of decision-making (Churchland et al., 2008; Dorris & Glimcher, 2004; Gold & Shadlen, 2007; Platt & Glimcher, 1999; Roitman & Shadlen, 2002; Rorie et al., 2010; Shadlen & Newsome, 1996, 2001; Sugrue et al., 2004; B. Zhang et al., 2021).

Existing models of decision-making capture activity dynamics only in specific temporal intervals during decision-making tasks, or across trials in specific task paradigms (Hart & Huk, 2020; Hunt et al., 2012; Louie et al., 2014; X.-J. Wang, 2002; Wong & Wang, 2006), and thus typically do not generalize across tasks. In contrast, via gated disinhibition driven by the external action instruction. Controlling the timing of valuation-to-WTA regime transition enables the LDDM to replicate neural dynamics in diverse task paradigms with different stimulus and action timing schedules (Kiani et al., 2008; Roitman & Shadlen, 2002; Rorie et al., 2010; Shadlen & Newsome, 2001).

#### Biological plausibility and fast modulation of disinhibition

The top-down control of normalization via disinhibition mirrors recently proposed mechanisms for flexible modulation of contextual processing in sensory circuits (Coen-Cagli et al., 2012, 2015; Schwartz & Coen-Cagli, 2013) and input-scaled disinhibition implements a self-sparing (‘donut-like’) inhibition motif central to midbrain models of categorical selection (Mahajan & Mysore, 2022; Mysore & Kothari, 2020). The micro-circuit structure underlying donut-like inhibition has been revealed as a mechanism of localized disinhibition from VIP neurons to PV/SST neurons in the cortex (Karnani et al., 2016). Recent research on neuromodulatory control of disinhibition offers biologically plausible mechanisms for such top-down control of circuit dynamics. In addition to evidence that VIP neurons are recruited by long-range projections from distanced regions (S. Lee et al., 2013; S. Zhang et al., 2014), VIP neurons are recruited by neuromodulatory projections such as acetylcholine (Fu et al., 2014) from the basal forebrain and pedunculopontine nuclei and serotonin from the red nucleus. With ionotropic acetylcholine receptor (nAChR) and serotonin receptors (5HT3aR and 5HT2R), VIP neurons depolarize to acetylcholine and serotonin (Alitto & Dan, 2013; Pfeffer et al., 2013; Rudy et al., 2011; Tremblay et al., 2016). The spiking mode of a major type of VIP neurons in layer II/III of the cortex switches from an input-insensitive burst-quiescent mode to an input-sensitive tonic mode under cholinergic and serotonin modulation (Prönneke et al., 2020). Such a mode-switching feature allows the disinhibitory neurons to receive excitatory projections with different gain under different level of neuromodulation, providing a mechanism to modulate network dynamics via disinhibition without a change in network structure*.* *In* *vivo* studies show that disinhibition mediated by cholinergic activation is triggered in a surprisingly fast time scale of tens of milliseconds (Alitto & Dan, 2013; Hangya et al., 2015; Letzkus et al., 2011), supporting a fast modulation mechanism of disinhibition and network plasticity.

#### The contribution of LDDM over existing disinhibition models

Disinhibition has been previously linked in separate models to computational functions exhibited in a unified manner by the LDDM. For example, a computational model employing dendritic disinhibition captures flexible information routing in a context-dependent decision task, with dendritic disinhibition gating on specific inputs to a circuit while gating off other pathways (Yang et al., 2016). However, disinhibition plays a different role in this model (context-dependent input gating) from in the LDDM (transition from value coding to WTA selection and mutual competition). In another example, PV neuron activation within a disinhibitory circuit motif can produce a divisive normalization of tuning curves in a model of visual cortex (Litwin-Kumar et al., 2016). This division can arise from different circuit mechanisms, such as reduced tuned input and firing rate nonlinearities. Finally, disinhibition has also been proposed to underlie the long timescales of information processing seen in working memory, as enhancing inhibitory-to-inhibitory connections stabilizes temporal dynamics and improves working memory performance in recurrent neural networks (R. Kim & Sejnowski, 2021). Taken together, previous results and our current work reinforce the importance of incorporating disinhibition in circuit models of decision-making.

