Fig. 1 Multistable perceptual rivalry. The fragmented images presented to the left and right eyes in **a** can lead to the coherent percepts shown in **b** Kovacs et al. (1996). **c** An example of the stimuli presented to the left and right eyes in Jacot-Guillarmod et al. (2017). Gratings were always split so that halves with the same color and orientation could be matched via interocular grouping, but were otherwise randomized across trials and blocks (See Jacot-Guillarmod et al. (2017) for experimental methods). **d** Subjects typically reported seeing one of four percepts – two single-eye and two grouped – at any given time during a trial. **e** A typical perceptual time series reported by a subject, showing the stochasticity in both the dominance times and the order of transitions between percepts

that involves different levels of visual cortical processing by building a hierarchical neural network model of binocular rivalry with interocular grouping. Our model captures the qualitative dynamics of perceptual switches reported by human subjects in experiments described by (Jacot-Guillarmod et al. 2017) involving the visual stimuli shown in Fig. 1c. When presented with these stimuli, subjects reported alternations between four percepts, two *single-eye percepts*, and two *grouped percepts* that combined two halves of each stimulus into a coherent whole (See Fig. 1d).

Levelt's four propositions (1965) capture the hallmarks of bistable binocular rivalry by relating *stimulus strength*

of the visual hierarchy. Our model thus suggests constraints on the interactions between neural populations in the visual system.

Our study thus shows that more complex visual stimuli can be used in perceptual rivalry experiments to drive the development of more detailed mechanistic models of perceptual processing R3.29412841w10 0 6Fnstraints

2003; Lamme and Roelfsema 2000). However, each level could also describe multiple functional layers of the visual system (Sterzer et al. 2009).

First level of the visual hierarchy The activity of each neural

generalized Proposition II when the grouped percepts were stronger. When one class of percept is much stronger (e.g., single-eye percepts), we expect them to completely suppress percepts of the other class (e.g., grouped percepts). Percept strengths used in the

while keeping them equal (See Fig. 5b). When grouping strength, β, is sufficiently high ($\beta >$

dominate. Hence, simultaneously increasing the value of α and β while keeping them equal, is approximately equivalent to increasing the input . Since the period of the associated deterministic model decreases as input strength, ,
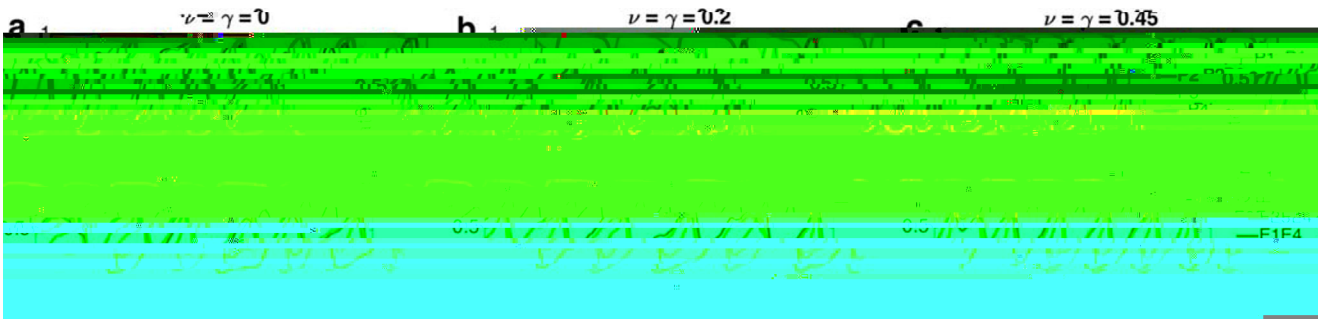
Fig. 7 Time series with different mutual inhibition at the upper level. Each upper panel shows the neural activity of percepts (populations at the higher level of the hierarchy), and lower panels show inputs from the lower to the higher level of the hierarchical model; e.g., $E1E$
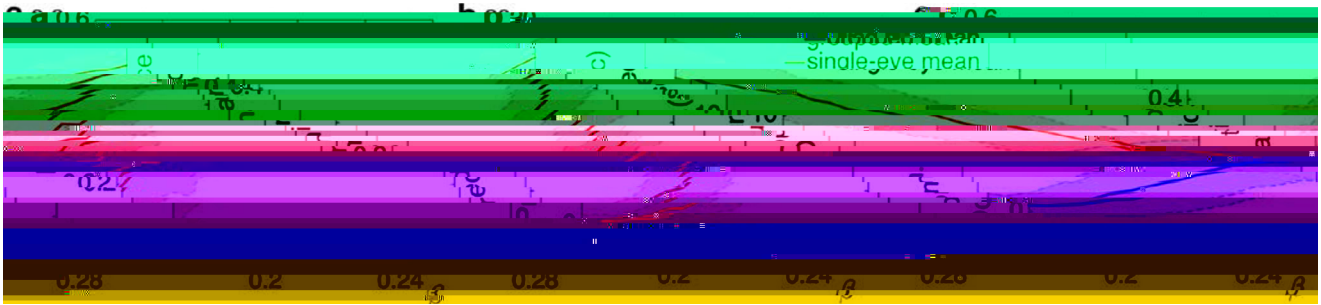
Fig. 9 Simulation results with feedback from the higher to the lower level of the hierarchy. Simulations indicate that the model can capture the key experimental results in Jacot-Guillarmod et al. (2017) even with feedback from the higher level to the lower level: **a** Predominance of grouped percepts increased as the interocular grouping strength increased; **b** The average dominance duration of single-eye percepts decreased while the average dominance duration of grouped percepts remained approximately unchanged (when $\beta < \alpha$ but close to the value α); **c** The ratio of the number of visits to the grouped percepts increased as the interocular grouping strength increased. Here $\quad = \quad = 0.1$ in Eq. (5), with other parameters as in Fig. 3

