Two paradigms of bistable plaid motion reveal independent mutual inhibition processes

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Perception is sometimes bistable, switching between two possible interpretations. Levelt developed several propositions to explain bistable perception in binocular rivalry, based on a model of competing neural populations connected through reciprocal inhibition. Here we test Levelt's laws with bistable plaid motion. Plaids are typically tristable, either a coherent pattern, transparent with one component in front, or transparent with the opposite depth order. In Experiment 1, we use a large angle between component directions to prevent plaid coherence, limiting the ambiguity to alternations of grating depth order. Similar to increasing contrast in binocular rivalry, increasing component speed led to higher switch rates (analogous to Levelt's fourth proposition). In Experiment 2, we used occlusion cues to prevent one depth order and limit bistability to one transparent depth order alternating with coherence. Increasing grating speed shortened coherent motion periods but left transparent periods largely unchanged (analogous to Levelt's second proposition). Switch dynamics showed no correlation between the experiments. These data suggest that plaid component speed acts like contrast in binocular rivalry to vary switch dynamics through a mutual inhibition model. The lack of correlation between both experiments suggests reciprocal inhibition mediates bistability between a variety of neural populations across the visual system.

Introduction

Our vision of the world is generally stable, even though perception is fundamentally probabilistic and reflects the most likely interpretation of the input stimulus (Gibson, 1979; Kersten, Mamassian, & Yuille, 2004; Gregory, 2009). One consequence of this is that perception can sometimes exhibit multistable behavior and switch back and forth between several possible interpretations. Perceptual bistability comes in many forms, with binocular rivalry (Von Helmholtz, 1967/1924–1925; Breese, 1899; Levelt, 1968; Blake & Fox, 1974; Lack, 1978; Logothetis & Schall, 1989; Leopold & Logothetis, 1996) being the most commonly studied example in the laboratory. Binocular rivalry is a unique form of bistability as it results from dichoptic stimulation (Wheatstone, 1838), whereby each eye views an image that cannot be fused with the other eye's image (Liu, Tyler, & Schor, 1992), setting up a competition between early monocular neurons (Blake, 1989; Alais & Blake, 2005). Bistability is not limited to dichoptic stimulation and, indeed, most other forms are experienced when binocularly viewed. Among many other forms of bistable perception are ambiguous depth from motion (Wallach & O'Connell, 1953), perspective ambiguity (e.g., the Necker cube and Schroeder's stairs; Necker, 1832; Schröder, 1858) and figure/ground ambiguity (e.g., Rubin's Face/Vase illusion; Rubin, 1921). While all these examples involve visual ambi-

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guity, bistability also occurs in the auditory modality (Warren & Gregory, 1958; Van Noorden, 1975; Pressnitzer & Hupé, 2006) and the somatosensory modality (Carter, Konkle, Wang, Hayward, & Moore, 2008; Liaci, Bach, Tebartz van Elst, Heinrich, & Kornmeier, 2016). This illustrates that perceptual ambiguity is a widespread phenomenon that will elicit bistable behavior under many circumstances (Schwartz, Grimault, Hupé, Moore, & Pressnitzer, 2012).

Although perceptual ambiguity in general has been widely examined, it is notable that binocular rivalry and ambiguous figures have been historically independent streams of research. In the case of binocular rivalry, the perceptual alternation involves one image being completely suppressed from consciousness awareness, while for ambiguous figures the phenomenal alternations are less dramatic as only the choice between two competing interpretations switches. Some have argued that this points to low-level sensory mechanisms underlying binocular rivalry (Fox & Check, 1968; Levelt, 1968; Blake & Fox, 1974) while high-level cognitive processes drive the perception of ambiguous figures (Gregory, 1970; Rock, Hall, & Davis, 1994). However, others have pointed out that both forms of ambiguity may share common processes (Walker, 1975; Riani, Tuccio, Borsellino, Radilova, & Radil, 1986; Leopold, 1997). Consistent with this, work emerged which suggested a new interpretation that rivalry occurred after the level of interocular grouping (Diaz-Caneja, 1928; Kovacs, Papathomas, Yang, & Feher, 1996; Logothetis, Leopold, & Sheinberg, 1996). This demonstrated that percept competition played a role rather than the interocular competition thought to underlie binocular rivalry (Leopold & Logothetis, 1999). This work advocated a set of "general rules": exclusivity, randomness, and inevitability, which have been shown to apply to ambiguity in audition (Pressnitzer & Hupé, 2006) and somatosensory (Carter et al., 2008).

The dynamics of binocular rivalry also follow specific, nonintuitive properties relating input strength to percept duration, described by Levelt (1968). The most striking result obtained by Levelt is known as his second proposition: When increasing the luminance or the contrast of the stimulus presented to one eye, while keeping constant the input to the other eye, the average percept duration for the manipulated eye did not change while percept duration decreased for the other eye. Brascamp, van Ee, Noest, Jacobs, & van den Berg (2006) showed that this phenomenon was in fact valid only within a limited range of parameter values (see Discussion). But even within this limited range, Levelt's result strongly constrains the underlying model: Rubin & Hupé (2005) stated that it demanded that two independent populations of neurons coding the competing representations be functionally connected through reciprocal inhibition, as indeed implemented in most, if not all, models of binocular rivalry accounting for Levelt's laws (Lehky, 1988; Mueller & Blake, 1989; Wilson, 2003; Noest, van Ee, Nijs, & van Wezel, 2007; Seely & Chow, 2011; see more references in the supplemental information by Alais, Cass, O'Shea, & Blake, 2010). There is also psychophysical evidence revealing the dynamic inhibition of suppressed percepts, therefore supporting the reciprocal inhibition model (Alais et al., 2010). In addition to coupling, key roles have been demonstrated for both adaptation (Suzuki & Grabowecky, 2002; Blake, Sobel, & Gilroy, 2003; Long & Toppino, 2004; Pastukhov & Braun, 2011) and noise (Brascamp et al., 2006; Moreno-Bote, Rinzel, & Rubin, 2007; Shpiro, Moreno-Bote, Rubin, & Rinzel, 2009; Pastukhov et al., 2013; Huguet, Rinzel, & Hupé, 2014) in triggering switches between the competing populations of neurons as the dominant response wanes.

