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Review

Multistability, perceptual value, and internal foraging

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SUMMARY

Substantial experimental, theoretical, and computational insights into sensory processing have been derived from the phenomena of perceptual multistability—when two or more percepts alternate or switch in response to a single sensory input. Here, we review a range of findings suggesting that alternations can be seen as internal choices by the brain responding to values. We discuss how elements of external, experimenter-controlled values and internal, uncertainty- and aesthetics-dependent values influence multistability. We then consider the implications for the involvement in switching of regions, such as the anterior cingulate cortex, which are more conventionally tied to value-dependent operations such as cognitive control and foraging.

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Multistable perception—the dynamical alternation that arises when a single sensory input has more than one interpretation or explanation (see also Figure 1 and Box 1: Multistable perception)—is a remarkable phenomenon that has been studied for at least a quarter of a millennium (see e.g., Dutour, 1760) and has attracted the attention of a wide range of brain scientists. The existence and dynamics of switching have been investigated with a diverse range of tools and approaches: psychophysics (Klink et al., 2012), electrophysiology and imaging (Blake and Logothetis, 2002; Koch et al., 2016), computational and theoretical modeling (Brascamp et al., 2017), pharmacology (see e.g., Carter et al., 2007; Mentch et al., 2019), neuropsychology (see e.g., Valle-Inclán and Gallego, 2006), and even with tools from genetics (see e.g., Chen et al., 2018). Furthermore, various aspects of perceptual multistability have been found to differ in a range of psychiatric conditions (e.g., Jia et al., 2020 report that, compared with healthy volunteers, the rate of perceptual switches is typically slower in major depressive disorder and faster in generalized anxiety disorder). Lastly, multistable perception is not restricted to human and non-human primates but has been reported in a wide variety of species, including insects, fish, and reptiles (Carter et al., 2020).

Seen as a scientific tool, multistable perception is one of the most straightforward, and least invasive, ways of putting the brain in what might be thought of as a non-conventional operating regime (in the sense of receiving an uncommon sensory input and engaging in an uncommon visual task; see e.g., Arnold, 2011). Examining such modes is a fruitful method for gaining an integrative understanding of neural function. Thus, multistable perception has been used to ask a broad range of questions from the core principles of information processing in the brain,

such as perceptual inference (Brascamp et al., 2017), all the way to high-level aspects of behavior, such as visual awareness (Logothetis, 2006) and perceptual decision-making (Parker and Krug, 2003; Krug, 2020). It is impossible for us to do full justice to this wonderful wealth of work on multistable perception. Therefore, we have had to select the few references that underpin our argument; we refer the reader to the excellent reviews of Blake and Logothetis, 2002 and Brascamp et al. (2017) for both complementary and more comprehensive historical treatments.

A convenient (though contestable) way to structure a theoretical investigation of perceptual multistability is via Marr's computational, algorithmic, and implementational levels of analysis (Marr and Poggio, 1979). The computational level concerns information-processing goals. For perception, this is prominently an inference about the contents of the sensory world (Doya et al., 2007), combining likelihood information from the input (which, if ambiguous, has distinct modes for the multiple potential contents) with prior expectations (which, in some cases, suggest that the contents might change over time). The algorithmic level contains process models or effective procedures, often specifying deterministic or stochastic dynamical mechanisms that give rise to the dominance of single percepts and the switching. Finally, the implementation level concerns the neural substrate—typically excitatory and inhibitory lateral, feedforward, and feedback connections in a hierarchy of sensory cortical areas.

In multi-level explanations, the implemented neural circuits realize algorithms that instantiate the computations (e.g., Dayan, 1998; Cao et al., 2021). Other accounts mainly consider two adjacent levels, focusing on computations and their algorithms, exemplified by Markov chain Monte Carlo inference in, for instance, Gershman et al. (2014)'s perceptual processing model, or on implementations and algorithms, such as Cohen et al. (2019)'s treatment of chaos/noise in neural populations engaged
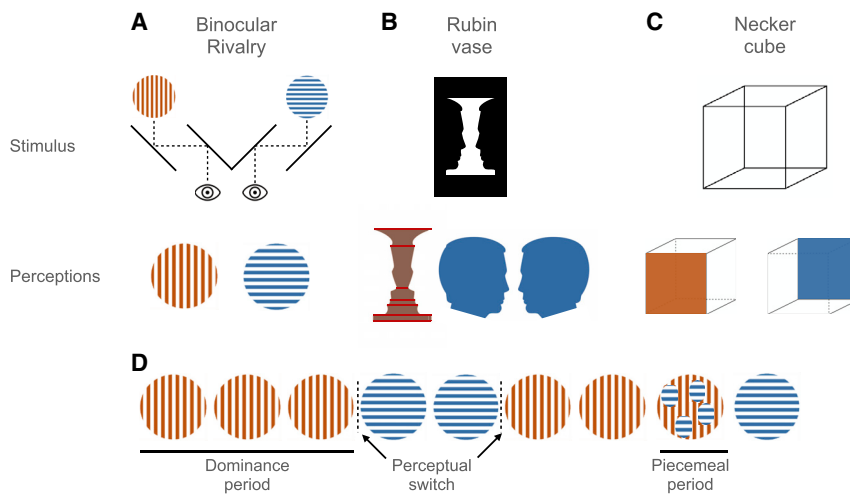
Figure 1. Multistable perception
(A–C) Three examples of multistable stimuli. The stimuli are cartooned above and the main percepts below. (A) Binocular rivalry involves a participant's two eyes seeing images that differ by more than just depth disparity. Participants typically perceive one of the presented images, horizontal (left, red) or vertical (right, blue) gratings. (B) The face-vase figure ground illusion. The participant might perceive the vase in the foreground (left) or the two faces (right) in the background (B is created with free avatars from "macrovector_official"/Freepik). (C) The Necker cube can be perceived as if the cube is viewed from bottom (left) or from top (right).
(D) In binocular rivalry, a participant's typical perceptual experience consists of dominance period (when either the left or right image is exclusively perceived) and perceptual switches (transition from one percept to the other). Perceptual switches can also be slow, with piecemeal perception arising when participants experience a mixture of both images (see Box 1 for more details).

in mutually competitive dynamics. Others still concentrate mainly on single levels, such as the Ising-model (Bialek and DeWeese, 1995) analogies for the computations involved in perceptual processing, or the very many suggestions (to which we return in the section 'concluding remarks and future directions') that multistable dynamics are primarily a consequence of biophysical and circuit properties, without reference to a computational end (e.g., Gao et al., 2006).

