

broader role in many types of neuron [12] and does not function uniquely in the adult brain as a regulator of learning and memory. The situation is further complicated by the fact that p190 RhoGAP is very closely related to the protein p190-B RhoGAP, which is also widely expressed in brain [24] and the disruption of which in mice is associated with neural defects [25]. The degree of functional redundancy between these two RhoGAPs has not yet been determined. Interestingly, mice lacking p190-B RhoGAP exhibit a nearly complete loss of phosphorylation of the cAMP-response-element-binding (CREB) transcription factor in brain [25], and CREB mutant mice reportedly exhibit defects in several aspects of fear conditioning [26]. Thus, it is possible that both p190 RhoGAPs participate in fear conditioning through distinct regulatory mechanisms. Overall, it is becoming increasingly clear that the response to fear is, at the molecular level, complex, involving numerous signaling proteins that undoubtedly perform multiple functions in both the developing and the mature nervous systems. With hindsight, it could be argued that the identification of the amygdala as a crucial brain region that mediates fear conditioning was relatively easy, and that the hard part has just begun.

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Research Focus Response

Response: Binocular rivalry and perceptual multi-stability

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We appreciate Nava Rubín's commentary [1] concerning our work on multi-stable binocular rivalry [2], articulating its relationship with conventional bi-stable binocular rivalry and with pervasive mutual exclusivity in visual processing.

She indicated that our results have opened up a 'multi-stable front', promising to provide new constraints for modeling the neural interactions that generate coherent unitary percepts from ambiguous retinal stimulation. Here, we focus on additional ways in which our results could contribute to elucidating cortical visual processing.

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Obtaining a stable and unambiguous interpretation of retinal input is a crucial goal of visual processing (partly because motor response selection tends to produce a serial bottleneck). As indicated by Nava Rubin, perceptual multi-stability provides a convenient laboratory paradigm for understanding how perceptual stability might be achieved under normal circumstances. However, the spontaneous shifting from one perceptual interpretation to another (evident in binocular rivalry as shifts from one image to another) is also ubiquitous and perhaps crucial for continued sampling of the visual world [3–4]. For example, even in the absence of eye movements, attention spontaneously shifts from one object to another, from one feature (e.g. color) to another (e.g. shape), and from one organization (e.g. of grouping, and/or of figure and ground) to another – perhaps in search of potentially important information. The neural interactions that control the timing and the course of these perceptual transitions are likely to be structured to optimize processing of information from a dynamic and multi-faceted visual environment. Extensive research on bi-stable binocular rivalry has addressed the time series of perceptual transitions for the simplest case of two-state transitions [5–8]. If all transitions among multiple images exhibited identical transition probabilities, investigations of bi-stability would be sufficient for understanding multi-stability [9–11]. Thus, our crucial finding is that transition probability can be path-dependent – that is, the probability of making a transition to a particular image can depend on what image is currently perceived. Furthermore, the fact that transition probabilities were elevated between certain classes of pattern (e.g. ‘opponent’ shapes as defined by brief shape after-effects [12–16], and symmetric images) suggests that the path of perceptual multi-stability offers a tool to understand the structure of pattern coding, with elevated transition probabilities providing a measure of pattern ‘relatedness’.

Path dependence also suggests that any model of perceptual multi-stability should accommodate image stability (duration) and transition probabilities as distinct components. A framework based on potential-energy wells (or attractors) [17–19] might initially prove useful. Intuitively, the duration of each image can be affected by the depth of its potential trough, whereas transition probabilities can be affected by the height of the barriers separating the troughs (e.g. relatively frequent transitions between images that are separated by lower potential barriers and relatively infrequent transitions between images that are separated by higher barriers). This framework parsimoniously accommodates our paradoxical result that, while perception was trapped within a pair of opponent images, duration of those images increased whereas the transition probabilities between them decreased – presumably owing to ‘high-level’ adaptation to perceptually selected images [2]. The presence of adaptation effects also suggests that path dependence reflects short-term plasticity in neural interactions, in addition to stable aspects of neural connections.

Finally, the literature on bi-stable rivalry suggests that the selection, dynamics and the mutual exclusivity of rivaling images depend on processing in multiple cortical

visual areas [3,7,8,20]. For example, the degree of mutual exclusivity tends to be enhanced when multiple grouping factors (e.g. the eye of origin, color, pattern coherence and synchrony) support competition between a particular pair of images [21–24]. Thus, although our study demonstrated the dependence of perceptual multi-stability on pattern coding, future research examining its dependence on processing of other visual attributes (e.g. color and motion) will provide insights into how multiple visual areas interact to direct the course of spontaneous visual exploration. Further, given that perceptual multi-stability is characterized by two parameters – image duration and transition probability – an unresolved question is how their respective underlying neural mechanisms might be related. To answer this, it is essential to examine carefully how the two parameters are influenced by basic psychophysical manipulations. For example, we are now investigating how image duration and transition probability are jointly influenced by pattern characteristics, as well as by short-term modulatory factors such as pattern pre-adaptation, temporal- and feature-based image grouping, priming of transitions, and intentional efforts of observers [25–28]. We are optimistic that perceptual multi-stability will provide a unifying framework to facilitate an integrative understanding of pattern coding, short-term neural plasticity and cognitive factors such as intention.