Some of the models cited above were developed for ambiguous figures, with the supposition that inhibitory coupling originally developed to account for Levelt's rules (e.g., Lehky, 1988), hence Levelt's rules (at least implicitly), apply to all types of perceptual competition. Such a generalization was suggested by Logothetis et al. (1996), who showed that Levelt's second proposition also applied to percept rivalry in case of interocular grouping. A few studies tested ambiguous stimuli for Levelt's second proposition and found results similar to binocular rivalry (Carter & Pettigrew, 2003; Klink, van Ee, & van Wezel, 2008; Bonneh, Donner, Cooperman, Heeger, & Sagi, 2014). However, a fundamental ambiguity remains in those studies, because testing Levelt's proposition requires being able to manipulate the strength of the input to only one of the competing interpretations, P1 or P2. Any modification of an ambiguous image favoring P1 relatively to P2 may do so by providing either more absolute weight to P1 or less absolute weight to P2 (or a combination of both), leading to opposite interpretations for Levelt's second proposition. In the cited studies, the knowledge is missing of the precise physiological mechanisms involved in building up the competing images, so the effect of the stimulus manipulations on perceptual competition could only be speculative.

In the search for finding another, hopefully more definitive, proof of the generalization of Levelt's laws, we use moving plaids (Wallach, 1935). Plaids are stimuli composed of two drifting gratings that move in different directions and are superimposed to form a kind of checkered pattern. Even though each grating moves in a different direction, the pattern is ambiguous and can be perceived as two gratings sliding over each other in transparency or as a single fused pattern moving in an intermediate direction (Alais, Wenderoth, & Burke, 1994; Hupé & Rubin, 2003). Plaids have been very widely studied from the perspective of motion integration and segmentation (Adelson & Movshon, 1982; Stoner & Albright, 1993) but are also remarkable examples of perceptually ambiguous patterns because they are tristable. That is, plaids can be seen as a coherent single pattern, as transparent motion with one grating in the foreground, or as transparent with the reverse depth order (Hupé & Pressnitzer, 2012). Here we use this tristable property of plaids indirectly to test Levelt's fourth and second propositions in a way that was not possible in previous studies with other bistable paradigms.

Since Levelt's laws apply to bistable, not tristable, perception, we select plaid stimulus parameters to limit the multistable behavior of plaids to a bistable range, but we do so in two different ways. In Experiment 1, we set the angle between the drifting component gratings to very strongly support transparency and elicit a bistable competition between the two possible depth orders (P1 and P2). In Experiment 2 we adjust the plaid parameters so that they alternate between transparent (P1) and coherent (P3) patterns, by having one grating occluding the other. The critical originality compared to previous studies is the possibility to have the same percept (P1) competing with either a similar percept (P2) or a very different one (P3). As we shall explain, this allows us to overcome the ambiguity between relative and absolute manipulation of percept strength, without having to know the precise physiological mechanisms involved. In both experiments, we manipulate grating speed and show that, when considering both results together, speed acts analogously to contrast in binocular rivalry to produce plaid alternation dynamics consistent with Levelt's fourth proposition (Experiment 1) and second proposition (Experiment 2). We show finally that the switch dynamics in both experiments are not correlated, suggesting that reciprocal inhibition governs both kinds of bistability but it is instantiated between different neural populations in each case.

Methods

Observers

Fifteen observers (eight women, seven men; aged 21–46) participated in the experiment, including authors CMS (subject S1) and JMH (subject S15). We verified that all subjects had normal or corrected-to-normal eyesight, although one subject (S9) was excluded after running the experiment because we realized he was color-blind (he was the only subject for whom the color occlusion in the plaid bistability experiment was not efficient). The study was performed in accordance with the Declaration of Helsinki, and written, informed consent was obtained from all subjects, who received (except the authors) compensation for their time in the form of coupons worth 40 euros. Subjects, including the authors, were unaware of the purpose of the experiments concerning the potential effect of speed on percept duration: At the time of design, the purpose of the experiment was to find for each subject a specific set of parameters that led to equidominance. Speed was manipulated simply to explore a larger parameter range. Subjects were told that we were studying the dynamics of perception for ambiguous stimuli.

Apparatus

We presented stimuli on a 19-in. Sony Trinitron Multiscan G400 screen (26.25 cm vertical viewable screen size) at a frame rate of 85 Hz, controlled by a PC running Windows 7. The experiment was coded in MATLAB (MathWorks, Natick, MA) using the Psychophysics Toolbox extension (Kleiner, Brainard, & Pelli, 2007). Screen resolution was 1280×1024 pixels. Subjects were comfortably seated 54 cm in front of the screen in a dimly lit room, with their chin and forehead resting on a chinrest. Sighting dominance was estimated by asking subjects to point a distant target while closing each eye in turn. The dominant eye position was monitored at 2000 Hz with an EyeLink Plus (SR Research, Ottawa, ON, Canada). Subjects continuously reported their percepts using a 3-button mouse.

Stimulus and parameters

All stimuli comprised two moving, superimposed rectangular-wave gratings, presented through a circular aperture 5° in radius. The gratings comprised thin dark stripes (about 15 cd/m^2, duty cycle = 0.25) on a lighter background (27 cd/m^2) and appeared as dark stripes moving over the background (Figure 1). The luminance of the gray background outside the aperture was 23 cd/m^2, corresponding to the average luminance across the aperture. The gratings both moved at either 1.5 °/s or 5 °/s (measured in the direction normal to their orientation). The direction of the coherent plaid (corresponding to the motion of intersections) was either upwards or downwards, although coherence was almost never perceived for the plaids designed to be transparent, as in Figure 1a. A black fixation point (0.2° radius) was added over a 1° radius circular gray mask (23 cd/m^2) in the middle of the circular aperture, to minimize optokinetic nystagmus. The images of all stimuli were computed before the experiments, applying anti-aliasing, and stored in a movie.

