Early interactions between neuronal adaptation and voluntary control determine perceptual choices in bistable vision

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At the onset of bistable stimuli, the brain needs to choose which of the competing perceptual interpretations will first reach awareness. Stimulus manipulations and cognitive control both influence this choice process, but the underlying mechanisms and interactions remain poorly understood. Using intermittent presentation of bistable visual stimuli, we demonstrate that short interruptions cause perceptual reversals upon the next presentation, whereas longer interstimulus intervals stabilize the percept. Top-down voluntary control biases this process but does not override the timing dependencies. Extending a recently introduced low-level neural model, we demonstrate that percept-choice dynamics in bistable vision can be fully understood with interactions in early neural processing stages. Our model includes adaptive neural processing preceding a rivalry resolution stage with cross-inhibition, adaptation, and an interaction of the adaptation levels with a neural baseline. Most importantly, our findings suggest that top-down attentional control over bistable stimuli interacts with low-level mechanisms at early levels of sensory processing before perceptual conflicts are resolved and perceptual choices about bistable stimuli are made.

Keywords: rivalry, visual perception, perceptual memory, attention, adaptation, voluntary control, onset

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Introduction

How does one choose between alternatives that are completely equal in every possible aspect? This classic problem is known in philosophy as *Buridan's ass* and tells the story of an ass that starves to death because it is incapable of choosing between two equally distant stacks of hay that are of the same size and quality. A neurophysiological counterpart of this 14th century paradox can be found in the visual perception of bistable stimuli, containing equal evidence for two mutually exclusive percepts. When confronted with such a stimulus, the brain quickly chooses—in a non-random fashion—which interpretation will reach awareness (Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003; Noest, van Ee, Nijs, & van Wezel, 2007; Orbach, Ehrlich, & Vainstein, 1963). Classic decision theory, the accumulation of sensory signal toward a winner-takes-all decision, accounts for decisions based on unequal stimulus evidence (Gold & Shadlen, 2007) and thus predicts random percept choices for bistable stimuli. The fact that the visual system makes non-random choices between interpretations with equivalent stimulus evidence implies that this choice-process must rely on dynamically evolving internal states. Indeed, it has been found that percept choices at the onset of bistable vision depend on stimulus timing (Kanai & Verstraten, 2005; Noest et al., 2007; Orbach, Zucker, &

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Olson, 1966), preceding perceptual history (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007; Leopold et al., 2002; Maier et al., 2003), and both bottom-up (e.g., Chong & Blake, 2006; Mitchell, Stoner, & Reynolds, 2004) and top-down (Chong & Blake, 2006) attentional states.

A recent study (Noest et al., 2007) focused on finding the minimal neural mechanism that explains how the percept-choice process can yield perceptual repetitions when stimuli are presented with relatively long intermittent blanks (Kanai, Knapen, van Ee, & Verstraten, 2007; Leopold et al., 2002; Maier et al., 2003; Noest et al., 2007; Orbach et al., 1966; Pearson & Clifford, 2004) and perceptual alternations when the blanks are short (Noest et al., 2007; Orbach et al., 1966). The resulting low-level model is based on a dynamic balance between the adaptation levels of cross-inhibiting, percept-related neural pools and an interaction of this adaptation with a near-threshold neural baseline (for details, see Noest et al., 2007; and Appendix A). This interaction creates a small 'head start' for the more adapted neural population at the next stimulus onset that may overcome the effects of adaptation causing the more adapted neural population to become dominant and a perceptual repetition to occur. The model predicts and demonstrates that percept choices depend on the perceptual history and stimulus timing, both important determinants of the neuronal adaptation state. Importantly, the model only describes the dynamics of the single, core neural stage that resolves the rivalry. In reality, it is obvious that rivalry resolution does not occur at the first stage of neural processing, and there will be stages of neural processing that precede rivalry resolution.

These pre-rivalry stages exhibit general neural features like adaptation that will not change the nature of the percept-choice process itself but will nevertheless have clear effects. Reality thus forces us to consider these stages when comparing psychophysical data with model-driven predictions. In the current study, we extend the single-stage model of Noest et al. (2007) with the implementation of such adaptive pre-rivalry neural processing stages in their simplest possible form. They are assumed to have the same neural dynamics as the rivalry-resolving stages but lack cross-inhibition. The interaction of adaptation with the fixed neural baseline is functionally irrelevant for neural pools that do not interact (Noest et al., 2007) and is therefore not implemented in these stages. This model extension provides novel predictions that are consistent with the findings of our psychophysical experiments and help to understand the neural mechanism underlying percept choices at the onset of bistable stimuli.

An interesting feature of bistable stimuli under continuous viewing conditions is that subjects can, to a certain extent, voluntarily control their perception (Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005). It is however not known whether similar voluntarily control can be exerted over percept choices at stimulus onset. In this study, we investigate the possible effect and underlying mechanisms of voluntary control over percept choices at the onset of bistable visual stimuli. The minimal neural mechanism that can generate top-down choice biases can directly be derived from existing, well-established literature. Advances in the field of visual attention (e.g., Alais & Blake 1999; Chong & Blake, 2006; Ling & Carrasco, 2006; Ooi & He, 1999; Treue & Maunsell, 1999; Verstraten & Ashida, 2005; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006) in addition to the finding of common neural substrates for attention and voluntary control (Slotnick & Yantis, 2005) and the demonstration of stimulus-feature dependency of voluntary control (Brouwer & van Ee, 2006; Suzuki & Peterson, 2000) suggest that voluntary control influences perception by attention-driven gain modulations at early stages of visual processing. As noted before, these stages must exist preceding the previously modeled rivalry-resolution stage. Such early gain modulations cause an imbalance in the input signal of the rivalry-resolving stage, a situation that has previously been used to explain the existence of classic aftereffects that may override the influence of stimulus timing and perceptual history on percept choices (Noest et al., 2007). Our extended model predicts that a difference between the input signals to the rivalry-resolving stage of only a few percent causes a substantial bias toward choosing the high-gain percept. Furthermore, the non-linearities in the relation between adaptation and percept choices predict pre-stage gain imbalances to interact with stimulus timing and perceptual history, a notion that is confirmed by our second experiment in which we vary both stimulus timing and voluntary control instructions.

As a first step toward understanding the effects of voluntary control, we investigate how neural stages that precede the rivalry resolution influence the percept choices. Theoretically, adaptation that occurs prior to rivalry resolution will—to some extent—normalize the input to the rivalry-resolving stage. Longer stimulus ON-time durations will cause more adaptation in these pre-rivalry stages, thereby decreasing the amplitude of their output signal (which is the rivalry stage's input) while keeping the 'stimulus energy' (duration × amplitude) more or less constant (comparable to classic contrast normalization). Our model predicts that this pre-rivalry normalization process makes the build-up of adaptation in the rivalry stage independent of the stimulus ON-time duration. This effect emerges from the exact same minimal neural structure we will introduce to explain voluntary control but yields more simple predictions since it involves only two parameters (presentation duration and interstimulus interval) rather than three (voluntary control added to the mix). In our first experiment, two different types of bistable stimuli are used that may be resolved at different levels in the cortical hierarchy. It has been suggested that the visual competition for a set of binocular rivalry gratings takes place at a lower level of neural processing than that for perceptual rivalry such as a structure-from-motion-defined sphere with an ambiguous rotation direction (Meng & Tong, 2004; van Dam & van Ee, 2006b; van Ee et al., 2005). We demonstrate that this difference between stimuli is reflected in the amount of pre-stage adaptation that reveals itself in the relationship between stimulus timing and percept choices.

Our second and main experiment directly probes the effect of voluntary control on percept choices. The results demonstrate the existence of voluntary control over percept choice at the onset of bistable vision and are consistent with model predictions implementing small stimulus biases. They also confirm our prediction that voluntary control interacts with stimulus presentation dynamics and supports the proposal that top-down voluntary control indeed modulates neural gains at very early levels of visual processing.