When population $E_1(= E_2)$ dominates, it leads to the domination of percept 1 ($\quad_1$). Similarly, when $E_3(= E_4)$ dominates, then so does percept 2 ($\quad_2$). Alternations in elevated activity between populations E_1 and E_3 therefore correspond to rivalry between percepts 1 and 2. Hence, Eq. (1) generalizes existing models of rivalry, and can cap-

another (Hupe and Rubin 2004). In these cases subjects perceive either a grating or a moving plaid in alternation (three total percepts: moving to the left, moving the right and moving upward). Mutual inhibitory, adapting neuronal network models display dynamics consistent with data from such experiments, suggesting the mechanisms behind such rivalry may be similar to those driving conventional binocular rivalry (Huguet et al. 2014). This provides further evidence that the classical models of rivalry can serve as a foundation for models describing more complex settings.

Comparisons with previous models of perceptual multistability Our computational model is based on the assumption that perceptual multistability occurs via a winner-take-all process, with a single percept tempor98 2--r10 0 0 10 7-408.(78999939(m).5(o)15(v)-.30000001(ing)-404.3999939(to)-405.27572 Tmes

1999). However, a number of issues remain unresolved. The question of whether and when binocular rivalry is eye-based or percept-based has not been fully answered (Blake 2001). Activity predictive of a subject's dominant percept has been recorded in lateral geniculate nucleus (LGN) (Haynes and Rees 2005), primary visual cortex (V1) (Lee and Blake 2002; Polonsky et al. 2000), and higher visual areas (e.g., V2, V4, MT, IT) (Logothetis and Schall 1989; Leopold and Logothetis 1996; Sheinberg and Logothetis 1997). Thus, rivalry likely results from interactions between networks at several levels of the visual system (Freeman 2005; Wilson 2003). To understand how these activities collectively determine perception it is hence important to develop descriptive models that incorporate multiple levels of the visual processing hierarchy.

Collinear facilitation involves both recurrent connectivity in V1 as well as feedback connections from higher visual areas like V2 (Angelucci et al. 2002; Gilbert and Sigman 2007

Chow 2011; Wilson 2003). We then numerically found the same qualitative results hold for [1, 1.25].

Appendix B: Simulation procedure

To obtain the results shown in the figure, for each given parameter set we ran 100 realizations of the model for 300 seconds each and computed the dominance durations, predominance, and visit ratio for each percept. We pooled all dominance durations of one class of percepts (e.g., single-eye percepts or grouped percepts) and computed its average and standard deviation across occurrences and realizations.
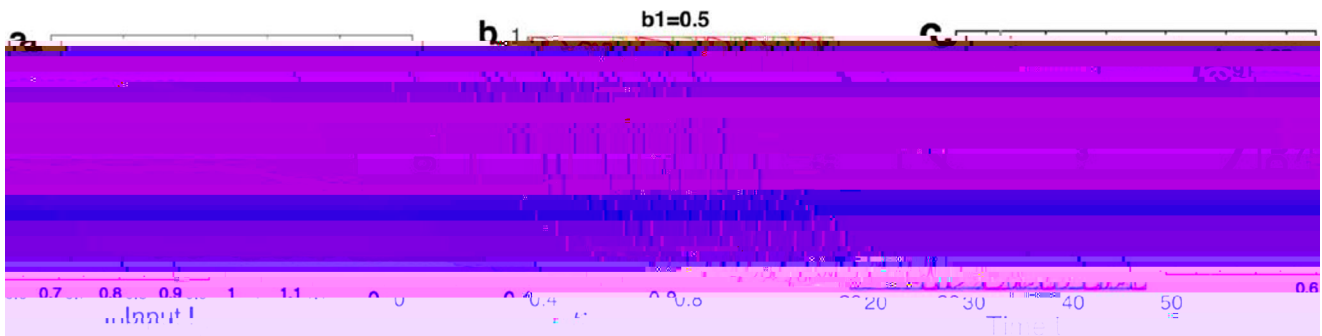

Fig. 11 Adaptation rate, κ, at the higher level of the hieararchy, and top-down influence. **a** The adaptation rate had little or no effect on the dominance duration of percepts. Parameter values as in Fig. 3. **b** Example of top-down influence from only one percept, here $_3$ ($_1 = _2 = _2 = 0$ and $_1 = 0.5$). Top down input from one

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