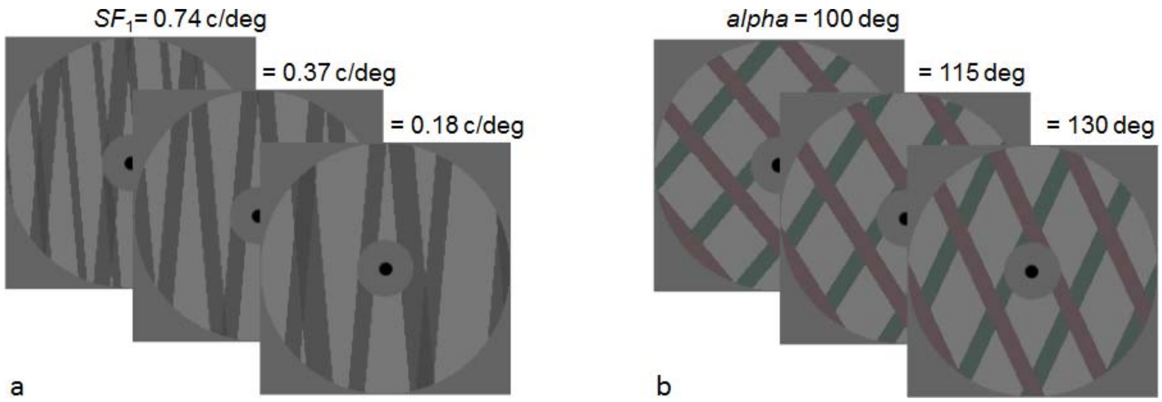

Figure 1. Examples of stimuli used to study (a) depth-ordering bistability and (b) coherent/transparent plaid bistability. SF_1 is the spatial frequency of the left tilted gratings, in c/°. The SF of the right oriented grating is 0.37. Alpha is the angle between the moving directions of the gratings (orthogonal to their orientations). The other manipulated parameters were grating speed (1.5 or 5 °/s), and the global direction of the plaid (up or down). For plaids shown in (a), the grating whose SF was manipulated was tilted either leftward or rightward. For the plaids shown in (b), the color of the occluding intersections was either red or green, and the red grating was tilted either rightward or leftward.

We studied perceptual alternation dynamics using three sets of plaid stimuli, each with carefully chosen parameter settings. The first two sets of plaids were set to strongly favor only two percepts out of the three possible plaid percepts. The first set (Figure 1a) was bistable, alternating between two possible grating depth orders and was almost never perceived as coherent. This was achieved by using a large angle between component directions, making coherent motion strongly unfavored. The second set (Figure 1b) was bistable between coherence and transparency, with one depth order strongly encouraged. This was done by allowing the red (or green) grating to occlude the green (or red) grating where they intersected. In this set of plaids, the percept of "transparency with green in front" was strongly unfavored (but not impossible, as observed for different set of plaids: Hupé & Rubin, 2000). A third set (not shown) was adjusted to encourage tristable plaid perception, but these data are not analyzed in the present study. We shall, however, describe their parameters as well (similar to those used by Huguet et al., 2014), because the plaids from the three sets were presented in an interleaved manner (see the Experiment section below).

To study depth-ordering bistability (Figure 1a), both gratings were gray (14.6 cd/m^2) and the luminance of the intersection was a bit darker (11.7 cd/m^2) to favor transparency. Gratings moved in directions 170° apart (angle alpha hereafter). The spatial frequency (SF hereafter) of one grating was 0.37 c/° while the SF of the other grating was either 0.18, 0.37, or 0.74 c/°. The factorial combination of the three parameters (two grating speeds, two plaid directions, and three possible SF) produced 12 stimuli. Each stimulus was repeated four times, twice for each tilt (the grating whose SF was modified could be tilted to the left or to the right) for a total of 48 stimuli.

To study coherent/transparent bistability (called plaid bistability hereafter, Figure 1b), one set of bars was greenish (CIE 1931 xyY = [0.267 0.298 14.8]), the other one reddish ([0.297 0.287 14.9]). One grating occluded the other one. The SF of both gratings was 0.37 c/°. Alpha was 100°, 115°, or 130°, grating speed was either 1.5 or 5 °/s and the plaid direction either up or down. The factorial combination of the three parameters (two grating speeds, two plaid directions, and three alpha values) produced 12 stimuli. Each stimulus was repeated four times, twice for each tilt (the red grating could be tilted to the left or to the right) and twice for each color occlusion (red or green occlusion), for a total of 48 stimuli.

The third set of plaids were gray, similar to those used for depth ordering, but with lower alpha values (100°, 115°, and 130°) and with the SF of both gratings equal to 0.37 c/°. The factorial combination of the two parameters (two directions and three alpha values) produced six stimuli, each repeated four times (total = 24 stimuli).

Experiments

Each subject ran four experimental sessions of about one hour. Each stimulus from the three sets of plaids (30 stimuli in total) was presented in each session. The stimuli were presented in a pseudo-random manner. Four different pseudo-random sequences were generated and run with the same order by each subject. The sequences were designed to avoid as much as possible adaptation to carry over trials. The constraints of the algorithm were: (a) never present two stimuli from the same set of plaids in a row; (b) never present two stimuli with both the same direction and alpha in a row; (c) only allow presentation of two stimuli with the same direction, same alpha, and same speed when at least two other stimuli were presented in between; (d) never present more than two stimuli in a row with the same direction of motion; and (e) never present more than three stimuli in a row with the same component speed.