Experiment 1: Percept choices and stimulus timing

It has previously been shown that the stimulus ON and OFF durations determine whether the intermittent presentation of bistable visual stimuli result in perceptual repetitions or alternations (Noest et al., 2007). This effect depends crucially on the build-up of adaptation during stimulus ON-time (T_{on}) and decay of adaptation during stimulus OFF-time (T_{off}) (Figure 1C). These predictions are based on an input signal to the rivalry-resolving stage that remains constant in amplitude during the stimulus presentation duration. Since visual rivalry is not resolved at the level of the retina, there will be stages of neural

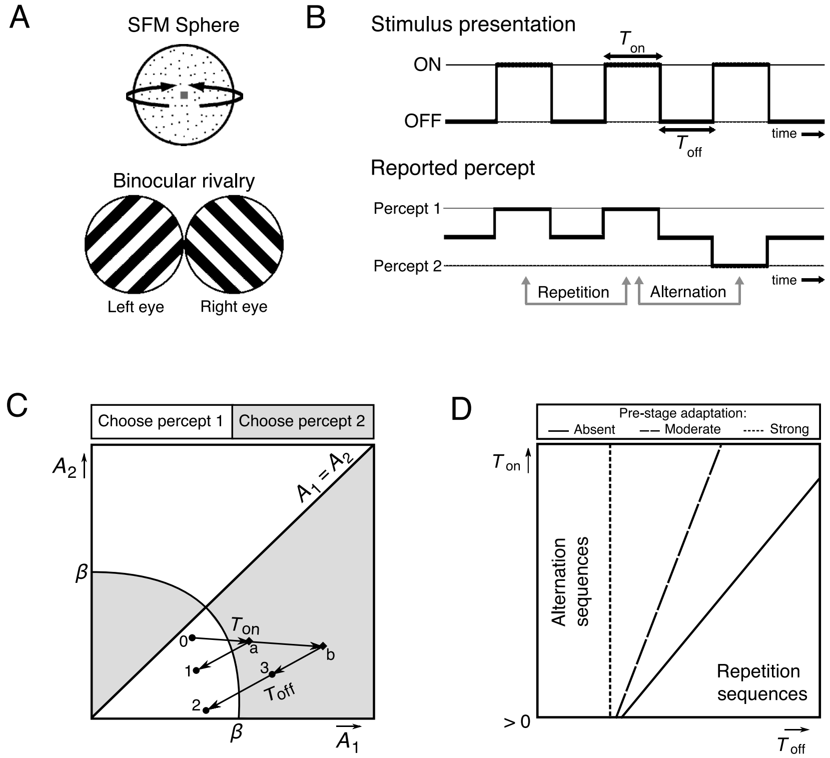

Figure 1. (A) Schematic representation of the stimuli. The structure from motion (SFM) sphere consisted of two random dot patterns moving in opposite directions with a sinusoidal speed profile that gives rise to a vivid impression of a rotating three-dimensional sphere with an ambiguous direction of rotation. The binocular rivalry stimulus consisted of an orthogonal set of gratings presented to the individual eyes. (B) Experimental procedure. Stimuli were presented intermittently with various durations of stimulus presentation (T_{on}) and interstimulus interval (T_{off}) (upper panel). During each ON-time, the subject reported the current percept (lower panel). Two subsequent percepts that are opposite are defined as an alternation; two similar percepts are defined as a repetition. (C) The model of Noest et al. (2007) predicts the percept choice to depend on the adaptation states of the rivaling neural populations at stimulus onset and the neural baseline parameter β. These adaptation states in turn depend on the amount of adaptation build-up during T_{on} and decay during T_{off}. If at stimulus onset '0', percept 1 is being perceived, the corresponding adaptation state A_1 will increase (solid arrow to the right) during T_{on} and decay during T_{off} (dotted arrow to the left). With short T_{on} (a), a short T_{off} suffices to get perceptual repetitions (1), while with longer T_{on}'s (b) the percept choice depends on the length of T_{off}: short T_{off}'s give alternations (3), long T_{off}'s repetitions (2). (D) With constant input to the rivalry-resolving stage, the transition from alternation to repetition sequences involves a positive correlation between T_{on} and T_{off} (solid line). Adaptation prior to the rivalry resolution stage normalizes the input and thus the amount of adaptation that is built up (the solid arrow to the right in C would be of a fixed length). The border between alternation and repetition sequence areas is steepened with increasing preceding adaptation until it becomes vertical for complete pre-stage adaptation (dotted line).

processing that precede the neural stage where the rivalry resolution takes place. These stages—like any neural system—will be subject to adaptation, causing the amplitude of the input to the rivalry-resolving stage to decrease for increasing ON-time. If the amount of adaptation is different for the two individual percept-related neural processes in pre-rivalry stages, it might result in unbalanced input to the rivalry stage leading to perceptual biases. But more in general, this pre-rivalry adaptation effectively functions as a normalization process that—if there is enough adaptation—will result in percept choices that are independent of the stimulus ON-time (Figure 1D). In this first experiment, we test this assumption using two bistable stimuli that are thought to rival at different processing levels. If our assumptions are correct, we expect to find that percept choices are relatively independent of stimulus presentation duration. Furthermore, if any effect of ON-time will still be present, it is more likely to occur with the binocular rivalry stimulus, which is generally regarded to be a more low-level kind of bistable stimulus.

Methods

Visual stimuli

Two different types of bistable stimuli were used: an ambiguously rotating, structure from motion (SFM) sphere and two orthogonally oriented gratings presented binocularly. The sphere was composed of two transparent layers of random white dot patterns on a black background moving in opposite directions with a sinusoidal speed profile (Figure 1A). Due to structure-from-motion effects, these moving dots created the vivid impression of a three-dimensional rotating sphere (Bradley, Chang, & Andersen, 1998; Dodd, Krug, Cumming, & Parker, 2001; for a review, see Andersen & Bradley, 1998). As no unambiguous depth information was present in this stimulus, the perceived rotation direction was bistable. The sphere was presented in the center of a computer monitor (1024 × 768, 85 Hz) at a distance of 122 cm, with a yellow fixation square (4.2 × 4.2 arcmin) in its center. It was 2 degrees in diameter, while the dots were 2.8 arcmin and moved with a sinusoidal speed profile with a peek angular speed of 60 degrees per second. The luminance of the white dots was 21.7 cd/m^2 and background luminance was 0.13 cd/m^2; the dot density was 40 dots per squared visual degree. The dot lifetime was infinite, but at the start of each stimulus presentation, the dots were randomly positioned to prevent tracking individual dots over stimulus presentations.

The binocular rivalry stimulus (Figure 1A) consisted of a dichoptically presented pair of sine wave gratings (spatial frequency = 1.75 cycles/degree) at orthogonal orientations using a mirror stereoscope. Each grating was multiplied by a two-dimensional Gaussian envelope (σ = 0.5 degrees), resulting in an effective stimulus size of about 2.4 degrees in diameter. At the peak of the Gaussian function the luminance measured 61 cd/m^2; the lowest luminance was ~0 cd/m^2. The gratings were kept in anti-phase throughout the experiment, while the orientations remained the same for each eye. The gratings were presented on a gray background with a luminance of 15 cd/m^2 and were accompanied by four dark gray lines (1.95 degrees by 0.12 degrees) presented to both eyes to support correct binocular fusion of the images. These lines had a luminance of 3.7 cd/m^2 and were positioned 2.9 degrees from the gratings. The binocular rivalry stimulus was presented on a computer monitor (1280 × 1024, 85 Hz) in the center of the screen, 47 cm from the subject.

Experimental procedure and subjects

Five subjects participated in the ambiguously rotating sphere experiments; four of these also participated in the binocular rivalry experiments. In both groups, two subjects were completely naive with respect to the aims of the experiments. Subjects ranged in age between 22 and 39 years and had normal or corrected-to-normal visual acuity. They were seated with their head restrained by a head and chin rest and were instructed to fixate on the square in the sphere experiment or the middle of the screen in the binocular rivalry experiments. They were instructed to press one button when the front (near) surface reversed from a rightward to a leftward direction and to press another button when the opposite occurred. Subjects could occasionally also perceive the stimulus as either two convex surfaces or two concave surfaces that are sliding on top of each other (Chen & He, 2004; Hol, Koene, & van Ee, 2003). Nevertheless, they still perceive one surface sliding in front of the other, meaning that our instruction to report the direction of the front surface is clear and unambiguous. Stimuli were presented intermittently, with different combinations of ON-time duration (T_{on}) and OFF-time durations (T_{off}) (Figure 1B). To avoid probing both the percept-choice process at stimulus onset and the percept-switch process present with continuous viewing, we chose to study ON periods short enough to prevent spontaneous percept switches during the stimulus presentation. Four different values of T_{on} (logarithmically spaced between 0.71 and 2.0 s) combined with nine different values of T_{off} (logarithmically spaced between 0.125 and 2.0 s) for the SFM sphere and 11 different values of T_{off} (logarithmically spaced between 0.125 and 4 s) for the binocular grating resulted in 36 and 44 different conditions, respectively, that were each presented twice in pseudorandom order in blocks of 2 min, resulting in 40 to 288 stimulus presentations and perceptual choices per condition. Percepts were reported with a button press. Subjects were instructed to respond only once per stimulus presentation and to report the first percept in the event a perceptual switch occurred during longer stimulus presentation. (Note that our selection of ON-durations ensured us that this rarely happened. As an indication, less than 9% of perceptual durations with continuous viewing were shorter than 1 s). If uncertain, they were to choose the percept that appeared strongest. An extra condition was added in which the stimuli were presented continuously ($T_{\text{off}} = 0$ s) for a block of 2 min that was presented twice, and subjects reported percept switches with the same two buttons.