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Research Focus

Binocular rivalry and perceptual multi-stability

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When different images are presented to the two eyes, binocular rivalry can occur – that is, perceptual alternations between the two monocular images (bi-stability) or between more than two percepts comprised of complementary portions of the two images (multi-stability). A recent paper reports important findings about the dynamics of multi-stable alternations in binocular rivalry.

When an observer is presented with one image to the right eye and simultaneously an unrelated image to the left eye, a phenomenon known as binocular rivalry occurs. The observer reports periods of seeing only one of the images, which alternate in a seemingly random manner with periods of seeing only the other [1]. Binocular rivalry is, thus, an example of perceptual *bi-stability*: a class of phenomena in which a particular stimulus gives rise to two different interpretations that alternate over time. Other known examples are ambiguous figures such as the Necker cube [2], Figure–Ground illusions such as the face–vase [3], and ambiguous motion displays such as the plaid [4,5]. What is common to all these stimuli is that they offer more than one plausible interpretation. What is common in terms of the perceptual response to these stimuli is that only one interpretation is perceived at any given moment. This suggests that the brain has built-in mechanisms to enforce *mutual exclusivity*: given a stimulus with more than one possible interpretation, the neural representation of only one of those interpretations is allowed to be active at each moment.

One of the reasons why bi-stability is interesting is that it could reveal general principles about brain architecture.

It is unlikely that the brain developed specialized mechanisms for bi-stability just so that it can deal with the rare cases of deeply ambiguous stimuli such as those mentioned above (which are typically encountered only in the laboratory). More likely, bi-stability – and the principle of mutual exclusivity it implies – occurs as a result of brain architecture that has evolved to deal with the far more common situations of ‘weak ambiguity’ present in many sensory stimuli. (For example, every retinal image could have arisen from a multitude of underlying scenes [6].) Normally, there is a wealth of cues in the environment to render one interpretation far more likely than the others, although often not to eliminate the others entirely. The fact that we (as perceivers) are not aware of ambiguity attests to the great success of the brain in implementing the principle of mutual exclusivity.

Although some of the most well known examples of ambiguous stimuli give rise to just two competing percepts, in certain cases a stimulus can have more than two plausible interpretations. In such cases, prolonged observation results in *multi-stability*: each of the competing interpretations enjoys periods of dominance, and the (three or more) percepts alternate in dominance in a seemingly random manner. Multi-stable phenomena, like bi-stable phenomena, therefore suggest an underlying principle of mutual exclusivity. In contrast with bi-stability, however, there has been rather little work on multi-stable phenomena, both experimentally and theoretically. In particular, in the domain of binocular rivalry, which in its very nature involves pitting two images against each other, alternations between just two percepts have been the focus of most studies. It is possible, however, to obtain multi-stability from binocularly rivaling stimuli.

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A recent paper by Suzuki and Grabowecky [7] brings the issue of multi-stability in binocular rivalry to front and center stage. The paper makes an important contribution towards turning binocular rivalry into a useful general model for how the brain deals with ambiguity. Given that sensory information can have multiple interpretations, moving from bi-stability to multi-stability is a much needed step if binocular rivalry is to reveal general principles about how the brain implements mutual exclusivity.

Inducing multi-stability in binocular rivalry

Suzuki and Grabowecky [7] took advantage of a recently re-discovered finding about binocular rivalry: the brain can 'piece together' parts of the two monocular images, from spatially non-overlapping portions of space, to form a unitary percept [8,9]. This phenomenon, known as inter-ocular grouping, is key to understanding how binocular rivalry can give rise to multi-stability. If images comprised of portions of each monocular image can enjoy periods of dominance, then the apparent limitation of only two competing percepts (those projected to the two eyes) is removed. However, it is still non-trivial to produce inter-ocular grouped stimuli that are suitable for a systematic study of multi-stability. For example, it is well known that binocularly rivaling images larger than $\sim 1^\circ$ can lead to 'mosaic' percepts comprised of fragments from each eye; however, these 'mosaic' images are fleeting and do not tend to recur reliably. To study multi-stability with binocular rivalry it is necessary to find stimuli that give rise to inter-ocular grouping percepts that enjoy robust, repeated periods of dominance – we term such percepts 'quasi-stable'.