At the beginning of each session, subjects were shown examples of tristable plaids (third set) and asked to report verbally the direction of motion. We waited until they experienced spontaneous switches of percept and reported them. Then we told them that when the bars moved together, we called that percept *coherent movement*; to report this percept (therefore upward or downward motion), they should keep pressing the middle mouse button as long as they were experiencing it; when the bars moved in opposite directions across each other, we called that *transparent movement*. Then, we asked them whether, when experiencing the transparent percept, they could tell which bars were in front. We waited until the participant identified the two possible percepts and then told them to keep pressing the right mouse button when they saw the bars in front moving to the right, and the left mouse button for the bars in front moving to the left. For participants who did not identify clearly the two transparent percepts, we showed them plaids composed of gratings with different SF, where depth ordering is generally more salient. We also tried to help them by indicating that the bars perceived in front were typically the ones that one pays more attention to and that capture the sense of motion (Hupé & Pressnitzer, 2012).

Participants kept practicing with different stimuli until they were familiar with the percepts and the button-press reporting. We told them that there was no correct nor wrong responses, and that if at times they were not sure of what percept they were experiencing, they should stop pressing any mouse button at all and that for some stimuli their percept may remain constant for the whole trial. We did not tell them that for most stimuli (from the two bistable sets shown in Figure 1) they should experience only two different percepts (meaning that subjects could report a coherent plaid percept for the depth ordering set, as well as, for example, red bars moving in front even when occluded by green bars for the plaid bistable set). These seldom expected third percepts were very rare across all subjects and, when they occurred, were very short, hence validating our procedure (see also the Pretreatment paragraph below in the Data Analysis section).

Participants were told that they would have to report their percepts as faithfully as possible for 30 1-min trials, while maintaining constant fixation on the black dot at the center of the screen. They were given "passive" viewing instructions, meaning that they should try not to voluntary hold or change a percept. They would initiate each new trial by pressing the space bar, so they could take breaks as long as they wished between each trial. The experimenter (second author CMS) was always present in the room, monitoring online the quality of the participant's eye fixation. When noticing deviations, the experimenter would encourage participants to try to fixate the center more accurately. He would also ask participants to take a longer break after 15 of the 30 trials were completed. Standard eye calibration was performed at the beginning of each session and after the long break (as well as after any long break initiated by the participant).

Data Analysis

Pretreatment

Perceptual reports were acquired through a three-button mouse, allowing subjects to press several buttons at the same time, even though subjects were told to be careful to avoid it. These multi-button reports needed to be disambiguated for the analysis. A semiautomatic procedure, detailed in Supplementary File S1 (Appendix A: Clean-up procedure) led to correction of 374 reports, representing only 4.3% of the total number of percepts. Only 101 modifications involved durations longer than 600 ms, for a total of about 300 s, corresponding to less than 0.4% of the total time across subjects.

Since the whole experiment relied on subjects reporting their percepts faithfully, we looked for objective indications that they actually did so. Unknown to the participants (except authors S1 and S15), our stimuli had parameters that systematically biased perception towards one or the other interpretation. For depth ordering bistability, lower frequency gratings are more often perceived in front (Moreno-Bote, Shpiro, Rinzel, & Rubin, 2008). For plaid bistability, plaids with higher alpha values are perceived more often as transparent (Hupé & Rubin, 2003). We tested if these manipulations were effective for every subject. In addition, we tested if we managed to put all participants in a bistability (not tristability) range, and whether they continuously reported their perceptual state for most of the trial period.

These analyses are detailed in Supplementary File S1 (Appendix B: Objective validation of subjective reports). We had to exclude two subjects for the depth ordering experiments, for whom the SF manipulation did not have a systematic effect across parameters. Participants could report a percept most of the time. Over 672 60-s long trials in each experiment, we removed five trials for depth ordering and one trial for plaid bistability because the continuous tracking record had blanks where no percept was reported for longer than 20 s. Bistable-only alternations were reported in most trials and subjects.

The unfavored percept (coherent for depth ordering, transparent with the occluded percept in front for plaid bistability) was reported sometimes, however, usually for very short durations (so possibly involving mistakenly pressing the wrong button). We removed all trials (13 for depth ordering and 38 for plaid bistability) in which the unfavored percept was reported for more than 5% of the time (3 s), to be sure to analyze only clearly bistable perception.

We therefore analyzed 559 trials (out of 576) across 12 subjects in the depth ordering experiment, and 633 trials (out of 672) across 14 subjects in the plaid bistability experiment

Statistical analysis

Analyses were performed in R, version 3.4.1. We considered two dependent variables, percept dominance and percept duration. Percept dominance was expressed as the percentage of time one percept was experienced in each 60-s trial. It was computed by ignoring the periods of no report and the rare and short periods reporting the unfavored percepts. For depth ordering bistability, we computed the dominance of the right moving grating perceived in front (dominance of the left moving grating in front was 100 minus this value). For plaid bistability, we computed the dominance of the coherent percept (dominance of the transparent percept, with the occluding grating perceived in front, was 100 minus this value). Percept dominance was used to test if parametric manipulations were effective in every subject (Supplementary File S1, Appendix B) and to find the parameters that led to competition closest to equidominance for each subject (Supplementary File S1, Appendix C and D).

The analyses related to our research question and presented in the Results section were performed on the duration of individual percepts across trials. The duration of the last percept, when interrupted by the end of the trial, could not be measured: It was therefore not included in the analysis, except when this was the only percept reported during the whole trial. In this case its full duration was underestimated, but this error was less detrimental to the analysis than if only keeping shorter percepts acquired for the same set of parameters. We analyzed the duration of transparent and coherent percepts independently. We used the R package lme4, version 1.1-18-1, to apply generalized linear models with a Gamma family and the identity link function, in order to compute the confidence intervals of effect sizes in seconds. We verified that the results were similar with linear models applied to the log of the response times (Hupé & Rubin, 2003, 2004; Hupé & Pressnitzer, 2012; Huguet et al., 2014). We computed mixed models for estimates across subjects.