Data analysis

For continuous viewing, the number of percept switches per minute was calculated. For intermittent presentation, two subsequent stimulus presentations with different reported percepts was defined as an alternation (see Figure 1B) and both the number of alternations per minute and the fraction of the total number of trials in which an alternation occurred (alternation probability) were calculated. In these percept-choice experiments, subjects were instructed not to report percept switches during the stimulus presentations. If subjects responded twice during one stimulus presentation, the second response was excluded. Trials in which the subject failed to respond were also excluded, along with their preceding and subsequent trials. Less than 3% of all trials were discarded based on one of these criteria.

The data were fitted with a descriptive two-dimensional cumulative Gaussian function (Equation 1). This function describes a surface of alternation probabilities in $T_{\text{on}}-T_{\text{off}}$-space, where x and y are the logarithms of T_{off} and T_{on}, respectively. Parameter a represents the base of the surface, b the amplitude, c the transition point of T_{off} in which the subjects change from more perceptual alternation to a perceptual repetition regime (*shift*), d the standard deviation of the cumulative Gaussian function and a measure of the steepness of this transition (*sigma*), and k the steepness of the change in the transition point for different T_{on} (*slope*).

$$\text{Choice alternation probability} = a + b/2 \cdot \operatorname{erfc}\left(\frac{x - (c + k \cdot y)}{d \cdot \sqrt{(2)}}\right). \quad (1)$$

Results

If percept choices crucially depend on the adaptation states of the underlying neuronal populations, this should become obvious from manipulations of the adaptation build-up during stimulus presentation (T_{on}) and decay during the interstimulus interval (T_{off}). Figure 2A

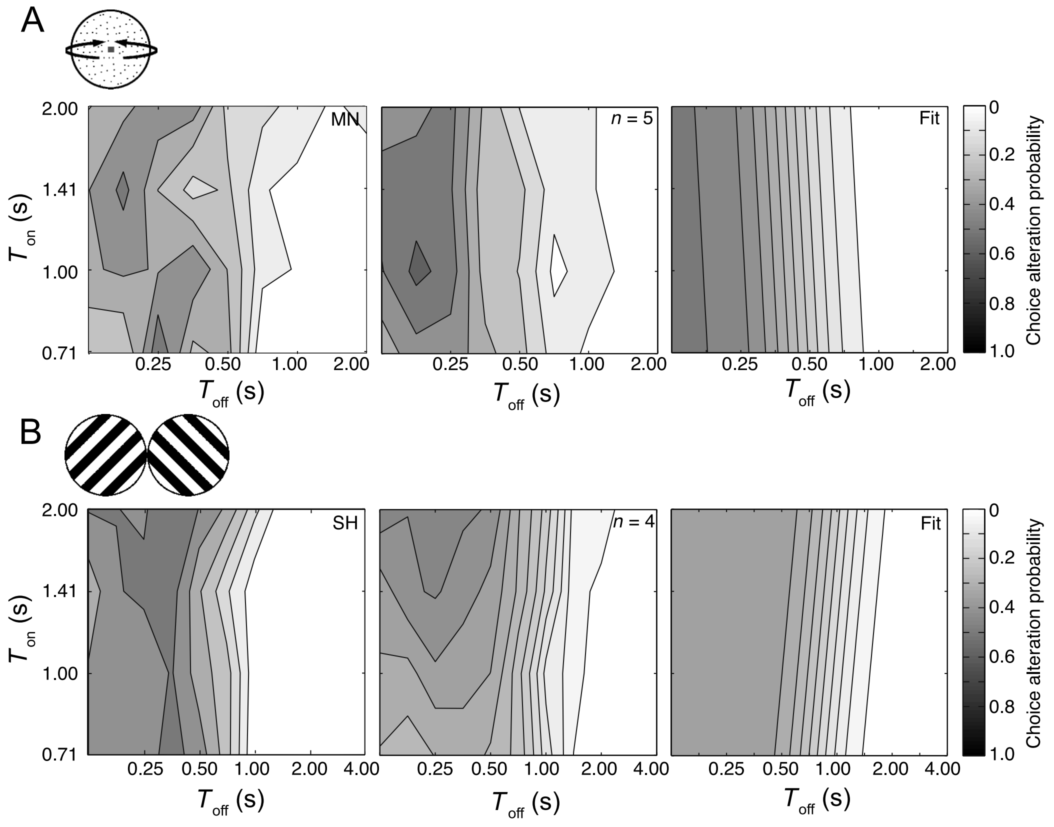

Figure 2. Alternation probabilities for intermittently presented bistable stimuli generally depend on presentation duration (T_{on}) and interstimulus interval (T_{off}) for (A) the ambiguous sphere and (B) the binocular rivalry stimulus. The left panels depict the data from a typical single subject, center panels show the averaged group data, and right panels show the fit. The influence of T_{on} is quite small, leaving choice alternation probabilities to be determined predominantly by T_{off}.

illustrates how alternation probabilities for perceptual decisions depend on both the T_{on} and T_{off} for the experiment with the ambiguously rotating sphere. The black coloring indicates high alternation probabilities, while the white coloring indicates low alternation probabilities. In the left panel, the data are provided for one typical subject. The same qualitative pattern of T_{off} dependency is present for all subjects, indicated by the average plot of all five subjects in the center panel. Short T_{off}'s lead to high alternation probabilities, whereas at longer T_{off}'s the alternation probability declines and perceptual stabilization occurs. Furthermore, these figures indicate that the change from alternation to repetition depends primarily on T_{off}, not T_{on}. A two-way ANOVA confirms this notion; for all individual subjects—and for the group data—T_{off} significantly influences the alternation probability ($p < 0.0001$), whereas T_{on} does not ($p > 0.20$). These findings confirm our predictions for the effective contrast normalization by pre-stage adaptation. The noisy boundary between the alternation and the repetition regime areas likely results from inevitable noise in the rivalry-resolving system (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006).

To quantify the results, we performed a descriptive fit on the data using a cumulative Gaussian function (see Methods section, Equation 1). The fitted data ($R^2 = 0.94$) of the average of all five subjects are shown in the right panel of Figure 2A. The transition T_{off} time for alternation to repetition regimes of percept choices (c in Equation 1) averages 0.48 s (±0.10 s). If percept choices with intermittent presentation and percept switches under continuous presentation are basically manifestations of the same underlying process, one might expect that the transition times from repetition to alternation regimes (intermittent presentation) and the average percept durations during continuous viewing roughly coincide or are at least correlated. However, the transition time is roughly 14 times smaller than the mean percept duration under continuous viewing conditions for the same subjects (6.70, *SD* ±3.62 s), and the absence of a correlation between the two measures ($r^2 = 0.01$) adds further evidence to the suggestion that percept choice (intermittent presentation) and percept switch (continuous presentation) are fundamentally different processes. The average steepness of the transition point (d in Equation 1) for the five subjects was 1.20 (±0.73), corresponding to 0.13 s (±0.02 s), and the average steepness of the change in transition point of T_{on} (k in Equation 1) was −0.13 (±0.22). This quantification indicates a vertical border and supports the statistical findings that the transition point depends on T_{off}, not T_{on}.

A qualitatively similar pattern is present for the binocular gratings (Figure 2B). The figure provides the data from a typical subject (left panel), the averaged group data (center panel), and the fit to the data (right panel, $R^2 = 0.95$). A two-way ANOVA confirmed that the effect of T_{off} on the alternation probability is significant ($p < 0.001$) for all subjects as well as the group data. Alternation probabilities decrease with increasing T_{off} ($a = 0.02 \pm 0.03$; $b = 0.48 \pm 0.04$); these values are in the same order of magnitude as the values for the SFM sphere ($a = 0.06 \pm 0.04$; $b = 0.54 \pm 0.07$). The average transition moment from an alternating to a repetitive regime lies at a T_{off} of 0.71 s (±0.12 s), which is roughly 8 times shorter than—and not correlated ($r^2 = 0.46$) with—the average percept duration during continuous viewing conditions (5.35, SD ±1.15 s). Compared to the SFM spheres the important difference is that, with binocular gratings, T_{on} has a small but significant effect on the alternation probability for all subjects as well as the group data (two-way ANOVA, $p < 0.01$). The average k value is 0.27

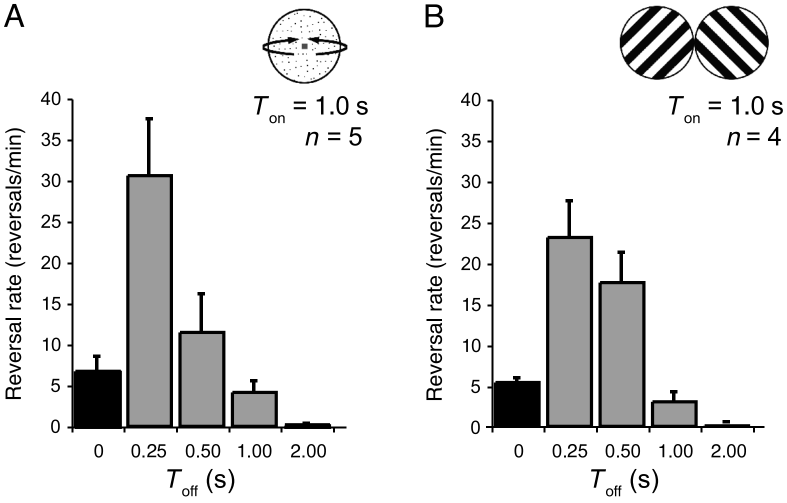

Figure 3. Mean number of reversals per minute (with *SEM*) of five subjects for continuous (T_{off} = 0 s) and intermittently presented stimuli (T_{off} > 0 s) for (A) the ambiguous sphere and (B) the binocular rivalry stimulus. Stimulus presentation duration (T_{on}) was 1 s for the intermittently presented stimuli. The effect of intermittent presentation depends on T_{off} and can result in either lower or higher reversal rates than in the continuous viewing condition.