#### Disinhibition in cortical-ganglia pathways: the similarity and the difference

While absent in standard existing cortical decision models, disinhibition is a key element of action selection in models of the cortical-basal ganglia (CBG) system (Bogacz & Gurney, 2007; Frank, 2005; Lo & Wang, 2006; Schroll & Hamker, 2013; Wei et al., 2015). In the basal ganglia direct pathway, GABAergic neurons in the striatum inhibit neurons in the substantia nigra pars reticulata and internal globus pallidus, which in turn send inhibitory projections to the thalamus. Cortical inputs to the striatum thus produce a disinhibition of thalamic outputs to cortex and brainstem motor areas, resulting in motor facilitation. Crucially, the activation of disinhibition in the CBG system is selective: the selection of a specific action requires a selective disinhibition driven by asymmetries in cortical inputs or striatal synaptic weights. This selective disinhibition is an essential element of computational models of the CBG system (Frank, 2005; Lo & Wang, 2006), including more complex models that incorporate global inhibition mediated by the indirect and hyper direct pathways (Bogacz & Gurney, 2007; Schroll & Hamker, 2013; Wei et al., 2015).

While both the LDDM and the CBG models utilize disinhibition to drive selection, however, they differ in two important ways. First, disinhibition in the LDDM functions in a novel manner that implements a transition between value coding and WTA selection states. This transition is mediated by a broad/non-selective activation of disinhibition across the decision circuits. The activation of disinhibition is not biased towards specific alternatives until a period of interaction with differential value inputs to option-specific subcircuits. Second, disinhibition in the LDDM is tightly integrated with the lateral inhibition that mediates competition between alternatives; consistent with the microarchitecture of cortex which it seeks to model (Fu et al., 2014; Karnani et al., 2016; Kepecs & Fishell, 2014; Pi et al., 2013; S. Zhang et al., 2014), disinhibitory, inhibitory and excitatory neurons are part of the same local circuit. In contrast, the basal ganglia is known to lack these local, lateral connections and mutual competition in the CBG models, which typically require both direct pathway disinhibition along with diffusive suppression of competing motor plans via the indirect or hyper direct pathways (Bogacz & Gurney, 2007; Schroll & Hamker, 2013; Wei et al., 2015). Thus, while conceptually similar to the CBG models, disinhibition in the LDDM is tightly integrated with competitive inhibition and provides a dynamic control of circuit state, both characteristics of decision-making in cortical brain areas.

#### Point-attractor and line-attractor persistent activity

An interesting feature of the LDDM is that it can produce both point attractor (Bathellier et al., 2012; Kopec et al., 2015; Niessing & Friedrich, 2010; Wills et al., 2005) and continuous/line attractor (Ganguli et al., 2008; Wimmer et al., 2014; Yoon et al., 2013) dynamics in persistent activity, a balance controlled by the level of disinhibition. Given ambiguous empirical evidence, it remains controversial whether persistent activity in neural circuits exhibit point attractor (Bathellier et al., 2012; Kopec et al., 2015; Niessing & Friedrich, 2010; Wills et al., 2005) or continuous/line attractor (Ganguli et al., 2008; Wimmer et al., 2014; Yoon et al., 2013) dynamics. Most existing circuit models of persistent activity exclusively predict either a point attractor (Amit & Brunel, 1997; Brunel & Wang, 2001; Hopfield, 1982; X.-J. Wang, 1999) or line attractor (Amari, 1977; Burak & Fiete, 2009; Compte, 2000; Ganguli et al., 2008; Seung, 1996). The LDDM achieves the flexible reconfiguration of line attractor and point attractor states under the control of disinhibition, suggesting that attractor dynamics might not be a fixed property of a network; rather, it may be adaptive and controllable by a top-down signal operating via gated disinhibition. Similar reconfiguration has been achieved by other circuit mechanisms. For example, a mutual inhibition network can capture the different regimes of sequential two-interval decision-making – stimulus loading, working memory, and comparison – by assuming a flexible reconfiguration of external inputs (Machens et al., 2005). Similar to the LDDM, this model can transition between point attractor (initial stimulus encoding), line attractor (working memory), and saddle point (comparison) dynamics. Interestingly, disinhibition may also play a role in this model, by providing a theoretical mechanism to switch the routing of external inputs within the circuit, which drives the switch from line attractor to comparison dynamics.