Suzuki and Grabowecky devised stimuli that gave rise to four quasi-stable percepts: each of the two monocular images, as well as two inter-ocular grouped percepts [7]. An example is shown in Fig. 1: the monocular images are an upright and an inverted triangle. At prolonged exposures, observers reported seeing not only those two percepts (at different times), but also two others: a left-skewed and a

right-skewed parallelogram. Those percepts resulted from grouping of the right-hemifield portion of one triangle with the left-hemifield portion of the other. The unique thing about these four possible percepts is that they cluster into two pairs of related stimuli: a pair of triangles and a pair of parallelograms. This allowed Suzuki and Grabowecky to examine an important question: given a stimulus that leads to multi-stability, is there any structure underlying the transitions from one quasi-stable percept to another? They found strong evidence that there is. Specifically, they found that perceptual alternations tended to become 'trapped' in sequences going back and forth between the two members of a related pair (e.g. 'upward triangle to inverted triangle to upward triangle'), with such trapping occurring a lot more often than expected by chance (i.e. if a triangle shape is as likely to follow one of the parallelogram shapes). Note that in this example, the pair of triangles and the pair of parallelograms resulted from single-eye dominance versus mixed-eye dominance (inter-ocular grouping), respectively. This presents a possible explanation for the trapping that is unrelated to their shapes: that there is a general tendency for the brain to switch eye dominance in a synchronized manner across the visual field. This would lead to sequences of back-and-forth single-eye dominance alternations, as well as sequences of mixed-eye dominance, occurring at above-chance probability. To test this possible explanation, the authors performed control experiments in which the inter-ocular-grouped images were no more related to each other than to the single-eye images. No trapping was observed. The authors concluded that the trapping they had observed was driven by the relatedness of the shapes in a trapping sequence.

Theoretical implications

Suzuki and Grabowecky [7] interpreted their results in the context of a theory postulating that each quasi-stable percept is an 'attractor' state, which is associated with a certain potential energy [10–12]. They proposed that related percepts (e.g. left-pointing and right-pointing parallelograms) had lower energy barriers separating them and that, therefore, the probability for a transition between related shapes was higher than that of a transition between less related shapes (e.g. a triangle and a parallelogram), giving rise to the observed trapping sequences. Further findings, that seem conflicting at first glance, might also be accounted for with this framework. As the alternation sequence progressed, the probability of continued trapping receded but the dominance durations of the individual percepts grew. The authors proposed that during a trapping sequence, 'the potential barrier separating the [related shapes] might rise, making the percept relatively more likely to break from the trapping...while at the same time increasing [its] dominance durations'.

Thinking of quasi-stable percepts as attractor states is an appealing idea, as it offers a link between multi-stable phenomena and more general theories about neural computation [10–14]. At the same time, it is not obvious how to relate this (attractor) framework to the existing body of theoretical work on binocular rivalry. The majority of models in this domain utilize an architecture consisting

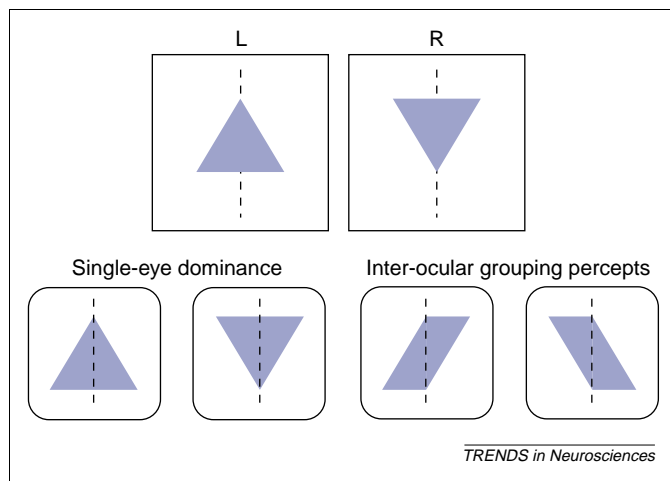


Fig. 1. Example of a stimulus used by Suzuki and Grabowecky [7]. Top: the monocular images projected to the left (L) and right (R) eye were an upright and inverted triangle (the dashed lines indicating the midline were not present in the stimuli). Bottom: four quasi-stable percepts alternated over time. These were the monocular images and, in addition, two inter-ocular grouped percepts depicting a left-skewed and a right-skewed parallelogram.

of reciprocal inhibitory connections between populations of neurons that represent the two competing percepts. This architecture implements mutual exclusivity via a 'winner-take-all' mechanism, allowing only one population to be active, or 'dominant', at any given time [15–19]*. Some of these models have been successful in reproducing key features of the dynamic behavior observed experimentally, such as the distribution of dominance durations and the effect of changing stimulus strength on those durations [1]. By contrast, it is not known whether attractor-based models or those based on transition probabilities can show the dynamic behavior observed experimentally. But then again, extending the present binocular rivalry models to account for multi-stability is not straightforward: positing reciprocal inhibitory connections between all competing percepts seems tenuous because the amount of required connections increases dramatically. By underscoring the relationship between binocular rivalry and multi-stability, Suzuki and Grabowecky [7] thus open a new front in the challenging task of finding appropriate models for these phenomena. Furthermore, they provide a rich set of data that impose new constraints on the models. Meeting the challenge could bring us closer to understanding not only multi-stability but also, more importantly, how the brain achieves the stability experienced most of the time.

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* There had been some debate over whether binocular rivalry reflects dominance and suppression of monocular cells in V1, or involves neuronal populations that represent higher-level abstractions of the stimuli (e.g. in inferotemporal cortex). The emerging consensus seems to be that rivalry probably takes place at both levels [20]. Many of the models are, however, sufficiently general for the reciprocal inhibition to refer to neuronal populations in either V1 or the inferotemporal cortex.

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