(±0.18), indicating a slightly sloped border between alternation and repetition regimes. The effect of T_{on} is smaller than that of T_{off} ($d = 1.12 \pm 0.34$), but its significance reveals that stages preceding the resolution of binocular rivalry are subject to less adaptation than the stages preceding the rivalry resolution for the sphere. Apparently the rivalry stage input signal has not been fully normalized in preceding neural stages.

While repetition probabilities reach unity for all conditions at long T_{off}, the average maximum alternation probabilities for the ambiguously rotating sphere and binocular rivalry stimulus at short T_{off}'s are 0.33 and 0.47, respectively. One could therefore presume that, instead of reaching an alternation regime, the system simply reaches a regime of random percept choice at short T_{off}. An analysis of the occurrence of longer sequences of alternating percepts however reveals that subjects truly perceived sequences of alternations at short T_{off} rather than random percepts (Figure 5A).

Finally, in Figure 3, we plotted the reversal rates expressed in alternations per minute for the continuous presentation and all the intermittent presentations with a T_{on} of 1 s to directly compare our results with a previous study that reported perceptual stabilization due to intermittent stimulus presentation (Figure 5B in Leopold et al., 2002). For both stimuli, the reversal rates for intermittent presentation decline with increasing T_{off}, and reversal rates with continuous viewing lie between those acquired with T_{off}'s of 1 s and half a second. Our range of T_{off}'s clearly demonstrates that intermittent presentation can result in percept-choice alternations and percept-choice repetitions (stabilization), ultimately depending on the length of the intermittent interval.

Experiment 2: Percept choices and voluntary control

In this second experiment, we directly probe the effects of voluntary control. Whereas voluntary control over continuously presented bistable stimuli has been known for some time (Meng & Tong, 2004; van Ee et al., 2005), it has never been shown for percept choices at stimulus onset. Interestingly, there are reports about the influence of voluntary object-based attention on the percept choices at the onset of binocular rivalry stimuli (Chong & Blake, 2006), and we argued that there is considerable evidence to interpret voluntary control as an attentional gain modulator that effectively biases the input of the rivalry-resolving neuronal stage toward one of two perceptual interpretations. For this interpretation, our new extended model provides some clear predictions. The topography of the 'percept choice-map' as related to the adaptation states (Figure 1C) changes under biased inputs (Noest et al., 2007). The area where the favored percept will be chosen increases in size, whereas those of the unfavored percept shrink (Figure 4B). This shrinkage depends on the size of the bias and is more dramatic in the area of low adaptation levels compared to the areas of high adaptation levels. These novel predictions imply that voluntary control should interact with the adaptation states and become more effective when stimulus OFF-times increase (lower adaptation levels).

Methods

In this experiment, we used the same stimuli and experimental procedure as in the first experiment. The only difference is that each block of stimulus presentations was now preceded by one of five possible instructions with respect to the voluntary control: (1) alternate; (2) hold the current percept; (3) hold leftward or (4) rightward rotation/orientation; and (5) baseline condition, exerting no control (passive condition). In our first experiment, we have shown that alternation probabilities for this stimulus are independent of T_{on}; therefore, we only varied the T_{off} in this experiment. T_{on} was always 1 second, and T_{off} was pseudorandomly chosen from 11 (sphere) or 5 (binocular rivalry) possible durations in the same range as in Experiment 1. All subjects' performance with all five instructions was also recorded with continuous presentation of the stimulus ($T_{\mathrm{off}} = 0$ s), presented twice in blocks of 2 min. Six subjects participated in the experiment with the sphere, including four who had also participated in Experiment 1. One of these six subjects (MS) was not successful in exerting voluntary control and was excluded from the group analysis. Four subjects participated in the binocular rivalry experiment. Subjects ranged in age between 22 and 39 years and had normal or corrected-to-normal visual acuity. For both stimuli groups, two of the subjects were naive with respect to the purpose of the experiments. As a descriptive fit to the data, we used a one-dimensional version of Equation 1:

$$\text{Choice alternation probability} = a + b/2 \cdot \operatorname{erfc}\left(\frac{x - c}{d \cdot \sqrt{(2)}}\right). \tag{2}$$

In this equation, x once again represents $\log(T_{\mathrm{off}})$, a is the baseline, b is the amplitude, c is the shift that represents the transition point, and d is the standard deviation of the cumulative Gaussian function.

Results

It is known that voluntary control over perceptual states for bistable stimuli is possible when the stimulus is shown continuously (Brouwer & van Ee, 2006; Hol et al., 2003),

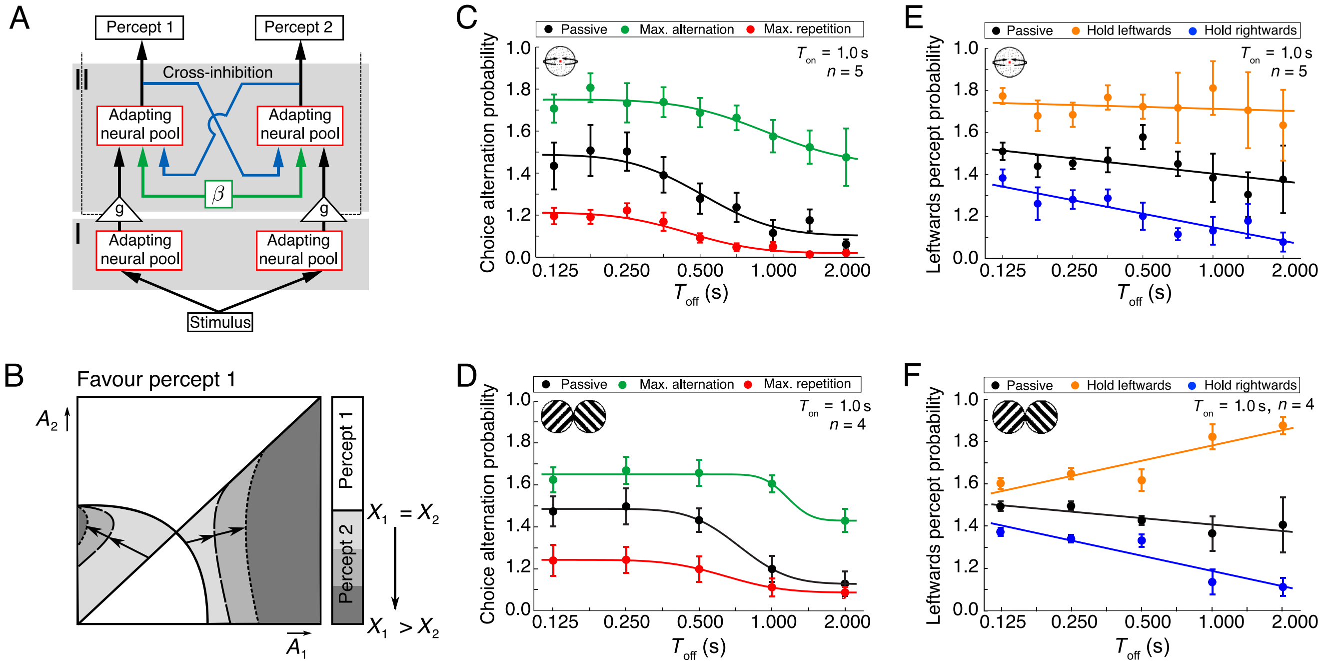

Figure 4. (A) A schematic representation of our two-stage model of perceptual decisions. The model consists of a pre-processing stage (I) where adapting neural pools process perceptual representations without inhibiting each other. The second—rivalry-resolving—stage (II) has similar adapting neural pools but these pools do exhibit cross-inhibition and an interaction with a neural baseline (β). Top-down biases are implemented as gain modulations (dashed lines, g) preceding the rivalry-resolving stage. (B) An input bias ($X_i > X_j$) caused by a gain imbalance re-shapes the percept-choice map in adaptation state space. The areas in which the unfavored percept gets chosen shrink (gray shades and arrows) in size. This shrinkage depends on the size of the imbalance and is faster in the area for lower adaptation levels (on the left side of the plot). (C/D) Average alternation probability for the sphere (C) and binocular rivalry stimulus (D) for all subjects as a function of T_{off} and three different instructions: maximize number of alternations (green), maximize number of repetitions (red), and view passively (black). T_{on} was 1 s in all conditions. Thick lines are fitted one-dimensional cumulative Gaussian functions. (E/F) Average probability of leftward rotation (sphere, E) or orientation (binocular gratings, F) percepts for all subjects as a function of T_{off} for three different instructions: hold percept leftward (orange), hold percept rightward (blue), and passive viewing (black). Thick lines are linear regression fits. Error bars are the *SEM*s. A profound effect of voluntary control is evident in all four plots.

but it was still unclear whether observers have voluntary control when stimuli are presented using varying $T_{\text{on}}/T_{\text{off}}$ sequences. Figures 4C (sphere) and 4D (binocular rivalry) demonstrate that when subjects were instructed to view the stimulus passively, the same T_{off} dependency of alternation probability occurs as in Experiment 1. High alternation probabilities occur at short T_{off}'s, and low alternation probabilities occur at high T_{off}. Perhaps more surprising is the presence of the same qualitative pattern for situations in which subjects were instructed to exert voluntary control to perceive either as many alternations or as many repetitions as possible. Furthermore, the average choice alternation probabilities of all subjects as a function of T_{off} clearly shifted in the direction of the instruction to repeat or alternate demonstrating the successful exertion of voluntary control.