These extensive and diverse body of experimental and theoretical studies have helped us understand much about perceptual multistability. However, there is a critical distinction between (1) computationally active, information-seeking, accounts of perception (e.g., for vision, Findlay and Gilchrist, 2003)—how animals choose what to look at, or what to attend to, in order to collect the data necessary to accomplish tasks in the world that might ultimately deliver reward or avoid punishment and (2) computationally (though not biophysically) passive accounts in which sensory systems process whatever input is delivered by the periphery. With some honorable exceptions (e.g., Wilbertz et al., 2014; Parr et al., 2019; Haas, 2021), most work on multistability is computationally passive, specifying a form of under-controlled inference about the contents of the world. In the same way that active vision involves externally visible eye movements, one can see paying attention as a form of internal neural action (Schütz et al., 2011). From this perspective, multistability might best be conceived as an internal, at least partly controlled, process (Dayan, 2012a, ; Leopold and Logothetis, 1999; Parr et al., 2019; Martin et al., 2021) that responds to the same sort of affective imperatives as other controlled processes. The most obvious expectation from this is that multistability should be influenced by values, both explicitly and implicitly via the information that percepts might provide to allow a valuable choice of actions. Indeed, this has quite widely been found. For instance, reward and punishments can modulate the dynamics of perceptual alternations (Balcetis et al., 2012; Wilbertz et al., 2014; Marx and Einhäuser, 2015; Wilbertz et al., 2017; Wilbertz and Sterzer, 2018); furthermore, prominent among those psychiatric disorders that lead to changes in the

dynamics of perceptual alternations are the ones involving impairments in value-based decision-making processes (see e.g., Ye et al., 2019).

In this review, we first provide an overview focusing on core computational and algorithmic aspects of perceptual multistability. We then introduce an internal decision-making perspective in which the brain is seen as making choices about what to perceive—a form of foraging for values and value-related information. We discuss this perspective from computational, algorithmic, and implementational viewpoints.

MULTISTABILITY AND PERCEPTUAL INFERENCE

Prevalent computational- and algorithmic-level accounts of multistable perception start from the seminal suggestion of von Helmholtz whose modern interpretation suggests that perception is a statistical inference in a generative model of the sensory world (Doya et al., 2007). For images, this generative model specifies what input activity would be generated if different objects are present—in particular, locations in a scene that an observer views under given lighting conditions. The observer then has the recognition task of inverting the generative model—going from retinal activities to calculate the percept—i.e., a description of the objects, positions, and lighting that could have generated the activities, and can thereby *explain* them. Given noise, occlusion, and the indeterminacy created by the fact that the observer only has two slightly different 2D retinal projections of a complete 3D scene, recognition is often considered in statistical terms—with sensory evidence being integrated with prior expectations or knowledge that is derived from evolution or experience to create a posterior distribution. This prior information acts to regularize the recognition, favoring certain potential percepts over others. Typically, though not in multistable cases, one percept has an overwhelmingly higher posterior probability than the others, and so it becomes the dominant account of the input. Although incomplete, for instance, lacking an account of selection (Zhaoping, 2014), this Helmholtzian perspective has been extensively explored. In

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Box 1. Multistable perception

Perceptual multistability is a well-studied perceptual phenomenon in which when humans (and some other animals) are exposed to some particular forms of ambiguous stimuli (see Figure 1), they experience more than one percept. Multistable perception arises across many modalities (see for example, Zhou and Chen [2009] for olfaction, Warren and Gregory [1958], Kondo et al. [2012] for audition, and Darki and Rankin [2021] for somatosensation). However, we focus on the case of vision, which is the source of most examples.

Binocular rivalry is one of the most intensively studied forms of visual multistability (Blake, and Logothetis, 2002). It involves a participant's two eyes being shown images that differ structurally (for instance, with vertical bars in one and horizontal ones in the other). Shortly after initial presentation, just one percept (typically one image) is apparent to the participant—it is said to *dominate* (particularly for low contrast images, the first percept can involve fusion of the two images before exclusive perception and switching takes over; Brascamp et al., 2015). Over the course of prolonged exposure to such binocular-ambiguous stimuli, the participant experiences apparently spontaneous *switches* from one percept to the other—the length of each stable period is called a *dominance duration*.

Dominance durations in binocular rivalry (and other bistable stimuli) share common statistical properties, for example, more (Pastukhov et al., 2013) or less (Brascamp et al., 2005) gamma-like distributions, and have also been shown to exhibit scale-free fluctuations (Gao et al., 2006). Scale-free fluctuations are characteristic properties of scale-free phenomena. These fluctuations can be precisely defined and described based on their statistical properties, but, intuitively, they satisfy a dynamic analogy to the self-similarity property of geometrical fractals (e.g., the van Koch curve) in time series. For instance, for the case of perceptual multistability, if one creates a time series from the observed sequence of dominance durations, the Fourier transform of the resulting time series has amplitudes of spectral components inversely proportional to their frequencies (Figure 5b of Gao et al., 2006).

Dominance durations can also be manipulated (to be shorter or longer) by changing different attributes of a stimulus such as contrast (see Levelt's well-known propositions; Brascamp et al., 2015) and through learning (Klink et al., 2010; Suzuki and Grabowecky, 2007). Participants can also exert some voluntary control to avoid perceptual switches, although, in general, this has been shown to be difficult (for a review, see e.g., Scocchia et al., 2014). Notable exceptions are cases in which extensive perceptual training leads to nearly exclusive dominance of the rival image that contains the visual features used in the training phase (Dieter et al., 2016).

In binocular rivalry, in particular, switches can take substantial time during which the participants may perceive a mixture of both percepts—called *piecemeal perception*. Piecemeal perception also tends to manifest with a characteristic dynamic—for instance, with a wave of one of the percepts propagating over the visual field (also known as a perceptual traveling wave; Lee et al., 2005). Furthermore, it has been reported that during the time that the competition has not been fully resolved (e.g., close to switching times), attentional cues can help the resolution of perceptual conflict. For instance, Dieter et al. (2015) presented feature-based cues (a congruent or an incongruent visual pattern presented in the surroundings of the main stimulus) close to switching times and found that the cues that were congruent with the dominant stimulus prolonged the dominance durations, whereas the cues that were congruent with the suppressed stimulus expedited switching, consequently shortening the dominance period.

The difficulty of studying a phenomenon such as perceptual switching that is largely endogenous has led to the introduction of a number of other paradigms offering finer-grained experimental control. Examples include *onset rivalry* (Carter, and Cavanagh, 2007) in which participants perceive only one image upon simultaneous sudden presentation of both images on the left and right sides (called *perceptual predominance*) and different kinds of flash suppression paradigms (Tsuchiya et al., 2015) in which one stimulus can be suppressed in a controlled fashion via the sudden presentation of the other stimulus in the contralateral eye.

Lastly, perceptual multistability also shares some statistical properties with exploratory eye movements. Along with a postulated (Hancock et al., 2012), though disputed (Law et al., 2015), correlation between the saccade rates in an eye movement task and the rate of the perceptual switches in binocular rivalry, it has been shown that piecemeal and dominant perceptions exhibit scale-free fluctuations (Bakouie et al., 2017; Gao et al., 2006), which are also established statistical properties of eye movements (see e.g., Brockmann, and Geisel, 2000). This means that the dynamics of these processes are not memoryless in spite of the stochasticity of the switches—thus, in binocular rivalry, successive dominance durations tend to be positively correlated. Such statistical properties have been discussed in terms of underlying optimality principles (Brockmann, and Geisel, 2000) and/or neural dynamics (Gao et al., 2006).