#### Conclusions

In conclusion, here we introduce a novel, biologically-plausible architecture for decision-making based on local disinhibition, unifying the characteristic decision-making features of normalized value coding, WTA competition, and persistent activity into a single circuit. The LDDM captures psychometric and chronometric aspects of behavioral choice and predicts realistic neural dynamics in standard decision-making tasks. Local disinhibition provides a mechanism for top-down control of local decision circuit dynamics, enabling the LDDM to replicate variable task-dependent timing in diverse decision-making paradigms and implement speed-accuracy tradeoffs. These results suggest a new circuit mechanism for decision making, and emphasize the importance of incorporating interneuron diversity, local circuit architecture, and top-down control into models of the decision process.

# Methods







#### Equilibria and stability analysis of the LDDM

In **Figs. 3** and **5**, we showed that the LDDM exhibits different pattern of equilibria and stabilities under normalized value coding and WTA competition, mediated through disinhibition. Here we provide detailed mathematical analysis about the equilibria and stability of this dynamic system under different states of disinhibition.

Equilibria of the system were solved by taking the intersection of the nullclines of all units, i.e., the steady states of each unit. This is obtained by setting , , and all equal to 0 in Eqs. 1-3. The solution of the equilibrium state of *R* units (*Ri\**) can be written as:

|  |  |  |
| --- | --- | --- |
|  |  | (5) |

For a binary input system (*N* = 2), the six differential equations can be simplified to two equations with only the *R* units explicitly in the expression (Eqs. 6 and 7). Each equation describes the nullcline of a single *R* unit.

|  |  |  |
| --- | --- | --- |
|  |  | (6) |
| (7) |

Given that the equilibrium states of the system can be reduced with only *R* units explicitly in the expression, these equilibrium points can be visualized in the space of *R1* and *R2* activities as the intersection of the nullclines of the two *R* units (as shown in **Figs. 3** and **5**). The stability of each equilibrium point was then examined by checking the eigenvalues of the Jacobian matrix around it. The equilibrium point is attractive and stable when all of the eigenvalues have negative real parts; the equilibrium point is divergent and unstable when there exist any positive real parts of eigenvalues. By denoting as the differential equations for all units in their steady states, the Jacobian matrix around the point can be written as Eq. 8:

|  |  |  |
| --- | --- | --- |
|  |  | (8) |

We examined the configuration of nullclines and checked the eigenvalues of the Jacobian matrix across a wide range of parameter values and . was set as a unit value of 1 for the sake of simplicity. and were set as zero in the following visualization.

The property of the system under equivalent inputs is a critical test since it determines whether the system is able to implement a WTA choice and select an option. Thus, we examined the property of the system for WTA under equal inputs. Examining the full space of and revealed five territories distinguished by the number of equilibrium points and their stabilities (**Figure 5-figure supplement 1A**). For each territory, the configuration of nullclines are illustrated in **Figure 5-figure supplement 1** labeled by color. **Dark green region**: When disinhibition is smaller (), and show a trade-off in generating WTA competition. When both and are small, the system generates a unique equilibrium point of normalized coding (dark green region in **Figure 5-figure supplement 1A**, nullclines shown in **Figure 5-figure supplement 1B**). Eigenvalues in this regime show all negative real parts on this equilibrium point, indicating it is a stable equilibrium. **Blue region**: As values increase (at smaller values), the system generates three equilibrium points (**Figure 5-figure supplement 1D**), with two high-contrast (stable) attractors at the peripheral and one (unstable) repellor in the center of space *R1*-*R2*. Neural activities of *R1* and *R2* with equal initial values bifurcate into the high-contrast attractors to realize WTA competition (example traces shown in red and blue lines). **Green region**: When the strength of disinhibition increases (), most of the regimes (yellow and red regions) show the properties of WTA competition except for a small regime when (an almost invisible region between dark green and yellow). In the green region, the nullclines of *R1* and *R2* still intersect on three equilibrium points but, in contrast to the blue region, the two points with high contrast of *R1*-*R2* activities are unstable and the equilibrium point in the center is stable, therefore, the system maintains normalized coding (**Figure 5-figure supplement 1C**). **Yellow region**: When disinhibition is large (), most of the parameter regime in the yellow region shows only one repellor at the center (**Figure 5-figure supplement 1E**). The activities of *R1* and *R2* bifurcate from the center repellor to the high-contrast corners. The restriction of maximum activity depends on the value of . When , the model predicts limited value of activity on each *R* unit as () (vertical and horizontal dashed lines in **Figure 5-figure supplement 1E**). When , the model predicts no boundary on the maximum activities (though a boundary may still need to be considered because of biological constraints). **Red region**: When disinhibition is extremely large (), the two nullclines show no intersections (**Figure 5-figure supplement 1F**). Most of the other features in this region are similar to the yellow region. The neural activities of *R1* and *R2* bifurcate from initial values from the center to the corners of high contrast (example traces shown in red and green thin lines). The boundary of neural activity is predicted when and not accounted when .