We used a balanced two-way ANOVA to test the influence of instruction and T_{off} on alternation probability for statistical significance. For the sphere, both the effects of instruction ($p < 0.001$) and T_{off} ($p < 0.001$) are significant, no interaction is evident between the two factors ($p = 0.88$). For all three individual instructions, there is a significant effect of T_{off} ($p < 0.01$) and a significant difference between individual subjects ($p < 0.01$). Despite this difference between subjects, all individual subjects demonstrated a significant instruction effect ($p < 0.01$); all but one (CK) had a significant T_{off} effect ($p < 0.01$). Results for the binocular rivalry stimulus are highly similar. A two-way ANOVA once again revealed significant effects of instruction ($p < 0.001$) and T_{off} ($p < 0.001$) and the absence of a significant interaction between the two ($p = 0.37$). For all the three instructions, this T_{off} effect was significant ($p < 0.001$). All the individual subjects demonstrated a significant instruction effect ($p < 0.001$), and all but one (RW) demonstrated a significant effect of T_{off} ($p < 0.01$).

We fitted the averaged data to a cumulative Gaussian function. For the sphere, the average quality of the fit for individual subjects was good ($R^2 = 0.72$, *SD* ±0.29), but the individual fits for binocular rivalry lacked statistical power. For the group data, we performed weighted fits. The individual data points received a weight-factor proportional to the inverse of their squared standard error. The average quality of this fit over the three conditions was very good for both stimuli (sphere: $R^2 = 0.93$, SD ±0.01; binocular rivalry: $R^2 = 0.93$, SD ±0.01). Figures 4C and 4D demonstrate that for both stimuli and both types of instructions, the fitted curves shifted vertically with respect to the "passive" curve toward their intended goals of maximal and minimal alternation probabilities. This can also be seen in the estimated parameters of a, representing the base of the fitted curve (sphere: $a_{\text{passive}} = 0.10 \pm 0.01$; $a_{\text{repetition}} = 0.02 \pm 0.03$; $a_{\text{alternation}} = 0.44 \pm 0.02$; binocular rivalry: $a_{\text{passive}} = 0.13$; $a_{\text{repetition}} = 0.08$; $a_{\text{alternation}} = 0.43$). We must be cautious in comparing other parameter estimates, such as the transition point (c) or amplitude (b), between the different instruction conditions since the shapes of the curves for repetition and alternation seem to be influenced by saturation.

Figures 4E and 4F show the fraction of trials in which subjects reported leftward percepts as a function of T_{off}, when they were instructed to hold one specific percept: a leftward rotating vs. a rightward rotating sphere or a leftward tilted vs. a rightward tilted grating. We compared these two instructions with the passive condition. The data points indicate averaged values of leftward percept probabilities for five subjects while error flags depict the standard errors of the mean. To fit the data, we used weighted linear regressions. Data points received a weight factor proportional to the inverse of their squared standard errors.

For the sphere, the data points for the passive condition in Figure 4E are positioned around 0.5 but are negatively correlated with T_{off} indicating a small bias toward rightward percepts, which becomes obvious especially at longer T_{off}. This is the reason why the curves for 'hold leftward' and 'hold rightward' are not mirror images of each other in the chance axis (probability = 0.5). An additional analysis confirmed the presence of a small bias for rightward percepts (data not provided). The curves for holding one percept are shifted in the intended direction indicating that subjects are able to exert voluntary control over their percept choice. A two-way ANOVA on the data set reveals that the instruction effect is significant for all individual subjects ($p < 0.02$), as well as for the group data ($p < 0.01$). The effect of T_{off} was significant only for two subjects ($p < 0.02$), and when we examined the instruction conditions separately, a significant effect of T_{off} occurred only in the "hold rightward" condition ($p < 0.01$). From Experiment 1, we know that the number of alternations drops with increasing T_{off}, which results in the larger standard errors at longer T_{off}'s. An analysis of longer sequences of alternations revealed that subjects are not reporting random percepts at short T_{off}'s but true sequences of alternations or repetitions (Figure 5B). It also demonstrates that the fraction of alternations that is still present when subjects try to maximize the number of repetitions is predominantly due to very short repetition sequences (Figure 5B). The opposite is true when subjects try to maximize repetitions.

The results for the binocular rivalry stimulus, shown in Figure 4F, are very similar to the findings with the sphere. A two-way ANOVA revealed that the effects of instruction are highly significant ($p < 0.001$), and although the T_{off} effect only approaches significance ($p = 0.06$), when investigated separately, all instructions did show a significant of T_{off}. The interaction between instruction and T_{off} was also significant ($p < 0.001$). This pattern is present with all subjects ($p < 0.01$). The weighted linear regressions reveal a small bias in passive condition, but the 'hold-curves' are near perfect mirror images in the chance axis.

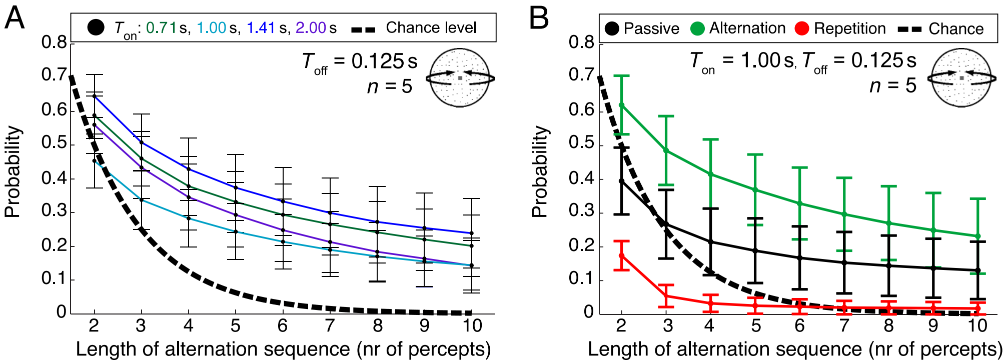

Figure 5. When longer sequences of alternations are taken into account, it becomes obvious that subjects are not reporting random percepts, but perceive true alternation sequences even if the alternation probability is around chance level at short T_{off}. The dashed line in both panels represents the chance level for the occurrence of alternation sequences of increasing length. (A) Thin-colored lines represent the probabilities of alternation sequences of increasing length in the data of Experiment 1, for the sphere with a T_{off} of 0.125 s. Even though the lines are around chance level for the shortest possible alternation sequence of 2 percepts, they are all well above chance for longer alternation sequences. (B) The data from Experiment 2 for three instructions, "passive viewing" (black solid line),"maximize alternations" (green), and "maximize repetitions" (red), clearly demonstrate that subjects perceive sequences of alternations rather than random percepts at a T_{off} of 0.125 s. It becomes clear that any alternations that are still present when subjects maximize the number of repetitions are predominantly due to very short sequences of alternations. Error bars represent *SEM*s.

In addition, for the continuous viewing condition ($T_{\text{off}} = 0$ s), all subjects were successful in exerting voluntary control over the stimuli. Mean percept durations were significantly shorter (ANOVA, $p < 0.01$) when subjects tried to maximize their alternation probability compared to when they tried to minimize the alternation probability (for the sphere on average 4.05 times shorter, *SD* ±2.10; for binocular rivalry on average 2.58 times shorter, *SD* ±1.27). When instructed to hold one of the two percepts, all subjects were again successful. Mean percept durations were significantly longer (ANOVA, $p < 0.01$) for the percepts that subjects were instructed to hold compared to the alternative perceptual interpretation (for the sphere on average 1.81 times longer, *SD* ±0.32; for binocular rivalry on average 1.47 times longer, *SD* ±0.31).