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particular, given the structure of the visual system, and the complexity of visual scenes, it is common to think of multilayered generative and recognition models. The latter can be realized in bottom-up connections in a hierarchy of cortical areas and the former in top-down connections between the same areas (Dayan et al., 1995; Bastos et al., 2012).

Multiple aspects of perception fit such a Helmholtzian account, including many visual illusions (Geisler and Kersten, 2002). It of-

fers a particularly attractive basis for understanding multistable perception. The idea is that some sensory input is substantially ambiguous in such a way that multiple, radically different, and incompatible percepts offer nearly equally good (or in the case of binocular rivalry, nearly equally bad) explanations of the input—having nearly equal posterior probabilities. Without an overwhelmingly favorite explanation, a full probabilistic description of recognition would be a multi-modal posterior

distribution over these percepts. However, rather than realize the whole distribution at one time, the brain chooses a particular mode as a current percept but then switches to other modes over time. Differences in posterior probabilities of alternative modes would then lead to differences in dominance durations of their associated percepts.

There are many theoretical accounts of multistability along these lines (Brascamp et al., 2017). They differ according to their computational and algorithmic rationales and methods for picking particular modes and switching between them. Particular attention has been paid to algorithmic features—for instance, sculpted excitation and inhibition, which allow one percept at a time to dominate; deterministic adaptation, which limits the length of this domination and can model expectations about perceptual change over time; and noise, which can make dominance durations stochastic and can model sequential exploration of multiple potential modes of the posterior distribution.

Hints about the relevance of this Helmholtzian perspective for multistability come from the consideration of uni-modal and multi-modal aspects of the likelihood of stimuli. For a uni-modal instance, it has been shown that there is perceptual preference for natural images (Baker and Graf, 2009), visual objects that match their context (Brascamp and Shevell, 2021), and even visual stimuli that correspond with our intuition about real-world physics (Gilroy and Blake, 2004; Jackson and Blake, 2010) (although not necessarily actual physical principles; Pastukhov et al., 2018). Such stimuli should have higher likelihood in a reasonable generative model. In multi-modal terms, many studies have considered cases in which the input in the non-visual modalities is either congruent or incongruent with one of the potentially rivaling visual stimuli. Typically, congruence will increase the overall likelihood; incongruence will decrease it; and as expected from this, the former case is endowed with longer dominance durations (e.g., Conrad et al., 2010). Perhaps surprisingly, there is evidence that this goes beyond pure sensory information and also applies at the level of semantics (Chen et al., 2011) and abstract representations/relationships (Lee et al., 2015). For instance, Lee et al. (2015) used musical notes rivaling with a simple grating and showed that *only* for participants who can read music, presentation of an auditory melody matching the note prolonged the duration of that note's percept.

However, we have so far only discussed passive and affectless aspects of posterior distribution over interpretations of visual input. As we noted, perception is actually a highly active process—observers make decisions about where to move their sensory apparatuses (e.g., how to saccade and/or pay attention) in the light of the information that they need to gather about the world to be able to choose actions that increase reward and decrease punishment over the long run (Findlay and Gilchrist, 2003; Whitehead and Ballard, 1990). These sensory decisions greatly affect what participants will perceive and for how long. A wealth of this work concerns saccades and attentional focus *within* single images or image parts (Li, 2002; Zhaoping, 2014). For multistability, the issue can also be at the coarser level of selection *between* images.

The animating question for the current review is whether this active perspective can illuminate aspects of multistability—

with internal decisions of what to perceive and when to switch being analogous to external decisions of what to look at and when to saccade, with both being influenced by values. Indeed, there is already much evidence that rewards and punishments can modulate the dynamics of perceptual alternations (e.g., Wilbertz et al., 2014; Marx and Einhäuser, 2015; Wilbertz et al., 2017; Wilbertz and Sterzer, 2018) and perceptual decisions (Cicmil et al., 2015) in tasks involving multistable stimuli.

In the next sections, we discuss this evidence and provide a roadmap for a new conceptualization.

VALUES IN CONVENTIONAL AND MULTISTABLE PERCEPTION

Elevating visual perception from a mere sensory inference to being a key contributor to affective decision-making requires us to consider how the *values* of sensory objects influence what we look at and also how we interpret what we see. There are prominent examples of value-laden interpretations of images (for a review, see Martin et al., 2021); however, we focus on what we *choose* to look at. Indeed, it is known that different aspects of eye movements (e.g., velocity, amplitude, reaction time, and gaze duration) are modulated by various sorts of values in visual-based affective decision-making tasks (see e.g., Shams-Ahmar and Thier, 2020).

The sources of values for visual stimuli can be categorized in various ways: we consider explicit and implicit contributions. Explicit values largely concern the emotional content and aesthetic hedonics of images—the pleasure or pain derived from looking at particular pictures. Implicit values are more amorphous: one potential example derives from the information about the world that comes from looking at an image—this information can turn into a value by helping determine which action might lead to the greatest reward or least punishment in the future. The extra net utility expected to be available—because the image was looked at—can be seen as the value of the choice to look at it. Implicit values can also accrue if there is explicit conditioning of reward (or punishment) to an image, as in classical or Pavlovian conditioning. Most of these factors have been studied very extensively in regular vision; we concentrate on the cases in which they have also been considered in the context of perceptual multistability.

Explicit values

There is ample evidence that stimuli that are affectively charged with emotional content or aesthetic values can grab attention and influence oculomotor behavior (see e.g., Mulckhuyse, 2018). Indeed, faces with emotional content have frequently been used in binocular rivalry experiments (Alpers and Pauli, 2006; Alpers and Gerdes, 2007; Bannerman et al., 2008; Bannerman et al., 2011; Sterzer et al., 2011; Gayet et al., 2016). For instance, Alpers and Pauli (2006) demonstrate that emotional facial expressions predominate over neutral expressions, and they are more often the first percept and are perceived for longer durations. A later study by Alpers and Gerdes (2007) confirmed this finding, also using simple emoji-like emotional faces to rule out potential confounds from low-level features such as color content.

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Yang et al. (2007), Sterzer et al. (2011), and Hedger et al. (2015) used continuous flash suppression (CFS), measuring how long it takes a contentful image presented to one eye to "break-through" suppression from dynamic patterns presented to the other eye. Faces with fearful expressions gain access to awareness more quickly than neutral or happy expressions. There are at least two explanations for observations such as the ones reported by Yang et al. (2007), Sterzer et al. (2011), and Hedger et al. (2015). On one hand, Yang et al. (2007) and Sterzer et al. (2011) argue that fearful faces are privileged because of their emotional content, operating via the involvement of higher level cognitive processes; by contrast, Hedger et al. (2015) argue that such privileges are rooted in low-level features of the stimuli (e.g., with fearful faces having higher effective contrast). The speculation is that such sensory privileges are gained either through learned adaptation or evolution (to facilitate transmission of such important social signals). Both of the explanations are compatible with the core idea that emotional content of the images plays a role in the visual competition. Interestingly, it has been also observed that for participants suffering from major depression disorder (MDD), faces with sad expressions were suppressed for shorter periods than for healthy volunteers, while faces with happy expressions were suppressed for longer periods than for healthy volunteers (Sterzer et al., 2011). Altogether, this suggests that emotional content of images can bias the visual competition in a way that varies across healthy and psychiatric populations.