Taken together, the five territories can be simplified to two regions based on the properties of the system in implementing either normalized coding or WTA competition as discussed in the main text (**Fig. 5E**). These two regions show clear-cut dichotomous separation in the two-dimensional space of recurrent excitation weight () and local disinhibition weight ().

|  |  |  |
| --- | --- | --- |
|  |  | 9 |

the

#### Fitting the LDDM and the DNM to the neural firing rates of normalized value coding

In order to quantify the performance of the LDDM in fitting to the neural dynamics of normalized value coding and compare with the original DNM, we fit the equilibrium values of the LDDM and DNM to the dataset of normalized value coding (the Fig. 4 in Louie et al., 2011). In this task, monkeys are asked to represent the reward targets (1, 2, or 3) on the corresponding location of the screen. The neural activity in the response field receiving direct input *V1* is recorded. Different combinations of *V1*, *V2*, and *V3* are provided to the monkeys based on the associated volumes of juice in the presented targets (varying from 50, 100, 200, and 250 µl or omitted target marked as 0), resulting in 28 data points.



























To fit the DNM, we employed the following differential equations,

|  |  |  |
| --- | --- | --- |
|  |  | (10)  (11) |

To fit LDDM, we employed Eq. 1-3.

The direct input value () to each pool takes the value of the volume of juice reward () plus a baseline input value . was set as 1. In the LDDM, there are additional terms of self-excitation weighted by , baseline gain control input fed into , and coupling between and the disinhibitory neurons weighted by .

To fit the predicted activities to the empirical mean firing rates during the sustain phase, we fit the predicted activities during the equilibria of these models. The equilibria of the two models were solved in Eq. 12 and Eq. 13 respectively by taking the differential equations (Eqs. 10-11 and Eqs. 1-3) to zero.

For DNM,

|  |  |  |
| --- | --- | --- |
|  |  | (12) |

For LDDM,

|  |  |  |
| --- | --- | --- |
|  |  | (13) |

To fit the empirical activities with normalized scale, we need another scaling parameter to capture the arbitrary rescaling, which result in the following equations (Eq. 14 and Eq. 15).

For DNM,

|  |  |  |
| --- | --- | --- |
|  |  | (14) |

For LDDM,

|  |  |  |
| --- | --- | --- |
|  |  | (15) |

Since we assume the disinhibition modules in LDDM keep silent during representation, takes zero. For a trinary input system, the equilibria of the two models can be described by the following equations (Eqs. 16-18 for DNM and Eqs. 19-21 for LDDM).

For DNM,

|  |  |  |
| --- | --- | --- |
|  |  | (16)  (17)  (18) |

For LDDM,

|  |  |  |
| --- | --- | --- |
|  |  | (19)  (20)  (21) |

From Eqs. 19-21, we realized that and share the same term and cannot be independently identified. Thus, we combined these parameters as one in our model fitting.

Based on the above analyses, two free parameters were estimated for the DNM (Baseline input and the scaling parameter ). Three free parameters were estimated for the LDDM (, *S*, and a combined parameter ). The Bayesian adaptive direct search algorithm (BADS)(Acerbi & Ma, 2017a, 2017b) was implemented to minimize the ordinary squared error between the steady state of the predicted neural firing rates on *R1* and the empirical data.