Because percept durations varied a lot between subjects, therefore leading to very different numbers of values across subjects, we first applied models independently for each subject and experiment in order to detect outliers using residual analyses. Values with *z*-score values above |3.5| were removed. For the depth-ordering experiment, these values were always obtained for short percepts, possibly corresponding to involuntary button presses or errors. We removed 10 outliers across five subjects. Eight percepts were shorter than 1 s; the other two were 1.7 and 1.8 s long, but percept durations for similar stimuli and for the same subject were on average 13 s long. For the plaid bistability experiment, we had to remove only three outliers across two subjects (two values shorter than 750 ms, one value lasting almost 60 s). Overall, the percentage of outliers removed was very small (0.23%).

In order to be able to estimate the effect of speed across different parameters, we had to test for the presence of interactions between speed and the other main parameter (*SF* or alpha). We used the Multi-Model Inference R package (MuMIn, version 1.42.1; Burnham & Anderson, 2002) to compare linear mixed models on the *log* duration with and without interaction, based on the Akaike information criterion. In the depth ordering experiment, the model without interaction between speed and *SF* was slightly better (ΔAICc = 0.9). In the plaid bistability experiment, the models without interaction between speed and alpha were better both for transparent percepts (ΔAICc = 10) and coherent percepts (ΔAICc = 5.4). These analyses show therefore the lack of interaction between speed and SF ratio and speed and alpha (as already observed by Hupé & Rubin, 2003). We performed similar analyses with generalized linear mixed models on percept durations (not log transformed) and observed significant interactions in the depth ordering experiment and for coherent percepts in the plaid bistability experiment. These interactions were due to a larger effect of speed for alpha or SF ratio parameters leading to longer durations. In other words, the effect of speed was proportional to the average duration, as expected given the absence of interaction on the log scale. However, we used the generalized linear models for display purpose in order to show the effects on a meaningful scale.

Results

Depth ordering experiment

By increasing the speed of the two opposed gratings, we increased their relative speed and therefore the level of motion contrast, providing cues for easier segmen-

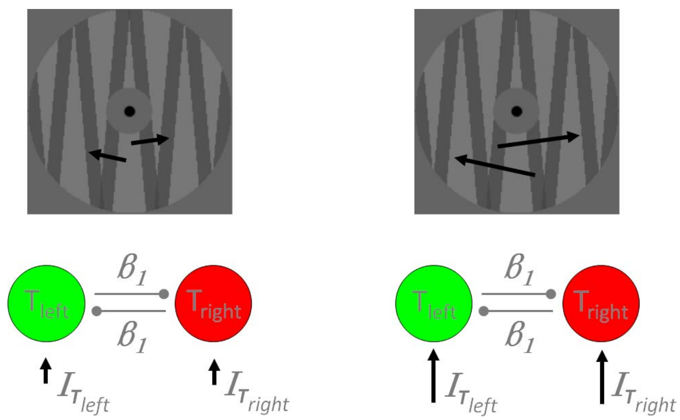

Figure 2. Illustration and interpretation of the effect of speed in the depth ordering experiment. Top: examples of stimuli used. The length of the arrows denote the speed of the gratings (1.5 or 5 °/s). Bottom: model interpretation of the manipulation of speed. We suppose that two independent populations of neurons (in green and red) compete with each other for the depth ordering of transparent motion, with either the grating moving to the left in front (T_{left}), or the grating moving to the right in front (T_{right}). The vertical black arrows denote the intensity of the input to each population, which we suppose are stronger for higher speeds. β_1 denotes inhibitory connections.

tation of the two surfaces. For our stimuli, even at the slower speed, motion transparency and the related perception of depth ordering were well above threshold and competition occurred for which surface should be perceived in front, the one moving to the right or the one moving to the left. By increasing the relative speed, we (supposedly) provided stronger input to both depth-ordering interpretations, in a way similar to increasing luminance or contrast to both eyes in binocular rivalry (Figure 2). Importantly, the input manipulation was identical for both percepts.

Intuitively, one may expect that increasing the strength of one perceptual interpretation would make it more stable, leading to an increase of that percept's duration. In binocular rivalry, however, Levelt (1968) showed that this manipulation led to systematically shorter percept durations, an observation known as Levelt's proposition IV. This proposition, as for his proposition II, is well accounted for by a model in which the two neural representations of the competing percepts are coupled by reciprocal inhibition (Rubin & Hupé, 2005), as illustrated in Figure 2.

Figure 3 shows that all included subjects (12 out of 14, see Supplementary File S1, Appendix B, Figures B1 and B2) experienced shorter percepts for faster speeds, therefore demonstrating that Levelt's proposition IV applied to depth ordering bistability and validating the model of Figure 2. The size of the effect was large: the percept duration estimated across subjects decreased from 22 s for the slow speed to 11 s for the fast speed. The 95% confidence interval (CI) of the decrease across subjects was [7 14] s. The min and max values of the decrease across subjects were 4 s (subject S6) and 24 s (subject S8). If selecting only trials leading to equidominance of the depth ordering interpretation (see Supplementary File S1, Appendix C, Figures C1 and C2), the 95% CI of the estimated decrease was similar ([5.8 12.2] s, min = 3 s, max = 24 s).