In another category of studies, it has been shown that aesthetic aspects of an image can bias the perceptual preference in binocular rivalry and other related paradigms (Huang and Hsieh, 2013; Mo et al., 2016; Shang et al., 2020; Tsikandilakis et al., 2019). Even in the frequently used case of rivalry between face and house images, faces, which occupy a special position in our aesthetic judgments (Rhodes, 2006), enjoy longer dominance (Persike et al., 2014). This suggests that the aesthetic value of sensory objects can have a clear and robust influence on the perceptual dynamic, i.e., changing dominance durations.

In sum, stimuli with emotional contents (particularly emotional faces) and aesthetic values (where again faces are particularly important) are typically associated with an explicit values. Such stimuli not only modulate oculomotor behavior but also perceptual dynamics, such as extending dominance periods, and lead to privileged access to perceptual awareness.

Implicit values

Beyond emotional contents and explicit aesthetic values, there is a collection of other imperatives for visual choice. We have already mentioned issues of salience and controlled attention, largely operating *within* images; here, we consider issues that may be associated with forms of values. This turns into a form of *information-based implicit value*, which is the revealed preference of our evident willingness to look at parts of a scene for the information that will accrue there, thereby helping us make better sense of the scene or make better choices based on the contents of the scene (Gottlieb et al., 2013; Bromberg-Martin and Monosov, 2020). Analysis of the exploration-exploitation trade-off in natural vision can also be viewed in similar terms (Ramos Gameiro et al., 2017).

There is at least suggestive evidence that some multistable percepts can be favored over rivals because of the informational value. For instance, prior to a binocular rivalry task, Anderson et al. (2011) paired "gossip" information with different images of neutral faces, i.e., they presented neutral faces with a description conveying gossip about the person; the gossip could be neutral, negative, or positive, putatively implicitly posing an informational problem about the facial correlates of this information. The dominance durations of the faces paired with negative gossip were longer than those paired with neutral and positive gossips. The same turned out to be true in a later experiment in which faces paired with "immoral characters" (e.g., theft, lying, and violence) dominated longer than those endowed with "virtuous" or "neutral" characteristics (Mo et al., 2016). Whether negative connotations are particularly powerful because they are relatively uncommon or because of the extra importance of threat in the context of survival, is not clear.

Klink et al. (2010) present an unusual result that might be interpreted as a novelty-based form of informational value. They report that over the course of around an hour of binocular rivalry, the proportion of time devoted to exclusive perception decreased, leaving a greater amount of piecemeal or superimposed perception. Piecemeal percepts are, of course, highly unusual and novel. It is also known that participants who are more open to exploration (based on measures of personality) experience longer duration of piecemeal percepts (Antinori et al., 2017).

Another generator of the implicit value is a visually guided task (Paffen et al., 2008; Dieter et al., 2016; Moreno-Sánchez et al., 2019; Wang et al., 2021). For instance, Dieter et al. (2016) trained participants (over a period very much longer than the few minutes of typical binocular rivalry experiments) to discriminate the aspect ratio of a bull's eye that was presented during a binocular rivalry task. They observed that the percepts containing the task-relevant features dominated longer than the rival stimuli (that lacked the task-related features). Surprisingly, the privilege of the task-related percept was observed to be extreme—to the level that this percept enjoyed almost exclusive dominance. Notably, although these studies involved a task, participants did not receive extrinsic reward. Nevertheless, as we discuss below, reward or punishment can also induce such privilege.

A separate case of learning involves pairing the *perception* of neutral images with reward or punishment—which is known to affect binocular oculomotor competition both in human (Bucker et al., 2015) and in non-human primates (Ghazizadeh et al., 2016). Along these lines, Wilbertz et al. (2014) and Marx and Einhäuser (2015) showed that perceptual conditioning affects the duration of dominance periods in binocular rivalry. In an instrumental procedure called *percept conditioning*, they paired one of the (affectively neutral) rivaling stimuli with a punishment or a reward in the form of money loss or gain when it was dominant (applying appropriate checks on dominance). Both studies reported that the dominance durations of rewarded percepts were longer than those of non-rewarded percepts, and also the dominance durations of punished percepts were shorter than those of non-punished percepts. However, the results subsequently became more complicated, for instance, with only the subset of participants who showed meta-cognitive awareness of conditioning exhibiting statistically significant modulation of the

dominance time according to reward (Wilbertz et al., 2017) and with no significant modulation of dominance when the pairing was with an aversive white noise stimulus (Wilbertz and Sterzer, 2018).

A different, Pavlovian, scheme called *stimulus conditioning*, involves training participants on the relationship between visual stimuli and reinforcers *before* those stimuli are used in the rivalry (Wilbertz and Sterzer, 2018). Indeed, Wilbertz and Sterzer (2018) suggest that this paradigm is more reliable than percept conditioning. In the stimulus conditioning case, when the reinforcer was an aversive sound, the paired stimulus had increased dominance. However, there is richness in the whole collection of results using very similar experimental designs, with punishment associations during percept (instrumental) conditioning sometimes leading to shorter dominance durations and sometimes (statistically insignificant) trends toward longer ones. There are various interpretations for the discrepancies (see Wilbertz and Sterzer, 2018 for an in-depth discussion); we suggest a further one in the next section.

In a similar vein, a few other studies used onset rivalry and different kinds of flash suppression paradigms (see Box 1 for more details) to show that conditioned stimuli gain preferential access to awareness. Gayet et al. (2016) used an aversive conditioning in CFS perceptual paradigm and showed that fear-conditioned stimuli (whose aversive association had been trained before the onset of ambiguous stimulation) broke into awareness faster, in line with previous studies employing actual fearful content rather than conditioned stimuli (Alpers et al., 2005; Yang et al., 2007).

The existing data suggest that not only in conventional visual tasks but also in perceptual multistability, the informational value of sensory input, task relevance, and different kinds of conditioning can manipulate the dynamics of perception through the implicit (and explicit) value they induce.

VALUE-BASED MULTISTABILITY

We can reassemble the results in the previous section to suggest that stimuli dominate in multistable cases (and are preferentially selected in normal visual scenes) if they are likable (e.g., attractive faces), provide information that is useful for gaining potential reward (e.g., associated with task performance) or avoiding potential punishment (e.g., faces with negative expressions such as fear or threat) or both (exploration versus exploitation), or, possibly, if the stimuli themselves have been associated over the course of learning with reward and/or punishment.