#### Fitting the RNM to the neural firing rates of normalized value coding

In order to quantify the performance of the RNM in predicting normalized value coding, we fit the reduced form of RNM (Wong & Wang, 2006) with 4 free parameters (JNi,i,i, JNi,j,k(i≠j≠k), I­0, and a scaling parameter *S* applied to the predicted neural firing rates) to a normalized value coding dataset (Fig. 4 in Louie et al., 2011). Other parameters are set the same as reported in the original paper (Wong & Wang, 2006), except that the noise term is set as zero. The RNM is expanded to a trinary choice circuit, with three selective populations wired together based on the same rules specified in the original paper (Wong & Wang, 2006). We study the predicted neural activity on the pool 1 that receives direct input from *V1* and investigate how the activity of pool 1 changes with the values of contextual inputs *V2* and *V3*. The BADS algorithm was used to minimize the mean squared error between the predicted neural firing rates of pool 1 and the empirical neural firing rates data reported in Fig. 4 of Louie et al., 2011. The best-fitting result shows that the RNM explains 89.2% of the variance, worse than the DNM and LDDM we reported in the main text (Best-fitting parameters: = .0055, = .0861, = .3511, *S* = 1.074).

#### Fitting the LDDM to empirical behavioral data

The LDDM with seven free parameters (the weights of self-excitation () and disinhibition (), the variance of Gaussian white noise in the Ornstein-Uhlenbeck process (), the scaling parameter of input (*S*), and time constants for three types of units , , and ) was fit to choice behavior (RT and choice accuracy) in a classic perceptual decision-making dataset (Roitman & Shadlen, 2002). was set to zero since any positive values will worsen the accuracy performance. was fixed as zero since it shows high collinearity with (**Fig. 6-figure supplement 3**). We employed the commonly used quantile maximum likelihood estimation (QMLE) method (Heathcote et al., 2002; Ratcliff & McKoon, 2007). The rationale of QMLE is to minimize the differences between the predicted data and the empirical data on the proportion of number of trials located in each RT bin. Choice accuracy was implicitly estimated because the algorithm accounts for the proportion of number of trials between correct and error trials. Nine quantiles (from .1 to .9 with .1 of step size) were used resulting in ten RT bins, with correct and error trials accounted for separately at each coherence level. Because the LDDM has no closed-form analytic expression for the RT distribution, we evaluated the prediction by Monte Carlo simulations (10240 repetitions for each input coherence). In each simulated trial, the initial values of *R1* and *R2* activities were set as 32 Hz to be comparable to empirical data (Churchland et al., 2008; Roitman & Shadlen, 2002). Visual stimulus (motion) inputs were defined as *S*\*(1+c’) and *S*\*(1-c’) for *V1* and *V2*, where the free parameter *S* models input scaling and the coherence c’ replicated values in the original experiment (0, 3.2, 6.4, 12.8, 25.6, and 51.2 %)(Roitman & Shadlen, 2002). At visual stimulus onset, a gap period (90 ms) was implemented in order to capture the commonly observed initial dip in empirical firing rates (Roitman & Shadlen, 2002). Gated disinhibition was activated along with inputs after the gap. A decision was reached when either of the *R* unit activities reached a decision threshold of 70 Hz, the biological threshold observed in the empirical data (Roitman & Shadlen, 2002). 30 ms was added to the RT of threshold hitting to capture the delay in the down-streaming motor execution. After the decision, the input values, α, and were reset to zero. The negative loglikelihood (nLL) of QMLE was minimized using BADS algorithm in Matlab (Acerbi & Ma, 2017a). The estimation was conducted using GPU (NVIDIA Tesla V100) parallel computation on a high-performance cluster (NYU Langone), with 160 chains of random initial parameter values to prevent local minima. The chain with the smallest nLL in its fitting result was selected as the best-fitting result.

The visualization of the predicted RT distribution (**Fig. 6A**) was calculated based on 60 evenly distributed RT bins, with correct and error trials calculated separately under each coherence. The predicted neural dynamics (**Fig. 6D**) were generated using the model best fit to behavior. *R* unit activities were aggregated across correct trials, segregated by units associated with the chosen and unchosen sides. As in the original experiment data visualization (Roitman & Shadlen, 2002), activity early in trials was aligned to stimulus onset and data within 100 ms of boundary crossing were omitted to reduce the impact of decision dynamics on visualizing early-stage ramping dynamics. Early activity traces were cut off at the median value of RT for each coherence level to ensure that the average trace was based on at least half of the trials. Activity late in trials was aligned to the time of the decision, and data within 200 ms of stimulus onset was omitted.