We believe that the novel implementation of adaptive pre-processing stages with a gain factor under the influence of voluntary control is physiologically plausible, widely supported by existing evidence, and elegant in its simplicity. The tight qualitative match between the extended model predictions and our data (for numerical simulations, see Appendix A) suggests that the mechanism of voluntary control is a top-down, attention-driven gain modulation on the independent perceptual interpretations of a bistable stimulus (Blaser, Sperling, & Lu, 1999; Suzuki & Peterson, 2000; van Ee, Noest, Brascamp, & van den Berg, 2006), influencing the percept-choice process at an early stage of visual processing.

Eye movements

It has been found that even though eye movements are not essential for perceptual alternations during continuous viewing, they can be facilitating (Brouwer & van Ee, 2006, 2007; Toppino, 2003; van Dam & van Ee, 2006a, 2006b). Alternations could be triggered, either due to the acquisition of 'fresh' neural tissue after an eye movement (Blake, Sobel, & Gilroy, 2003) or by tracking individual dots resulting in optokinetic nystagmus. We controlled for the possible effects of eye movements on voluntary control with an extra experiment resembling Experiment 2, for which we recorded eye movements. Three subjects that also participated in the first two experiments viewed a rotating sphere consisting of white and black dots on a gray background (30.7 cd/m^2). T_{on} was always 1 s, but three T_{off}'s were used (0.25, 0.71, and 2.00 s). All four voluntary control instructions were present (maximize alternations/repetitions, hold left/right), and each experimental condition was presented twice in random order in blocks of 60 s. Gaze position and eye movements were recorded using a head-mounted infrared camera-based Eyelink system (SMI/SR Research, Berlin, Germany) with a sample frequency of 250 Hz. The raw gaze position data were median-filtered and converted to Fick angles; eye movement velocity was calculated using a five point sliding window (Engbert & Kliegl, 2003; van Dam & van Ee, 2005). After blink-removal, saccades were detected and filtered using a separate threshold for horizontal and vertical velocities. Alternation probabilities were calculated the same way as in the previous two experiments.

All subjects were successful in exerting voluntary control. Both the effect of controlling the number of alternations ($p < 0.02$) and choosing one of two percepts ($p < 0.01$) was significant for all subjects and the group data ($p < 0.001$). The average magnitude of voluntary control can be expressed as the difference in alternation or percept probability between two opposing instructions (maximize alternations vs. maximize repetitions and hold left vs. hold right). These magnitudes were comparable in the control experiments with eye movement recording (0.47, *SD* ±0.18 for controlling the alternation probability; 0.52, *SD* ±0.14 for choosing a percept) and in the main experiment without eye movements monitoring (0.53, *SD* ±0.21 and 0.52, *SD* ±0.29, respectively). The occurrence of blinks was very low (on average 3.15 blinks/min), making it highly unlikely that they influenced perception during the much more frequent stimulus presentations. The gaze position was split up in an x- and a y-coordinate; only one subject showed a significant difference in x-coordinate between perceptual states ($p < 0.01$). When she reported the sphere to rotate leftward, the mean gaze position was 0.03 degrees left of the fixation dot, while rightward-rotating percepts had a mean gaze position 0.01 degrees right of the fixation dot. No significant difference in y-positions was evident for any of the subjects ($p > 0.15$). None of the subjects demonstrated significant differences in gaze position over different instructions ($p > 0.65$) or interstimulus intervals ($p > 0.19$). None of the subjects showed a significant difference in saccade direction between the voluntary control-related task instructions (2-way ANOVA, AR: $p = 0.15$; CK: $p = 0.07$; MN: $p = 0.14$) or the perceptual states (AR: $p = 0.46$; CK: $p = 0.61$; MN: $p = 0.95$). Two subjects had a significant difference in saccade directions ($p < 0.01$) between T_{off}-conditions, but the mean directions remained in the same quadrant of directions (AR: 96, 108, and 132 degrees; MN: 159, 150, and 167 degrees), making it highly unlikely that it played a role of any importance in the percept-choice dynamics. Eye movements could very well play a role in the perception of bistable stimuli and the exertion of voluntary control under less constrained conditions, but the results presented here clearly indicate that the successful exertion of voluntary control over an intermittently presented sphere cannot be explained by mechanisms solely based on eye movements.

Discussion

Stimulus timing

We studied the mechanisms underlying perceptual choices at the onset of bistable stimuli. In accordance with previous studies (Kanai & Verstraten, 2005; Leopold et al., 2002; Noest et al., 2007; Orbach et al., 1966; Pearson & Clifford, 2004), we found that perceptual repetitions occur at stimulus OFF-times lasting longer than approximately half a second. At short OFF durations, the opposite of percept repetition occurs and alternation rates increase dramatically. We demonstrate that this regime change primarily reflects the balance between true alternation and repetition sequences and not random percept choices at short OFF durations. Within our range of stimulus ON and OFF durations, the transition from perceptual repetition to alternation regimes depends primarily on the stimulus OFF duration, not the ON period. The use of longer ON-times for the study of perceptual choices at stimulus onset is not possible because spontaneous perceptual switches (a fundamentally different process) will then occur within the stimulus presentation episodes.

Models of perceptual bistability invariably include two terms: (1) Mutual inhibition of two percept-related neural pools (cross-inhibition) (Bradley et al., 1998; Dodd et al., 2001; Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Maier, Logothetis, & Leopold, 2007; Parker, Krug, & Cumming, 2002; Wilson, 2007) and (2) adaptation of these neural pools at a rate that depends on the magnitude of their activity (e.g., Blake et al., 2003; Lankheet, 2006; Wilson, 2007). These two components alone predict perceptual alternations at any OFF-time duration and thus cannot account for percept repetitions with long OFF-times. Recently, a single-stage, low-level model was proposed that introduces an interaction of the adaptation level with a fixed neural baseline in addition to adaptation and cross-inhibition (Noest et al., 2007). This model can explain both perceptual alternations with short OFF-times and perceptual stabilization with longer OFF-times. Our experiments reveal that the implementation of an extra adaptation stage with a gain modulation mechanism preceding the stage of rivalry resolution is necessary and sufficient for the model to explain our findings (Figure 4A) and conform to realistic constraints.

The single-stage, low-level model is based on a dynamic balance between the adaptation levels of cross-inhibiting, the percept-related neural pools, and an interaction of adaptation with a near-threshold neural baseline (for details see Noest et al., 2007; and Appendix A). In essence, this interaction term introduces an additional effect of adaptation by producing an elevated baseline activity and a reduced effective membrane time constant of the adapted population. For low adaptation levels, this baseline activity causes the more adapted neural population to 'win' the rivalry and percept-choice repetitions occur (Figure 1C). This explanation for perceptual stabilization has no need for an implicit perceptual memory (Kanai & Verstraten, 2005, 2006; Leopold et al., 2002; Maier et al., 2003; Pearson & Clifford, 2004), unless one would propose that the low-level balance between the key terms of the model is in fact the implicit perceptual memory trace (see also van de Grind, van der Smagt, & Verstraten, 2004). Consequently, a major difference from classic accounts of perceptual memory would then be that this type of perceptual memory does not require any active monitoring of the current percept but is a passive result of the shifting balance between neural pools.

Despite large differences in stimulus composition between a set of binocular rivalry gratings and an ambiguously rotating sphere, the relation between perceptual choices and stimulus timing was very similar. Interestingly, the only difference that we observed is the role of stimulus ON-time. Whereas the percept-choice dynamics of the SFM sphere are independent of T_{on}, the percept-choice dynamics of the binocular rivalry stimulus do show a small, but significant, ON-time dependency. Our model can account for this observation by assuming different amounts of adaptation preceding the rivalry resolution. Apparently, our binocular rivalry stimulus has undergone less pre-rivalry-stage adaptation than the sphere stimulus. Even though we can only make firm statements about the amounts of adaptation, it is likely that less adaptation also indicates less neural processing. This interpretation would be consistent with previous suggestions that binocular rivalry is a much more low-level, stimulus-based type of rivalry compared to the perceptual rivalry present in the SFM sphere or a Necker cube (Meng & Tong, 2004; van Dam & van Ee, 2006a; van Ee et al., 2005).

Previous studies on the perception of bistable stimuli have mainly focused on spontaneous perceptual alternations during prolonged presentation (for a review, see Blake & Logothetis, 2002). Although this percept-switching process may be closely related to the percept choice investigated here (Pearson & Clifford, 2004), the two are not necessarily based on the same mechanism (Carter & Cavanagh, 2007; Long & Toppino, 2004; Noest et al., 2007). In our study, we find a very low or absent correlation between the average percept-switch duration and the point of transition from an alternation to a repetition regime, which supports the notion that the percept choices at stimulus onset and percept switches during continuous viewing are fundamentally different processes.