What remains necessary is a more comprehensive multi-level theory that might unify these disparate results. As mentioned, we suggest the overarching idea that switching is a (mostly unconsciously) controlled process that optimizes long-run expected values. Thus, a computational description should cover the sources of values and the logic of the maximization. An algorithmic analysis should provide concrete process models for realizing this maximization. An implementational account should indicate which neural circuits are responsible for these processes. As we will see, not all levels can be described at an equal level of detail, and there remain many speculative points.

Computational level

Consider first an agent observing a conventional binocular visual environment with zero, one, or more visually guided tasks in mind. How might we characterize the way that this agent moves their eyes, sampling different portions of the scene for different periods of time and potentially emitting other actions associated with their task(s)?

One general formalization of this problem is that of a partially observable Markov decision process (POMDP) (Littman, 2009). In brief, humans and animals frequently encounter situations in which they repeatedly need to choose one action among multiple alternatives. Each action in a sequence must be made not only based on its immediate effect in terms of gaining reward or changing the circumstances of the actor but also any long-term ramifications for both of these. A Markov decision process (MDP) (Sutton and Barto, 2018) is a general framework for modeling a wide range of such decision processes. The four components of an MDP are states (specifying the circumstances of the human or animal in the external world), actions (the choice between available alternatives), transition probabilities (characterizing how the state of the world changes given each possible action), and rewards (which specify the loss or gain associated with the states, actions, and transitions). Although MDPs have proved very useful for characterizing many environments, one restrictive assumption is that the actor must know the state completely at all times, for instance, based on sensory input. This is called complete observability and is not valid for many real-world problems, including in our characterization, perceptual multistability, as the non-dominant percept is, almost by definition, a lesser determinant of state. Relaxing this assumption leads to a more sophisticated, but realistic, class of models that are called *partially observable* MDPs or POMDPs. POMDPs are MDPs in which the actor can be uncertain about the state of the world and therefore needs to form and maintain a *belief* about the state of the world.

We suggest that, similar to attempts made in active vision, perceptual multistability can be formalized in terms of a POMDP. In the following, we briefly describe this formulation, along with a more precise description of the corresponding POMDP. The decision-process portion of this reflects the fact that there is a state of the world underlying the full visual scene; this state can change (as visual scenes are wont to do); and there are various sorts of rewards and punishments that might be influenced by the agent's actions (eye movements and others). The change in state could also depend on the agent's actions. In a simple Markovian case, the change in state and the reinforcement only depend (perhaps stochastically) on the current state and action. The partial observability derives from the fact that the agent can only observe part of the visual scene at one time (hence the need for eye movements) and may have different resolution views even of the part that they observe (peripheral and foveal vision). Both of these are implementational constraints but with important computational consequences in terms of structuring the underlying decision-making problem. Furthermore, in Helmholtzian terms, even the full visual scene is only a stochastic reflection of the true underlying state that determines utility generation and transitions. Thus, the agent can only build and maintain a probabilistic belief about the state, which is

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determined by a combination of their history of observations and by priors, with the latter specifying the possibility of change in parts of the scene that the agent is not directly observing.

In such environments, the agent's task is usually to choose actions to maximize cumulative long-run summed utility based on the information that they have available—i.e., on their beliefs. A systematic mapping of beliefs to action (or to a probability distribution over actions) is called a *policy*. An optimal policy is one that maximizes this long-run summed utility. This includes giving up the short-term reward associated with the current view with an information gathering or observing action directed at another part of the scene, given the possibility that there might be even greater rewards or worse punishments available there.

This very general framework subsumes a number of other computational problems—for instance, we can expect the agent to engage in a form of visual *foraging* (Chukoskie et al., 2013), performing eye movements around a scene, and optimal foraging theories of patch leaving (Mangel and Clark, 2019) could inform parts of a policy of eye movements (Błażejczyk and Magdziarz, 2021). Indeed, Moreno-Bote et al. (2010) has already touched on the connection between perceptual multistability and foraging, and furthermore, the ecological relevance of perceptual multistability has been discussed (Miller et al., 2011).

Equally, if there is no difference in the value associated with any part of the scene, we can expect that the agents at some point will favor foveating parts of scenes that are poorly predicted by their current beliefs (Itti and Baldi, 2009; Li, 1999) since this will be an efficient way of reducing uncertainty about the state, which will generally facilitate the appropriate choice of action (Martin et al., 2021). In this case, switching will occur for reasons of both "push" and "pull": push, as all the available information about the currently foveated location is registered, with even all the multiple modes explored; pull, from known ignorance about previously uninspected parts of the scene and as beliefs about other locations become less sharp based on expectations about changes in the world.

We described this framework as applying to an agent that moves its eyes to parts of a complex visual scene. However, we suggest that the same applies to multistability—except that instead of an overt eye movement, the agent engages in internal interpretive and attentional actions, ultimately leading to percepts that are partial reflections of ambiguous images in the same way that a single glimpse of a complex scene is a partial reflection of the whole. Therefore, we can argue that switching is an internal analog of an external eye movement (Wilbertz et al., 2014; Parr et al., 2019). Of course, the analogy is not perfect—for multistable perception, it is typically the case that all the relevant information is simultaneously available in the input to the brain. Instead, it is a consequence of the hierarchical processing architecture that dominance is necessary. This is another example of an implementational constraint with critical computational consequences.

Given this perspective, what remains at a computational level is to specify sources of reward and punishment, and to consider the general strategies that the agent might adopt, to address the extreme computational complexities associated with calculating an optimal policy and building and maintaining beliefs. Here, we can only skim over these issues, many of which remain topics of substantial investigation.

We described various main sources of explicit and implicit values. Most straightforward from the POMDP perspective are the cases described above in which there are explicit visually guided tasks that mandate dominance of one of the percepts. As we noted, these exert a particularly powerful sway—even to the extent of forcing one percept to be favored almost completely (Dieter et al., 2016). This would be an obvious outcome when utility almost exclusively accrues from the associated choice.

Less obvious is the explicit value associated with percepts— the utility associated with scenes that does not derive from environmental or evolutionary tasks. Here, we turn to modern theories of aesthetic values, which suggest that utility is generated by the task of adapting the brain's sensory processing system to the demands of the stimuli that it expects to see now and over the long run. This theory synergizes well with the Helmholtzian perspective—arguing that the generative model underlying the sensory system is well adapted if it awards likely inputs high probability. The theory integrates the two popular classes of theory of aesthetic values: those arguing that stimuli that are processed fluently have high utility and those arguing that stimuli that generate substantial learning or change have high utility to the extent that they adapt the sensory processing system to be better adapted to processing future stimuli well. The latter are also closely related to information-based values—where the information is associated with future sensory processing— for both different parts of the current scene and future scenes as a whole (Brielmann and Dayan, 2022).