#### Fitting the RNM to empirical behavioral data

In order to compare the model performance in predicting choice behaviors, we fit the original RNM to the classical perceptual decision dataset (Roitman & Shadlen, 2002). We used the reduced form of the RNM (Wong & Wang, 2006). We set eight parameters in the reduced model (see the Appendix in its original paper) as free parameters to fit: self-excitatory coupling weights , mutual inhibitory coupling weights , non-selective input , noise amplitude of OU process , input scale , synaptic kinetic parameter , initial value , and time constant . The other parameters that describing the input-output relationship of a single cell were set as the same in the paper: *a* = 270 (VnC)-1, *b* = 108 Hz, *d* = 0.154 s. The time constant for the AMPA receptor was fixed as 2 ms. The task setting, non-decision time (90 ms delay after stimulus onset and 30 ms delay before saccade), and the optimization used were kept the same as in fitting the LDDM (see above). The time step *dt* was set as .001 s.

#### Fitting the LCA to empirical behavioral data

Another widely acknowledged decision circuit model – the leaky competing accumulator model (LCA) (Usher & McClelland, 2001) was fit to the behavioral data (Roitman & Shadlen, 2002). The dynamics of the two nodes in the LCA can be described using the following differential equations (Eq. 22).

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|  |  | (22) |

where () indicates the activity of each node; indicates the excitatory input value to each node; indicates the net leakage on each node after the cancellation of recurrent excitation; weighs the mutual inhibition strength from the other nodes; is a Gaussian random noise on each node with a standard deviation of .

The input values were set as 1+c’ for Option 1 and 1-c’ for Option 2, with c’ changing over 0 to .512. We fitted the threshold as a free parameter. In that way, the time constant can be taken as an arbitrary value (100 ms used in our case) since it was not independent from the threshold. Other than the parameters we mentioned above, non-decision time was fixed as 120 ms, sharing the same assumption with the other two models based on the empirical observed delays after stimulus onset (90 ms) and before saccade (30 ms). That gives in total four free parameters to estimate , , , and . Since the scale of the activities is arbitrarily defined, it would need rescaling when compared to the empirical data of mean firing rates in the unit of Hz. The task setting and the optimization used were kept the same as in fitting the LDDM (see above). The time step *dt* was set as .001 s.

#### Analysis of persistent activity

We showed in *Results* that the LDDM with recurrent excitation predicts persistent activity that maintains input information during delay intervals. Here we provide mathematical analysis of the LDDM differential equations to examine the properties and genesis of this persistent activity. In addition to examining the property of the system with symmetric gain-control weights (), we expanded our analysis to allow the gain-control weights to be asymmetric; this allows us to examine the robustness of LDDM properties to asymmetric weights.

Equilibrium states of the differential equations (Eqs. 1-3) after the withdrawal of inputs were considered. The gain control weights were split into two parts, with the local-option weight denoted as () and the cross-option weight denoted as (). The input values were set to zero and local disinhibition was assumed inactive (). Equilibria of the system were solved by taking the intersection of the steady states of all units, i.e., when , , and all equal to 0. When the input terms are set to zero, the solution degrades from Eq. 5 to Eq. 23 as a linear form,

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|  |  | (23) |

For a binary choice system, the solution of Eq. 23 is denoted in linear algebra as:

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|  |  | (24) |

The solutions of the equations depend on the value of recurrent excitation and baseline gain control . When , the equations do not provide a positive solution. This explains why the system without recurrent excitation () cannot generate persistent activity. When , the equations provide positive solutions. The model generates persistent activities in three different patterns depending on the symmetry of gain control weights, i.e., , , and .

First, by assuming and , the nullclines of *R1* and *R2* overlap on a line of attraction, as shown in **Fig. 8B (**the same as **Fig. 8-figure supplement 1B**). Any position on this line is an equilibrium point. This is a special case where the eigenvalues on each point have a real part of zero, therefore, linearization around the equilibrium points cannot tell us their stability. Thus, we checked instead the instantaneous change direction of neural activities across a wide range of initial values to see whether the system converges to the line of attraction. From the differential equations (Eqs. 1-3), the ratio of the instantaneous change rates of *R1* () and *R2* () keeps the same ratio as the ratio of original activities (*R1*/*R2*), given under the assumption of symmetric gain control weights. As a result, for any given initial values, *R1* and *R2* activities change in the direction that preserves the original ratio until reaching equilibrium on the line of attraction. The instantaneous changes of *R1* and *R2* are shown as a vector field (red arrows) in **Fig. 8B**. Thus, any positive initial values will drop into an equilibrium state with the ratio of *R1\**/*R2*\* maintaining the ratio of initial values, which preserves the ratio of inputs when the activities are inherited from the stage of value representation. **Fig. 8-figure supplement 1E**shows example dynamics of *R1* and *R2* under different ratios of input values (**Fig. 8-figure supplement 1G**). The activities show the characteristic dynamic of divisive normalization during the inputs and preserve this input information after withdrawal of inputs.