Voluntary control

The perception of bistable stimuli can be influenced by attention. This attentional modulation can be bottom-up, stimulus-driven (Carter & Cavanagh, 2007; Chong & Blake, 2006; Hancock & Andrews, 2007; Kamphuisen, van Wezel, & van Ee, 2007; Mitchell et al., 2004; Ooi & He, 1999), and top-down instruction-driven (Chong, Tadin, & Blake, 2005; von Helmholtz, 1866/1925; Hol et al., 2003; Lack, 1978; Peterson & Hochberg, 1983; Toppino, 2003; for a detailed comparison across various forms of visual rivalry, see Meng & Tong, 2004; van Ee et al., 2005). There is also evidence for an interaction of bottom-up and top-down modulation (Brouwer & van Ee, 2006; Suzuki & Peterson, 2000). Interestingly, some evidence suggests that for percept choices top-down attention is equivalent to a moderate bottom-up change in stimulus contrast (Chong et al., 2005; Chong & Blake, 2006). Recent advances in psychophysics (Blaser et al., 1999; Boynton, 2005; Ling & Carrasco, 2006) and physiology (Treue & Maunsell, 1999; for a review, see Reynolds & Chelazzi, 2004) have converged to conclude that the neural mechanism underlying attention involves shifting the balance between neural gains of feature-selective neural pools, even in early stages of visual processing (Felisberti & Zanker, 2005; Saalmann, Pigarev, & Vidyasagar, 2007; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1999; Wannig, Rodriguez, & Freiwald, 2007). To some extent, voluntary control and spatial attention shifts are associated with common activity in the posterior parietal cortex, suggesting voluntary control to be at least partially based on shifting the focus of attention (Slotnick & Yantis, 2005). The finding that the amount of voluntary control a subject can exert depends on stimulus features (Brouwer & van Ee, 2006; Suzuki & Peterson, 2000), and the demonstration of independent control over the two individual rivaling percepts (van Ee et al., 2006) further adds to the suggestion that voluntary control influences perception by independent, attention-driven gain modulations at early stages in visual processing.

Concerning voluntary control, we demonstrated (1) that voluntary control over perceptual decisions at the onset of bistable stimuli exists for both binocular rivalry and a bistable rotating sphere, (2) that it does not override the T_{off} dependency shown in our first experiment but interacts with it, and (3) that it is not driven by eye movements. Our subjects only indicated pure dominant percepts and no mixtures. This means that theoretically they may have changed their reporting criteria in the voluntary control conditions instead of their perception. We took special care in avoiding mixed percepts with our sphere stimulus (see Methods section in Experiment 1), but for the binocular rivalry experiment, this issue cannot be completely excluded. However, given the resemblance between the results of the sphere stimulus and the binocular rivalry, we are fairly certain we are probing a perceptual effect rather than a change in reporting criteria.

In Appendix A of this paper, we provide numerical simulations of our model that demonstrate a strikingly close resemblance between the experimental effects of voluntary control and simulations in which we implement voluntary control as a gain modulation in the two individual pre-processing stages (conform van Ee et al., 2006) (compare Figure 4C and 4E with Figures A1D and 4D and Figure 4F with Figure A1E). This resemblance suggests that voluntary control acts as a top-down attention-driven gain modulator in early visual processing stages. The fact that the perception of a bistable sphere and binocular rivalry gratings are similarly influenced by voluntary control together with the suggestion that binocular rivalry is resolved at a lower level of neural processing further supports the notion that voluntary control effects perception at very early levels of neural processing.

Attention and voluntary control both appear to influence bistable perception via early neural gain modulations. Voluntary control could thus be interpreted as the application of a non-specific attentional strategy to affect perception (it is the *reason for* rather than the *type of* attention). This would explain the resemblance between our voluntary control findings and experiments in which onset rivalry is influenced by attentional states (Chong & Blake, 2006). In their study, Chong and Blake (2006) demonstrated that feature-based attention influences binocular rivalry. They asked their subjects to attend to some stimulus feature preceding rivalry in the assumption that this feature-based attention would still be present at the onset of rivalry and influence perception accordingly. In our current study, we investigate the underlying mechanism of voluntary control without ever explicitly instructed our subjects to attend to any stimulus feature. The only instruction they received was to attempt to voluntarily control perception. It was never specified how they should do this, leaving subjects free to exploit any appropriate cognitive strategy to achieve the instructed effect on perception. The resemblance between our findings and those of Chong and Blake, together with existing literature on visual attention and our own novel computational efforts, strongly suggests that our subjects used some attentional strategy to exert voluntary control and influence perception. Differences in attentional strategy between individual subjects may account for differences in the extent to which they can exert voluntary control. Although in repeated tests observers produce highly replicable data with only small variation in drift and sequential dependence (Suzuki & Grabowecky, 2007; van Ee et al., 2005), they also benefit from initial training to become successful in exerting voluntary control. In this view, they may simply use this initial training to develop an appropriate attentional strategy. It remains an open question what attentional strategy our subjects used to be successful in exerting voluntary control. Previous reports provided evidence that voluntary control over the sphere does not interact with perception at the level of individual elements but at a higher level of surface representations (Brouwer & van Ee, 2006), dovetailing nicely with recent single cell recordings showing that attention can select surface representations to modulate activity as early as cortical area MT (Wannig et al., 2007).

The hallmark of bistable stimuli is that there is evidence in the stimulus for mutually exclusive perceptual interpretations. Voluntary control functionally appears to increase the relative value of the evidence for one of the possible perceptual interpretations thereby biasing the system toward a specific perceptual decision. The neural mechanism by which voluntary control achieves this gain-modulation could involve feedback connections from prefrontal and posterior parietal areas back to earlier areas of visual processing (Buschman & Miller, 2007; Saalmann et al., 2007) but is a topic that has to be addressed in future research.

Appendix A

The fact that perceptual stabilization only occurs at longer interstimulus intervals was predicted and qualitatively shown by a single-stage, low-level neural model for visual rivalry (Noest et al., 2007). Here we present a data-driven analysis of the influence of stimulus timing on perceptual rivalry revealing a relative insensitivity to stimulus presentation duration that is significantly stronger than was predicted in the original single-stage model. We demonstrated that an extension of the model easily accounts for this finding if a realistic stage of adaptation prior to the rivalry resolution is included. Furthermore, our experiments with voluntary control and variable stimulus timing confirm novel model predictions for input imbalances, suggesting voluntary control to act as a gain control mechanism preceding rivalry resolution. Figure A1A is a schematic representation of the model consisting of an adaptive pre-processing stage, a gain factor under top-down control, and a rivalry-resolving stage (as published by Noest et al., 2007). In equations, the entire model can be described by:

1. Pre-processing stage

$$\tau \partial_t \xi_i = x_i - (1 + a_i)\xi_i \tag{A1}$$

$$\partial_t a_i = -a_i + \alpha S[\xi_i]; i,j \in \{1,2\}, i \neq j \tag{A2}$$

2. Gain mechanism

$$X_i = g_i S[\xi_i] \tag{A3}$$

3. Rivalry-resolving stage

$$\tau \partial_t h_i = X_i - \beta - (1 + A_i)h_i - \gamma S[h_j + \beta] \tag{A4}$$

$$\partial_t A_i = -A_i + \alpha S[h_i + \beta]; i,j \in \{1,2\}, i \neq j \tag{A5}$$

The rivalry-resolving stage of the model describes two neural pools that are each coding for a rivaling perceptual interpretation. They adapt, inhibit each other through cross-inhibition, and their adaptation levels interact with a neural baseline. The basic model consists of fast 'local field' dynamics (Equation A4) and a slow shunting-type adaptation component ('leaky integrator', Equation A5). The fast dynamics are determined by the local field activity of one of two opposing percept-coding pool of neurons (h), which is translated into a spike rate via a sigmoid function (S) and depends on the neural input to the system (X); the adaptation dynamics (A); the amount of cross-inhibition (g); and a recently introduced term b, that can physiologically be interpreted as an intraneural baseline interacting with the adaptation levels (for details, see Noest et al., 2007). The addition of the b-term to the well-established adaptation and cross-inhibition terms is the only real novelty compared to classic models of visual rivalry (Blake & Logothetis, 2002), but it has been shown to be crucial for understanding the underlying mechanism of percept-choice repetitions (Noest et al., 2007). The intraneural baseline (b) effectively creates an elevated baseline activity and a reduced effective membrane time constant of the adapted neural population. This results in a small head start for the more adapted neural population at the next stimulus onset that may overcome the effects of adaptation causing the more adapted neural population to become dominant and a perceptual repetition to occur. The intraneural baseline thus determines at which combination of adaptation levels perceptual repetitions will occur (see Figure 1C in the main text).

Since visual competition is highly unlikely to be resolved at the very first stage of neural processing, reality forces us to consider neural processing preceding the rivalry resolution. We implement these stages in their simplest possible form. Neural stages preceding rivalry resolution are assumed to have the same type of fast 'local field' and adaptation dynamics as the rivalry-resolving stage (Equations A1 and A2) while lacking cross-inhibition. The interaction with a neural baseline (b) is functionally irrelevant here because the two pools do not interact (Noest et al., 2007) and it is therefore left out of the equations.