In particular, for the phenomena that we detailed above, this aesthetic theory justifies the agent favoring in dominance those stimuli that are explicitly liked (e.g., Mo et al., 2016); for reasons of fluency, those that are associated with congruent multimodal cues (e.g., Conrad et al., 2010) or congruent context (e.g., Brascamp and Shevell, 2021); natural images (Baker and Graf, 2009); and those that match our intuition about real-world physics (e.g., Gilroy and Blake, 2004). The opportunity for learning justifies longer dominance for complex than simple stimuli (Alais and Melcher, 2007) and for certain sorts of novelty (e.g., Antinori et al., 2017), and also, it provides a new computational rational for perceptual switches. That is, Brielmann and Dayan (2022) formalized an active form of *boredom* as being when the sensory system becomes tuned too narrowly to a particular sensory input to which it has been exposed for a prolonged period (e.g., during long periods of perceptual dominance). This reduces long-run values, because the sensory system becomes poorly adjusted for likely future stimuli. This is a "push" factor that adds to the one mentioned above.

Boredom can be a particularly important computational construct for perceptual multistability and can potentially explain, at least, part of the rich temporal dynamics of this phenomenon (e.g., Suzuki and Grabowecky, 2007). It has been reported that the length of perceptual dominance gradually increases (e.g., Suzuki and Grabowecky, 2007). This could match the characteristic temporal dynamics of a value due to boredom (gradual decay of the push factor we introduced above).

The lower aesthetic value that is associated with slower switching might provide a hint to an explanation of the reported

differences between psychiatric and healthy populations that concern the temporal dynamics of perception in binocular rivalry. For instance, the slower rate of perceptual switches that has been observed in a wide range of psychiatric disorders (see e.g., Jia et al., 2015; Ye et al., 2019; Mentch et al., 2019) could arise from reduced values, which are also widely reported. Anxiety is the exception that proves the rule, with its putatively enhanced information value.

Other sources of preferential dominance require more intricate computational arguments. For instance, images that are unpleasant or have dangerous associations can also dominate; one reason for this might be the utility of the information associated with threat (in fact, this can be the root for some observation in psychiatric conditions, e.g., Sterzer et al. 2011). Equally, images that are conditioned with rewards or punishments can be positively or negatively preferred—this might seem strange in a Pavlovian context when there is nothing that the agent can do by looking or not looking at them to influence these explicit utilities. For reward, we discuss one possibility below as an algorithmic heuristic. However, it is also possible, for instance, that the Pavlovian association makes the agent think that these images are more likely in the future and so gain the aesthetic value from the imperative to process them fluently. Equally, the attention paid to them during training could enhance their actual processing fluency. The conflicting results from the Pavlovian and instrumental conditioning paradigms (Wilbertz and Sterzer, 2018) might stem from these partially opposing influences (negative reward versus gained fluency during training).

In sum, the computational picture associated with the POMDP offers a rich and rather comprehensive view of different sources of, and influences over, dominance and switching. We have already appealed to implementational constraints to justify why a full, dynamic, and multimodal posterior cannot be maintained. However, we have yet to come to grips with the radical computational complexity that attends even good approximate solutions.

Algorithmic level

An algorithmic perspective should provide process models for the various components of the computational model—including the representation and calculation of the belief states, the utilities, and the policy for switch. Unfortunately, there is much uncertainty about all of these.

Certainly, general ideas about value-free Helmholtzian multistability (Brascamp et al., 2017) can provide some core methods and ideas. However, the dynamical picture is rather different—with the extra push and pull factors influencing dominance rather than, for instance, a value-free perceptual inferential Markov chain Monte Carlo method (Gershman et al., 2014) or circular inference technique (Leptourgos et al., 2020). Equally, substantial analysis is required to understand how circuit and/or connection dynamics realize approximately optimal policies. One possibility is that general factors such as utility would exert influence through neuromodulatory systems (Dayan, 2012b).

There is one algorithmic facet that might account for some of the results on conditioning. We noted that pairing neutral stimuli with the delivery of reward could lead to changes in dominance, a finding that is odd from the perspective of the POMDP, since

the pairing was Pavlovian, and so this reward would arrive irrespective of any aspect of dominance. This is rather reminiscent of the sort of Pavlovian misbehavior (Dayan et al., 2006) that affects conventional conditioning. Here, animals appear to have hard-wired policies such as approaching and engaging with stimuli that predict reward (called sign-tracking) or withdrawing from stimuli associated with punishment. The extent to which this is a source of individual differences in animals (Robinson and Flagel, 2009) and humans (in a study that was based on eye movements; Schad et al., 2020) could therefore be of interest also in perceptual multistability. The normal rationale for Pavlovian policies is that they obviate a substantial amount of individual learning—it is attractive to think that such convenient policies might also be available for the sort of POMDP that we have argued characterizes the value-based perception.

Implementation level

Belying the relative paucity of algorithmic notions, there are quite some hints about aspects of the implementation of the multistable computations. Various studies provide evidence on the involvement of multiple brain regions in perceptual multistability, including anterior cingulate cortex (ACC) (see e.g., Gelbard-Sagiv et al., 2018), striatum (see e.g., Baker et al., 2015), the locus coeruleus (LC) (at least using pupil size as proxy of its activation, see e.g., Einhäuser et al., 2008 but also see Brascamp et al., 2021), prefrontal cortex (PFC) (see, e.g., Kapoor et al., 2022) amygdala (see e.g., Kreiman et al., 2002), parietal cortex (see e.g., Bahmani et al., 2019), pulvinar (see e.g., Wilke et al., 2009), and various neuromodulators (see pharmacological studies of e.g., Carter et al., 2005 for serotonin and Sheynin et al., 2020 for acetylcholine). Each of these areas and systems is also known to play a crucial role in at least explicit value-based processing (see Figure 2), with visual aesthetics and most aspects of information-based values being less extensively investigated.

In particular, the involvement of the ACC in perceptual multistability is supported by previous fMRI studies (see e.g., Lumer et al., 1998) and also recent human electrophysiological (Gelbard-Sagiv et al., 2018) and EEG data (Drew et al., 2022). Furthermore, unconsciously processed visual input can be decoded from ACC (Levinson et al., 2021), and the region plays a role in information sampling (Boroujeni et al., 2021). This region also plays a crucial role in value-based decision-making and foraging behavior (for reviews, see Monosov et al., 2020; Holroyd and Verguts, 2021; Rudebeck and Izquierdo, 2022) and even has been shown to be involved in processing of aesthetics (Cloutier et al., 2008). There has long been speculation about the involvement of the ACC in conflict monitoring during binocular rivalry (see Botvinick et al., 2001); however, it is ripe for future investigation (Drew et al., 2022).