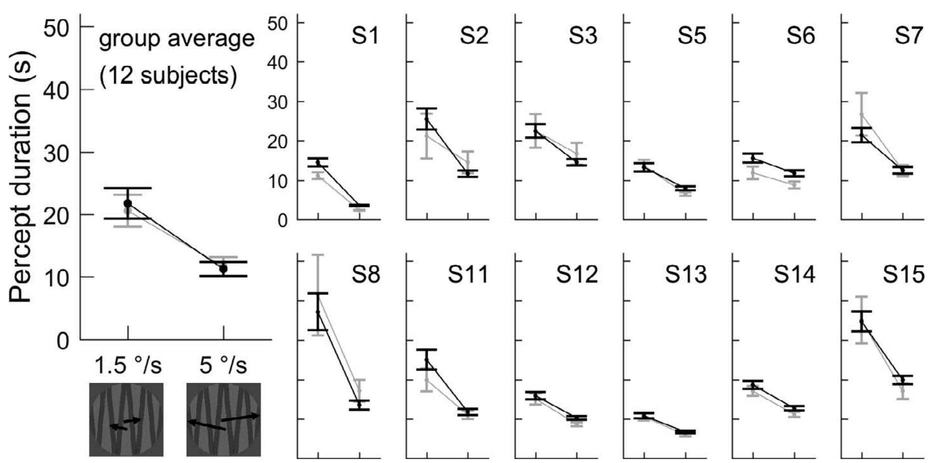

Figure 3. Estimated mean percept duration for the group and each subject, as a function of the speed of the gratings. The dark points and lines show means and ±*SEM* based on all data ($N = 2{,}243$). Light gray points and lines show the same for a restricted data set limited to trials producing equidominance of the depth ordering interpretation ($N = 735$). When including all data, the estimates of the group means and *SEM* were computed with a generalized linear mixed model, using the glmer function of the R package lme4, with the random factors (speed|subject), allowing therefore a different slope of the speed effect for each subject, and the fixed factors speed, SF ratio, global plaid direction (up or down) and direction of the grating perceived in front, using a Gamma family function and the identity link. The estimates for each subject were computed independently using generalized linear models (glm function) with the same fixed factors. For equidominance data, speed was the only fixed factor.

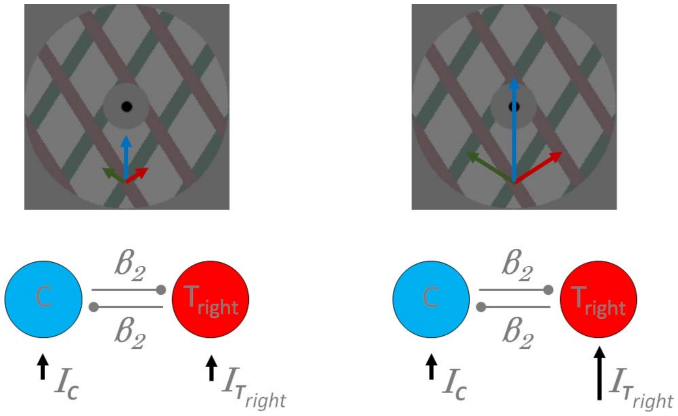

Figure 4. Illustration and interpretation of the effect of speed in the plaid bistability experiment. Top: Examples of stimuli used. The length of the arrows denote the speed of the gratings (1.5 or 5 °/s) and of the intersections (here for alpha = 115°, 2.8°, or 9.3 °/s). Bottom: Model interpretation of the manipulation of speed, when the red grating is occluding the green grating. We suppose that two independent populations of neurons (in blue and red) compete with each other. The vertical black arrows denote the intensity of the input to each population, which we suppose is stronger for higher speed only to the population of neurons representing the transparent interpretation (T_{right}). β_2 denotes inhibitory connections.

Plaid bistability experiment

In this experiment the angle alpha was decreased so that perceptual alternations would occur between transparency and coherence. To keep the dynamics within a bistability (not tristability) range, one grating occluded the other at the intersections—consistent with a nearer, overlaid grating—so that when transparent motion was experienced, only one depth interpretation was possible. We increased the speed of the gratings, as in the first experiment. By doing so, according to the results of the first experiment, we provided stronger input to the transparent motion interpretation, in a way similar to increasing luminance or contrast to only one eye in binocular rivalry (Figure 4). Levelt showed that, for binocular rivalry, such a manipulation leads to a decrease of percept durations for the eye whose input was not manipulated. (At this stage and without any independent evidence, we are making the hypothesis that speed does not modify the strength of the coherent motion interpretation: see Supplementary File S1, Appendix E for an a posteriori validation of this hypothesis).

Figure 5 shows that all 14 subjects experienced shorter coherent percepts (in blue) for faster speeds. The size of the effect was large: the percept duration estimated across subjects decreased from 12.6 s for the slow speed to 5.7 s for the fast speed. The 95% CI of the decrease across subjects were [7.7 11.8], [4.6 8.2], and [3.1 6.6] s for respectively, alpha = 100°, 115°, and 130° (model with interaction between speed and alpha). The min and max values of the decrease across subjects were 2.4 s (subject S7) and 14.5 s (subject S3).

The effect of speed on the duration of the transparent percepts (in purple) was not consistent across subjects. On average, increasing speed did not increase percept duration. If anything, the mean transparent percept duration decreased slightly: the percept duration estimated across subjects decreased