However, since the values of and are complementary on the line of attraction, any combinations of values with a constant sum satisfies the equilibrium. Thus, any disturbance to the system (e.g., random noise) will drive and to deviate from their original ratio resulting in a loss of the coded information about the inputs. Noise-driven drift on the line of attraction will cause decaying of the coded value information over time, consistent with the degradation attribute of working memory (Barrouillet et al., 2011; Barrouillet & Camos, 2012; B. Lee & Harris, 1996; Paivio & Bleasdale, 1974; Portrat et al., 2008).

In addition, under the special condition of symmetric gain control weights (), the formula in Eq. 24 can be easily expanded to multiple inputs with the equilibrium delay interval activities defined by:

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|  |  | (25) |

The summed value of all *R* units equals to a constant . When the number of inputs (*N*) increases, the activity shared by each *R* unit decreases and leads to a lower signal relative to noise scale. Thus, as the number of coded items increasing, the information kept during persistent activity may become less accurate considering lower signal-to-noise ratio. This may explain another important attribute of working memory – the constraint of working memory span (Cowan, 2010, 2016; Engle, 2001, 2002; Oberauer et al., 2016).

Second, by assuming and , the nullclines of *R1* and *R2* intersect on a unique equilibrium point, where *R1* and *R2* share the same value (**Fig. 8-figure supplement 1A**). The point is confirmed as attractive by linearization. Any positive initial values on the space of *R1* and *R2* will converge into this point, which is visualized in the instantaneous change ranges of *R1* and *R2* (red arrows) for a wide range of given initial values (**Fig. 8-figure supplement 1A**). Thus, *R1* and *R2* will gradually converge to be equal and the original information about input values will be lost. Nevertheless, the dynamic of information losing is based on the level of asymmetry of . For a close-to-symmetric matrix, the input information can be still preserved for a considerable amount of time. We showed example dynamics of information loss in **Fig. 8-figure supplement 1D**. After withdrawal of inputs, the *R* unit activities collapse into the same level and the coded ratio information gradually diminishes (simulation parameters: ).

Finally, by assuming and , the nullclines of *R1* and *R2* intersect on a unique equilibrium point, which is confirmed as unstable by linearization (**Fig. 8-figure supplement 1C**). Any initial values of activities on the space will diverge into the upper-left or bottom-right corner of the space generating high contrast between *R1* and *R2*, with the higher activity as and the lower activity suppressed to zero. The instantaneous change rates of *R1* and *R2* (red arrows) are visualized in the vector field in **Fig. 8-figure supplement 1C**. The instantaneous change direction bifurcates at the line of , biased to the side associated with higher initial activity. As an outcome, the *R* unit with higher initial values tends to increase while the opponent unit tends to be suppressed to zero, a process that implements WTA competition before the action stage but with constrained higher activity. Example *R1* and *R2* activity dynamics are shown in **Fig. 8-figure supplement 1F**. After withdrawal of inputs, *R1* activities with different preceding input values collapse onto the same level of high activity, while *R2* activities with lower input values are suppressed to zero. Thus, the system gradually switches from the normalized coding of inputs to a categorical coding of choice over the delay interval.

We also examined whether persistent activity could exist with active local disinhibition. We showed in **Results** that persistent activity in the working-memory task switches to WTA choice under the dynamic control of disinhibition (**Fig. 8D-F**). How does the transition from persistent activity to WTA choice happen? How might disinhibition change the dynamic pattern of persistent activity during a delay interval?