Multiple PFC regions have been shown to be important both for value-related processes and perceptual multistability; although involvement in the latter has recently been controversial (see, e.g., Safavi et al., 2014; Block, 2019; Raccah et al., 2021). The involvement of PFC regions in perceptual multistability is supported by a variety of experimental modalities, including fMRI and transcranial magnetic stimulation (TMS) (Brascamp et al., 2017), as well as primate electrophysiology
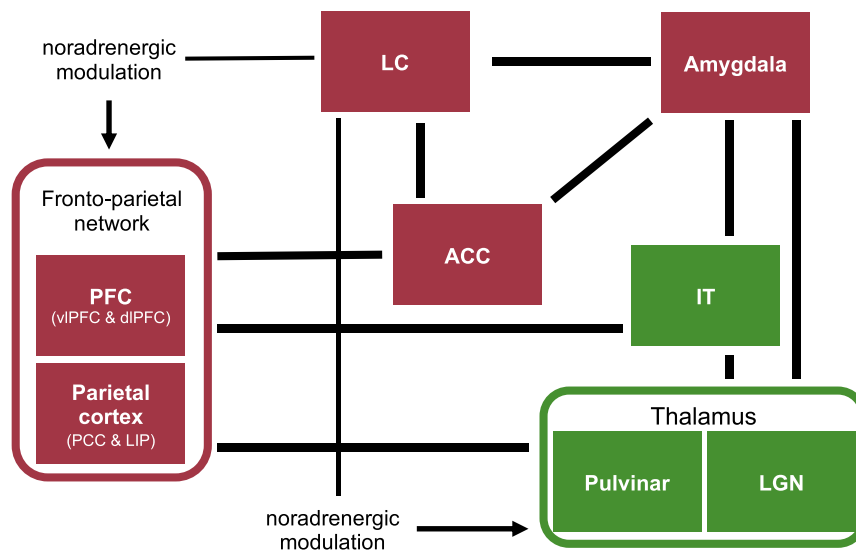
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Figure 2. Neural systems involved both in perceptual multistability and value-related processes
Schematic representation of the key systems involved both in value-related processes and perceptual multistability (red) and a subset of crucial sensory systems (green). Lines indicate the interactions between circuits, and the major noradrenergic inputs are indicated with arrows. Brain region abbreviations: LC, locus coeruleus; ACC, anterior cingulate cortex; PFC, prefrontal cortex; vlPFC, ventrolateral PFC; dlPFC, dorsolateral PFC; PPC, posterior parietal cortex; IT, inferior temporal; and LGN, lateral geniculate nucleus.

(Panagiotaropoulos et al., 2014). In particular, recent studies support the involvement of ventrolateral PFC (vlPFC) and dorsolateral PFC (dlPFC). vlPFC has been shown to be involved in perceptual multistability even in the absence of reports (Kapoor et al., 2022; Dwarakanath et al., 2020). The involvement of vlPFC is further supported by recent studies using causal intervention (Weilnhammer et al., 2021). Notably, the areas referred to as vlPFC in the non-human primate (NHP) electrophysiological studies relevant for our proposal (Kapoor et al., 2022; Dwarakanath et al., 2020; Ghazizadeh and Hikosaka, 2021) may overlap with human inferior frontal cortex (IFC) (Petrides et al., 2012), which has most consistently been implicated in perceptual switching in neuroimaging studies (Brascamp et al., 2017). The involvement of dlPFC has been a less consistent finding among fMRI studies (Brascamp et al., 2017), and no electrophysiology data are available from a no-report multistability paradigm. Nevertheless, recent causal studies with TMS support the role of dlPFC in perceptual multistability (Watanabe, 2021).

Both regions are also richly involved in value-related processes. Electrophysiological studies particularly support the involvement of vlPFC. It has been shown that neural responses in vlPFC represent the values of visual objects (Ghazizadeh and Hikosaka, 2021), the selectivity to sensory features in conventional visual paradigms (Hussar and Pasternak, 2009; Safavi et al., 2018), the contents of perceptual awareness during binocular rivalry (Kapoor et al., 2022), and also characteristic network dynamics during perceptual transitions (Dwarakanath et al., 2020). However, in spite of this varied evidence, and also the computational motivation, the role of PFC regions in mediating the effects of values on multistable perception has not been examined. For instance, it has been known that vlPFC is involved in coding the novelty and value of visual objects (Ghazizadeh et al., 2020), and as we suggest, both can play crucial roles in dynamics of the perceptual switches and dominance, but the contribution of vlPFC from this perspective has not been investigated.

Other regions, such as striatum and amygdala that are widely implicated in value-based processing (Schultz, 2015), however, have not had their association with perceptual multistability extensively investigated. Conversely, regions such as parietal cortex, pulvinar, and LC are rather less well understood in value-based terms, but they are particularly interesting on the perceptual side. For instance, parietal cortex, pulvinar (Fiebelkorn and Kastner, 2019; Fiebelkorn and Kastner, 2020), and LC (Aston-Jones et al., 1999) are closely associated with visual attention. Notably, parietal cortex (Kiani and Shadlen, 2009) and pulvinar (Komura et al., 2013) have also been associated with computing perceptual confidence. Lastly, there is a major projection from LC norepinephrine neurons to parietal cortex and pulvinar (Morrison and Foote, 1986) that highlights potential functional implication of LC. In spite of the relevance of mentioned networks, they are rather less well understood in value-based terms.

Lastly, some recent findings about neural correlates of perceptual multistability might be better interpreted in light of our proposal. For instance, we expect that at least some aspects of the value of even the suppressed percept should be computed and maintained. Processing of the dominant percept in higher cortical areas has been investigated for decades (Panagiotaropoulos et al., 2014) as it pertains to the content of conscious perception. By contrast, less is known about the processing of the suppressed percept although recent studies have pointed to the engagement of areas such as ACC (Levinson et al., 2021) and inferior temporal (IT) cortex (Hesse and Tsao, 2020).

A second set of relevant findings concerns the ACC. Apart from a few exceptions (see e.g., Drew et al., 2022), the involvement of this structure in perceptual multistability has mainly been discussed in the context of the recent debate on the role of frontal lobe in neural correlate of consciousness (NCC) (Safavi et al., 2014; Block, 2019; Raccah et al., 2021). Nevertheless, data from Gelbard-Sagiv et al. (2018), which have provided some of the clearest evidence about the involvement of this circuit, pointed to observations that are hard to explain in the context of NCC. Neural responses in ACC show anticipatory activity up to 2 s before a perceptual switch (in the form of a substantial elevation from baseline in the firing rate), with peak discriminability around (and slightly before the onset of) the perceptual switches, and thereafter they decay. This early activation might

indicate that ACC is a key initiator of the cascade that leads to perceptual switches. More importantly, the profile of the neural responses in ACC during the perceptual switches resembles the neural responses of ACC in a foraging task (Hayden et al., 2011), equating such switches (e.g., see Figure 5 of Gelbard-Sagiv et al., 2018) with saccade-based foraging (e.g., see Figure 4 of Hayden et al., 2011).

In sum, we outlined the neural components that we speculate to be involved in implementing the necessary computations we discussed in this review. Importantly, our value-based lens on perceptual multistability can potentially provide a more cohesive understanding of the neural substrates of this phenomenon, which involves sensory, decision-making, and value-processing systems. In particular, brain regions such as ACC, pulvinar, and LC that have been shown to be involved but cannot be easily integrated into existing views on perceptual multistability (such as predictive coding) can be part of a more general, value-based description. Moreover, given the findings pertaining to the involvement of a highly coordinated and large-scale network in perceptual multistability (see e.g., Blake and Logothetis, 2002; Panagiotaropoulos et al., 2014) and a recent study by de Jong et al. 2020), it is expected that neuromodulatory systems should play a crucial role, given their capabilities of these systems for implementing large-scale and distributed information processing (Dayan, 2012b).