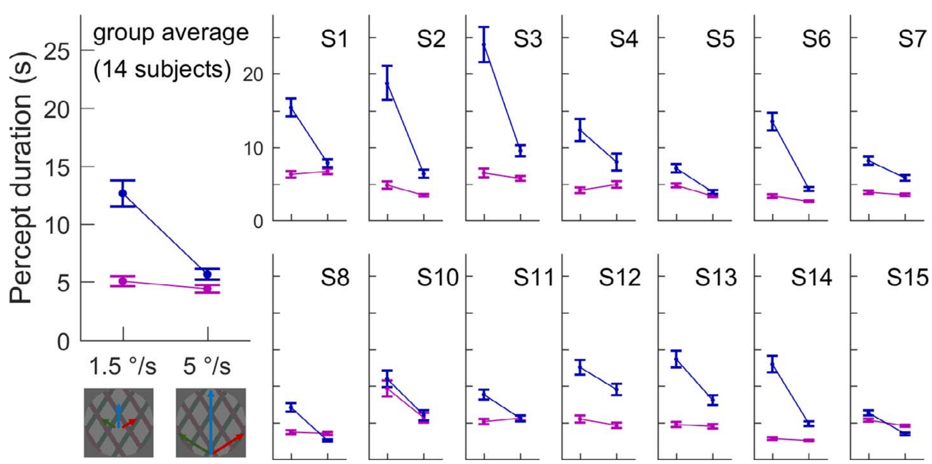

Figure 5. Estimated mean percept duration for the group and each subject, as a function of the speed of the gratings. The blue points and lines show means and ±*SEM* for the coherent percepts ($N = 2{,}925$). Purple points and lines show the same for transparent percepts (red in front or green in front, depending on the color of the intersections; $N = 2{,}930$). The group estimates were computed independently for coherent and transparent percepts with generalized linear mixed models (glmer function), with the random factor (speed|subject), allowing therefore a different slope of the speed effect for each subject, and the fixed factors speed and alpha, using a Gamma family function and the identity link. The estimates for each subject were computed independently using generalized linear models (glm function) with the same fixed factors.

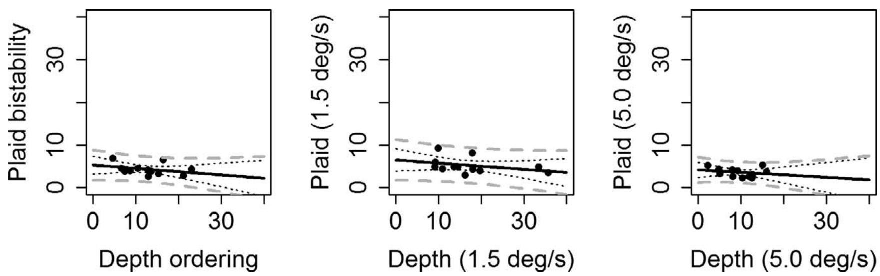

Figure 6. Average percept duration (in seconds) for the two tested speeds, together and independently, for depth ordering bistability (*x*-axis) and plaid bistability (*y*-axis), measured for each of the 12 subjects at equidominance. Bold continuous lines are the regression line, dotted lines and dashed lines show the 95% confidence and prediction lines, respectively. Average of both speeds: 95% CI for $R =$ [−0.76 0.30], 95% higher density interval (HDI, Bayesian analysis with a flat prior: Kruschke, 2015) for the slope = [−0.25 0.08]. Slow speed: 95% CI for $R =$ [−0.77 0.27], 95% HDI for the slope = [−0.20 0.07]. Fast speed: 95% CI for $R =$ [−0.71 0.39], 95% HDI for the slope = [−0.25 0.12].

from 5.1 s for the slow speed to 4.4 s for the fast speed. The min and max values of the change across subjects were a 4 s decrease (subject S10) and a 0.8 s increase (subject S4). The 95% CI of the decrease across subjects was [0.1 1.2] s, that is, negligible or weak. The linear models on the log of duration (which is more appropriate because effects sizes increase geometrically with percept duration) without the effect of speed was slightly better than with the effect of speed (ΔAICc = 1.9), confirming the very weak or inconsistent effect of speed on the duration of the transparent percepts. These results therefore suggest that Levelt's proposition II applies to plaid bistability.

Comparison of perceptual dynamics in both experiments

Percept duration varied a lot across subjects tested with the same stimulus parameters (Figures 3 and 5). Within our model interpretation of Figures 2 and 4, this suggests that the strength of inhibition (β parameter) may vary across subjects. A question then arises whether this strength of inhibition may represent an individual trait. Then, this trait would be constant whatever the perceptual competition involved, meaning that one would expect β_1 and β_2 to be equal or at least more similar within than between subjects. One cannot measure directly β_1 and β_2, but when the inputs to the competing neural populations are the same (and only when they are the same), percept duration is proportional to β. We therefore measured percept duration at equidominance in each experiment. Note that equidominance, though necessary, may not be sufficient to guarantee that the strength of the input is equal across subjects, due to idiosyncrasies (see the penultimate paragraph of the Discussion section).

The selection of parameters leading to equidominance, performed independently for each subject, is detailed in Supplementary File S1, Appendix C and D. For depth ordering bistability, some subjects displayed strong idiosyncratic biases related to the direction of motion, as detailed for other ambiguous stimuli involving the 3D interpretation of moving stimuli (Mamassian & Wallace, 2010; Wexler, Duyck, & Mamassian, 2015). We, therefore, sometimes had to choose stimuli with different SF and a particular direction of motion. The same set of parameters was chosen for both speeds tested, since speed has a strong effect on percept duration (Figure 3) but not on percept dominance (Figures 2 and B2). For plaid bistability, the global direction of motion (up or down) had almost no effect (see also Hupé & Rubin, 2004), as well as the color of the gratings and occlusion (chosen to be equiluminant). Equidominance was however observed for different alpha values across subjects. Since both alpha and speed affect dominance, independently (Figure B4), we had to choose a different alpha value for each speed (Figure D1).

The average percept duration for each subject was computed over all percepts of the selected trials, on the log scale, independently for slow and fast speed, and then averaged. We used the exponential of these log values to express the mean duration in seconds. For plaid bistability in the slow speed condition (1.5 °/s), plaids were perceived as coherent more often whatever the value of alpha in eight out of fourteen subjects (Figure D1). Mean percept duration at equidominance was then interpolated by fitting lines for the effect of alpha on average percept durations (log scale: see Figure D2 for an example).

Figure 6 shows that mean duration varied across subjects a lot more for depth ordering bistability than plaid bistability. Importantly, the slope of the correlation was almost flat, or if anything slightly negative, while we were expecting a positive correlation if β_1 and β_2 were similar within subjects. Even though our sample included only 12 subjects, this analysis was powerful thanks to the very large variability measured for depth ordering. The 95% CI analysis of the coefficient of determination indicates that, on average, the maximal positive correlation compatible with our data set could only account for 9% of the variance. Such a low value may authorize to conclude to the quasi absence of correlation. Correlation values were similar if performed on the log scale (not shown).