The analysis was based on the differential equations of the system with symmetric gain control weights and without inputs (Eqs. 1-3). The equilibrium solution is given by:

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|  |  | (26) |

With binary inputs, the solution can be thus written as:

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|  |  | (27) |

Besides the impact of recurrent excitation and baseline gain control discussed above, equilibrium responses are determined by the relative strength between disinhibition () and the gain control weight (). We examined three separate conditions: , , and . We have already shown the analysis for the special case when above (phase plane analysis and example dynamic shown in **Fig. 8-figure supplement 1B**) and replotted in **Fig. 8-figure supplement 2A** for the sake of comparison with other two conditions.

By assuming , the nullclines of *R1* and *R2* intersect on a unique equilibrium point, whose stability was confirmed as unstable after checking the eigenvalues of Jacobian matrix around the point (**Fig. 8-figure supplement 2B**). Any initial values on the space will diverge into the upper-left or bottom-right corner of the space, with the higher activity value as , and the lower activity value as zero. We show the instantaneous change rates of *R1* and *R2* at given initial values in the vector field (red arrows) (**Fig. 8-figure supplement 2B**). In **Fig. 8-figure supplement 2E**, we show example *R1* and *R2* activity dynamics (value setting kept the same as in **Fig. 8-figure supplement 1G**). All of the *R1* with larger input values converge into the same level of activity after withdrawal of inputs, while all of the *R2* with lower input values are suppressed to zero, implementing a WTA competition. Thus, the system gradually switches from normalized coding of input values to categorical choice from the early to the late stage of persistent activity.

By assuming , most of the features are similar to the previous situation, except that the model now predicts no constraints on the maximum activity (**Fig. 8-figure supplement 2C**). The system shows nullclines with an intersection at a unique repellor. The activities of *R1* and *R2* bifurcate at the line of . The example dynamics show that the activity of , which has higher initial value, increases to an unlimited level and thus will reach a decision threshold. The rising speed of depends on the advantage of over as defined by their initial values.

Taken together, these analyses show that persistent activity is present as normalized coding of input values only with symmetric gain control weights () and inactive disinhibition (). When disinhibition has a moderate strength (), the persistent activity gradually transitions from value coding to categorical choice coding but avoids hitting the decision threshold. When disinhibition is strong enough (), the system generates WTA competition and reaches the decision threshold.

#### Simulation of pharmacological manipulation of inhibitory activity

In **Fig. 10** we tested inhibitory potentiation (e.g., GABAergic agonist) manipulation effects in both the LDDM and RNM (Wong & Wang, 2006) by assuming different levels of enhancement of the inhibitory projections. For LDDM (**Figs. 10A-D**), we assumed , , input scale *S* = 256, decision threshold = 70 Hz, and *dt* = 1 ms. Panel **A** illustrated the temporal dynamic of excitatory pools (*R1* and *R2*) under input coherence of 25% between control (inhibitory connection weight = 1.0) and potentiation (inhibitory connection weight = 3.8) conditions (other parameters used were , , = 0, , and ). Panel **B** examined the predicted RT and choice accuracy over different input coherences (c’ = [0, 3.2, 6.4, 12.8, 25.6, 51.2] %) and levels of inhibitory weights (from 1 (control) to 4 (enhanced)) (, , = 0, , , and 10000 repetitions). Panel **C** showed the chromomeric and psychometric curves over a number of input coherences (1% – 100%) under the section between control and inhibitory potentiation (inhibitory connection weight = 1.8). Panel **D** scanned the full parameter space of and between the contrast of control and inhibitory potentiation (inhibitory connection weight = 1.8) (c’ = 3.2%, , = 0, and 10000 repetitions). For RNM (**Figs. 10E-G**), we used the parameters specified in Wong and Wang, 2006 for the mean-field rate model. Inhibitory potentiation was manipulated by weighting the inhibitory connection in the model. Panel **E** illustrated the noiseless neural dynamics of RNM using the same input coherences and inhibitory enhancement levels as in panel **A**. Panel **F** was set to compare with panel **B**, thus the input coherences and inhibitory enhancement kept the same as in panel **B**, with noise amplitude set as recommended by Wong and Wang, 2006. Panel **G** showed the chromomeric and psychometric function predicted by RNM under the same input and inhibitory potentiation assumptions as in panel **C**.

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#### Data and code availability

The empirical data presented in this paper and MATLAB code used for simulations and fitting the empirical data will be available upon publication at DOI 10.17605/OSF.IO/YGR57.

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