CONCLUDING REMARKS AND FUTURE DIRECTIONS

Extensive research on the phenomena of perceptual multistability has led to substantial insights into sensory processing. However, active sensing, which is a well-recognized approach to understanding a multitude of phenomena in conventional perception (Findlay and Gilchrist, 2003; Whitehead and Ballard, 1990), has only rather rarely been considered in the case of multistability (Parr et al., 2019). Instead, analysis by synthesis ideas, which are rather probabilistically purer, but value free, has dominated.

Here, we provided a computational and algorithmic picture of key facets of active sensing for the case of vision. Participants move their eyes to select particular image contents based on a number of factors—notably the explicit and implicit values that can be accrued by doing so. We then suggested that at least some multistable phenomena can be explained by assuming that the brain is accomplishing an equivalent feat, but replacing eye movements with hypothetical internal actions that switch perceptual dominance.

We justified this hypothesis both directly, using it to account for evidence of the influence of value in the choice and duration of dominance durations, and via inverse inference, noting the involvement in switching of neural structures such as the ACC that sit at the interface of value and cognitive control.

At first blush, this notion might seem rather absurd—one of the most important facets of overt eye movements is our conscious control over them, i.e., we can decide where to look or at least we are aware of the majority of overt eye movements (Marti et al., 2015). By contrast, control over multistable percepts is much more fragile—it is very hard to get a percept to flip merely by conscious control, even when, as for the

Necker cube, there are eye movement and attentional strategies that can at least help (van Ee et al., 2005). However, the overwhelming majority of eye movements is also unconscious (Clarke et al., 2017), and the complexities of the visual world are such that even those that are conscious are underpinned by the substantial bulk of under-the-surface unconscious computations.

The influence of aesthetic values is perhaps the more unexpected component of the account. In terms of Brielmann and Dayan (2022)'s (yet to be tested) suggestion for the generation of a value, one part of this is actually completely conventional—the value that accrues from fluent processing operationalized as log probability under a generative model. This is just the same implied value structure that underpins most of Helmholtzian vision. The second part, the value that accrues from the movement of the state of the brain toward the image presented, which quantifies the expected change in fluency with which future stimuli will be processed, may be less familiar. In our account, this can lead to an initial interest, but final boredom, with an image—and so encourages eye movements away from a current figure or perceptual switches. The active rejection of an image (due to the damage that specializing too closely it would do to the processing of *other* stimuli) is an additional computational-level rationale for switching, along with the expectation of change in the environment and stochastic sampling of a multimodal posterior.

Although brain imaging data and neural recordings implicate structures such as the ACC in switching, offering a substrate for a role for value, the question of how a switch is realized is not resolved. In the case of other internal actions such as the deployment or gating of working memory, it has been suggested that interactions between the basal ganglia and the cortex are involved (Hazy et al., 2006), and the striatum is indeed involved in binocular rivalry (Baker et al., 2015). However, there are not yet circuit-level findings to validate this. Likewise, the substrate of the calculation of aesthetic or informational values remains unclear. Therefore, simultaneous monitoring at a large scale during binocular rivalry is of paramount importance. Perhaps ACC and vlPFC can be among the first foci, given the clear evidence of their involvement in perceptual aspects of binocular rivalry and their *cooperative* role in value-related computations and conflict resolution (Monosov and Rushworth, 2022).

As mentioned earlier, multistable perception is not only revealing about neural processing in healthy volunteers but has also been extensively investigated in the context of psychiatric dysfunction, with switching rates being lower in most (Ye et al., 2019), but not all (Jia et al., 2020), cases. Although effects on switching in some conditions—notably schizophrenia—likely depend substantially on altered aspects of probabilistic generative and recognition processes (e.g., Weilnhammer et al., 2020), there are others in which the value may play a role. For instance, the switching rate is slower in depression and faster in general anxiety (Jia et al., 2020), the former being consistent with values being lower and the latter being consistent with an enhanced subjective information value for the unattended/unseen object. Consistent with the suggestion that perceptual switching and eye movements have some computational commonalities,

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abnormalities in eye movements have also been observed in psychiatric conditions (Bittencourt et al., 2013). For instance, Bestelmeyer et al. (2006) observed that schizophrenic patients exhibited fewer fixations, longer fixation durations, and longer saccade durations. Integrating the heterogeneous body of observations in psychiatric populations is an important task for future work, as is assessing whether particular aspects of perceptual multistability can be used as a reliable and non-invasive instrument in the clinical domain.

There are various avenues for testing this proposal. The hardest task will be finding experimental methods for separating out the various different components influencing dominance and dominance durations and to isolate those that depend selectively on the various aspects of values we have articulated. Nevertheless, it would be relatively straightforward to measure and manipulate the value structure before, during, and after multistable perception to see whether dominance hews to the theory.

Furthermore, as discussed earlier, perceptual multistability is an extremely rich phenomenon that has been investigated using many different methods, delivering a diverse collection of results over multiple scales. We considered the subset of these results concerning the role played by the value; it would be important to broaden the framework to encompass a wider range of effects, for instance, by integrating it with value-free aspects of inference based on Markov chain sampling (e.g., Gershman et al., 2014) and with aspects of sensory processing normally considered to arise at a lower level such as contrast adaptation whose computational foundations currently lie in different bodies of theory such as efficient coding (Zhaoping, 2014). These aspects of low-level sensory processing need to be integrated with high-level cognitive aspects, notably attention, which itself contributes at multiple processing stages of perceptual multistability (Maier and Tsuchiya, 2021).

Lastly, in this review, we mainly focused on computational constructs of perceptual multistability and the potential computational rationale underlying perceptual switching and dominance. Any such computation must ultimately be realized in neural circuits and synaptic biophysics. It is, however, important to acknowledge that much of the excellent work on circuit and synaptic principles such as attractor dynamics, adaptation, and mutual inhibition (Braun and Mattia, 2010; Deco et al., 2013; Theodoni, 2014), which can account for many characteristics of perceptual multistability (e.g., distribution of dominance periods), is agnostic to any higher computational purpose. Indeed, there are rivalry-like dynamics in anesthetized animals (Bahmani et al., 2014; Xu et al., 2016) and *in vitro* settings (Kogo et al., 2021). In general, it is pressing to integrate all these perspectives (as, for instance, in Brascamp et al., 2017; Leptourgos et al., 2020; Cao et al., 2021), highlighting both those elements of multistability for which we can tell a multi-level account, justifying such things as the influence of cognitively penetrable factors such as reward on dynamics, and those elements that obey neurobiologically rather than ethologically penetrable constraints.

In sum, we have presented a new treatment of perceptual multistability based on the involvement of values. According to this, the brain has substantial, albeit unconscious, agency in choosing what to perceive—doing so using internal actions

that occasion dominance and switching. This helps accounts for a wealth of suggestive data on modulation of multistable perception and also provides new ties to aspects of psychiatric dysfunction.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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