Figure A1B demonstrates how, at each stimulus onset, the flow field of the fast 'local field' dynamics (gray arrows) gives rise to trajectories (black lines) leading to one of two equilibrium points that represent the opposing percepts (P1, P2). The separatrix (dashed lines) at the intersection of the null-clines (red paired with either blue or green line) of the 'local field' dynamics groups trajectories that are destined for either equilibrium. At stimulus onset, the starting point of a trajectory with respect to the separatrix thus determines which percept will win the rivalry. Adaptation asymmetries between the opposing neural populations scale the corresponding null-cline (green to blue solid line) and shift the separatrix (purple arrow; green to blue dashed line). If the separatrix shift passes the starting point of a trajectory, this will change the corresponding endpoint to the less adapted percept, causing perceptual alternations. The inset demonstrates that the presence of an intraneural baseline (b) creates a fixed offset in the starting points of the trajectories giving them a head start toward the more adapted percept. If this offset is smaller than the adaptation-driven separatrix shift, the system will end up with

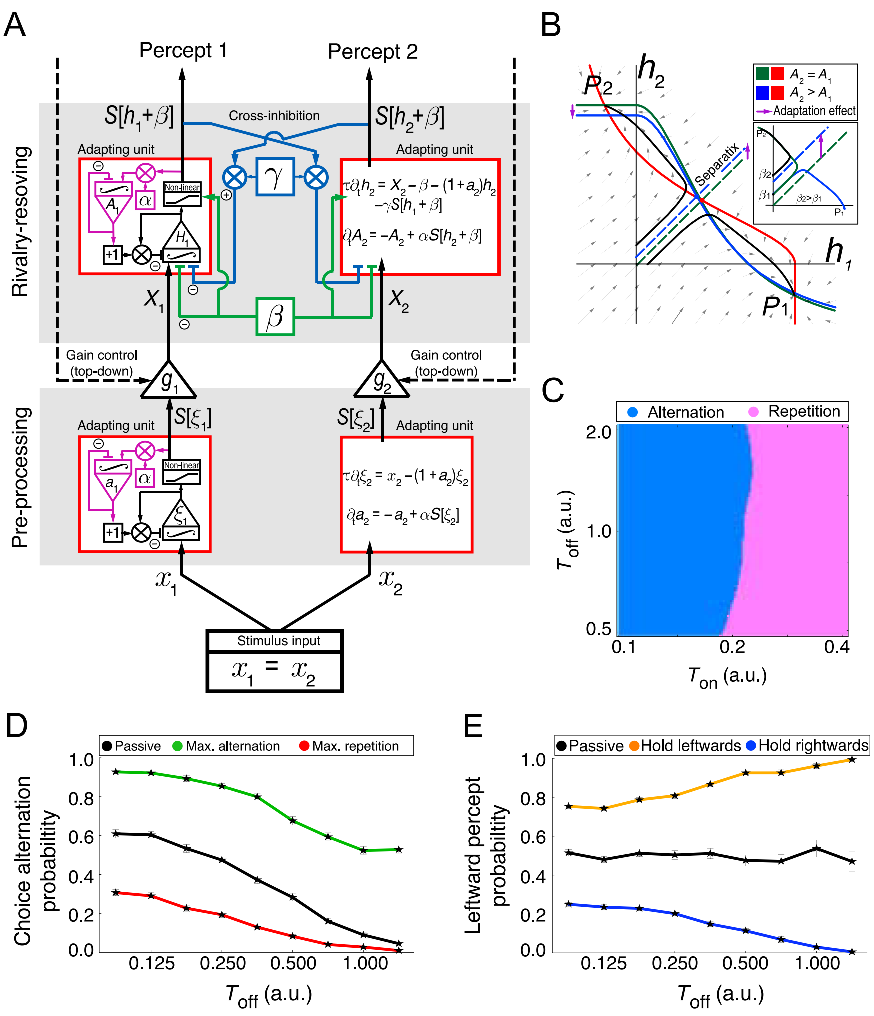

Figure A1. (A) Schematic representation of our complete percept-choice model for visual rivalry and its voluntary control. The model consists of two stages; a pre-processing stage feeds into a rivalry-resolving stage with a gain factor that is under top-down control. The dynamics of the model are determined by adaptation (purple lines), cross-inhibition (blue lines), and neural baseline (green lines). Both stages consist of adaptive neural pools coding for opposing percepts (red rectangles). On the left side of the scheme, the dynamics are displayed schematically, on the right side the corresponding equations are depicted. (B) The dynamics of the low-level neural model for perceptual choices in visual competition as defined by differential Equations A4 and A5. Depicted on the axes are the activity levels of opposing neural populations ('local fields,' h_i). When the adaptation levels of both are equal ($A_2 = A_1$), the red and green null-clines ($d_t h_i = 0$) determine the flow fields of the fast 'local field' dynamics creating the saddle point and corresponding separatrix at their cross-section. An imbalance in adaptation states with $A_2 > A_1$ scales one of the null-clines (for h_2) in the h_2-direction (green line) and causes the intersection and attached separatrix to move slightly up- and leftward. The intraneural baseline (β in the model) creates an offset of the starting points of the trajectories. The inset shows that trajectories (solid lines) for which the offset (β_1) is smaller than the separatrix shift (purple arrow) the trajectories are now on the other side of the separatrix (green dashed line to blue dashed line). This changes their endpoints to the less adapted percept, resulting in perceptual alternations (green to blue trajectory). If the adaptation-driven separatrix shift is however smaller than the offset (β_2), the trajectory endpoint remains unchanged (green to black trajectory), the more adapted percept prevails and perceptual stabilization occurs. Thus, with a fixed β, it is the size of the adaptation-driven separatrix shift that determines whether perceptual decisions alternate or repeat on subsequent presentations. (C) A simulation for the effect of pre-stage adaptation demonstrates a near-vertical border between alternation and repetition areas. (D) Simulations for instructions "maximize alternations" (green), "maximize repetitions" (red), and passive condition (black). (E) Simulations for instructions "hold leftward" (orange), "hold rightward" (blue), and the passive condition (black). Voluntary control was modeled in the pre-processing stage as a 2% increase of the gain for the favored percept. T_{on} and T_{off} are given in units of the adaptation time constant. Note the close resemblance between panels D and E and the data in Figures 4C–F. Simulations were performed with $x_i \in \{0,3\text{ g}\}$, $\alpha = 5$; $\beta = 4.4/(3\alpha)$; $\gamma = 10/3$; $g_1 = g_2 = 1.5$; $\tau = 50$. For panels D and E, T_{on} was set to 1.0, noise on the adaptation levels was added as 4% variance of the mean, and top-down gain control was modeled as a 2% gain increase for the favored percept.

perceptual alternations (b1; the green solid line is the trajectory for the original green dashed separatrix, the blue solid line is the trajectory for the shifted blue dashed separatrix), but if the offset is larger than the separatrix shift, the endpoints of the trajectories remain unchanged and perceptual stabilization occurs (b2; the black line is the new trajectory corresponding to the shifted blue dashed separatrix). With a fixed size for β, it is the adaptation-driven separatrix shift that determines whether perceptual decisions alternate or repeat on subsequent presentations (see also Figure 1C for the relation between β and the adaptation levels).

Figure A1C shows the result of a numerical simulation with our two-stage model and demonstrates that adaptation in pre-processing stages causes a steep border between areas of percept-choice repetitions and alternations (compare with Figure 3C in Noest et al., 2007) confirming our experimental findings. The addition of noise to the system would make the model more realistic but ‘blur’ the mentioned boundary, without influencing its shape (see Figure A4B in Noest et al., 2007) and is therefore left out of this simulation. Apart from the fact that existing empiric evidence dictates us to account for these pre-processing stages, no other simple parameter manipulations within the rivalry stage can produce the observed effect of stimulus timing.

Figures A1D and A1E show the results of numerical model simulations for voluntary control. Here we use a 2% gain imbalance to model an active preference for one of two perceptual interpretations at stimulus onset and realistic noise (4% variance of the mean) is added to the adaptation levels to obtain smooth curves. As a result of an increase in the number of repetitions, the error on the data points also increases with increasing T_{off}. Not only does existing empirical evidence favor the implementation of early gain modulations, manipulations of other model parameters—most importantly, those for the cross-inhibition and neural baseline—fail to yield results similar to our experimental data. An earlier suggestion that top-down voluntary control may be mediated through modulations of the β-parameter (Noest et al., 2007) are inconsistent with the vertical curve-shifts we demonstrate in our second experiment. Changing β would only affect the effect in the horizontal (T_{off}) direction. The one notable difference between the simulation and our data is due the small bias for rightward percepts that is present in the data, but not in the simulation. If such a bias would be added to the simulation the simulation would match the data even more.

Altogether, we have presented a relatively simple yet physiologically plausible, low-level neural model that is sufficient to explain the perceptual alternations, the perceptual repetitions (stabilization), the influence of stimulus timing, and the mechanism underlying top-down voluntary control for perceptual decisions at the onset of visual rivalry.

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