This analysis therefore indicates that the strength of inhibition may be different for different stimuli and subjects (β_1 and β_2 are not equal), and therefore is unlikely to represent an individual trait.

Discussion

In two experiments, we examined perceptual bistability in plaid motion patterns. Plaids are normally tristable, switching among coherent motion, transparent motion with one grating in front, or transparent motion with the opposite depth order. We limited this behavior to just two options, either by increasing the directional angle between the components to eliminate coherence (transparent plaids with bistable depth order), or by encouraging coherence while constraining the transparent depth order to just one interpretation by having one grating fully occlude the other at the intersections. In this way, we were able to study the bistable properties of each pair of competing percepts. We measured the effect of changing the speed of gratings in the two different sets of bistable plaids. In both cases, the speed manipulation affected the dynamics of bistability: for depth ordering bistability, increasing grating speed decreased the percept durations (Figure 3), while for plaid bistability, increasing speed strongly decreased the duration of the coherent plaid percepts and had little or no effect on the duration of the transparent percepts (Figure 5). We interpreted these effects within the framework of Levelt's (1968) propositions II and IV for binocular rivalry that relate percept duration with the strength of the inputs to two competing populations of neurons. If we suppose that increasing grating speed increases the input to the neural populations representing the competing transparent motions, in a similar way to increasing luminance or contrast boosts competition between populations in binocular rivalry, then the results can be seen to replicate Levelt's propositions II and IV. In depth ordering bistability, the decrease of percept durations (i.e., increasing switch rate) with increasing speed corresponds to Levelt's proposition IV, while in plaid bistability, the decrease of coherent percept durations with no corresponding increase of transparent durations corresponds to Levelt's proposition II.

Our reasoning when applying Levelt's propositions to plaids assumes that increasing grating speed increases the input to the neural population or network representing depth ordered transparent motion at the level where it competes *either* with the other depth ordered transparent interpretation *or* with the coherent interpretation. Without neuronal recordings from this hypothetic population or network and its response to speed, this assumption could remain speculative. However, our data show clearly that increasing grating speed had strong effects on percept durations (Figures 3 and 5), and we could demonstrate by reductio ad absurdum that increasing grating speed could not *decrease* the input to the neural population representing transparent motion. Our assumption is, therefore, the only one compatible with our full set of results (Supplementary File S1, Appendix E).

The possibility that Levelt's laws generalize beyond binocular rivalry has been suggested previously, although definitive proof of this, in our opinion, has been difficult to find. This is because of the difficulty of finding a stimulus manipulation that affects only one of the competing populations.

Klink et al. (2008) tested ambiguous rotating spheres created by two sets of dots moving in opposing directions, with the two sets differing slightly in luminance. The dots with the higher luminance were perceived more often to be in front of the dots moving in the other direction. The authors, followed by Moreno-Bote, Shpiro, Rinzel, and Rubin (2010), supposed that manipulating the luminance of only one set of dots should modify the input to only one interpretation. However, depth ordering may rather depend (in an unknown way) on the relative luminance between the two sets of dots, and, in that case, the luminance manipulation could affect simultaneously the inputs to both competing interpretations, making the results not interpretable anymore within Levelt's framework.

Similar arguments can be made when biasing ambiguous drawings (Fisher, 1967; Riani et al., 1986; these studies did not refer to Levelt, and only the second one measured average percept duration): adding visual cues in favor of one interpretation almost systematically corresponds to removing visual cues in favor of the other one. In his thesis, Leopold (1997, p. 173) showed (undocumented) results using Rubin's face/vase stimuli that fitted nicely Levelt's second proposition, but only by supposing that the *intended* manipulation on only one interpretation had the corresponding effect at the neuronal level. However, a similar interpretation of the manipulations by Riani et al. (1986) would lead to interpreting their results as opposite to Levelt's second proposition.

The two other attempts, which we are aware of, at generalizing Levelt's second proposition used motion induced blindness (Carter & Pettigrew, 2003; Bonneh et al. 2014). Carter and Pettigrew measured the disappearance of two orthogonal or parallel Gabor patches, instructing subjects to indicate "if either of the patches had disappeared" or "if they could see both Gabor patches in the display." Their paradigm therefore involved multistable perception reduced arbitrarily to two categories of percepts, preventing an interpretation in the terms of Levelt's proposition. Bonneh et al. (2014) monitored the disappearance of only one target and varied its luminance contrast. Increasing contrast was found to increase the proportion of time the target was visible, as intuitively expected, and that without affecting its average percept duration, in line with Levelt's second proposition. However, in their seminal paper, Bonneh, Cooperman, & Sagi (2001) had obtained the counterintuitive result that increasing target luminance increased disappearance. Bonneh et al. (2014) suggested that the opposite effects of the contrast manipulation could be due to the different eccentricity used in both experiments, but they did not provide any formal evidence nor precise explanation of such a differential effect.

The first author of the present study had also made previously several attempts to design protocols where only one of the competing populations would be affected by a specific manipulation. The results were in line with Levelt's second proposition (Supplementary File S1, Appendix F); however, without direct knowledge of the physiological mechanisms involved, the real effect of the manipulation on the competing neural populations remains speculative: In all those cases, some reasoning circularity could not be avoided. In the present study we have avoided this circularity by exploiting the tristable nature of motion plaids and isolating the same percept (a given depth ordering interpretation) involved in two different bistable competitions.

Our whole discussion so far on Levelt's propositions has been based on the original formulation by Levelt. Brascamp et al. (2006) have proposed a reformulation of proposition II, based on binocular rivalry data that differed significantly from predictions based on Levelt's propositions. Specifically, they observed that changing the contrast to one eye affected the durations of *both* percepts and differentially depended on the contrast of the fixed eye. When the fixed eye had a high contrast, as done originally by Levelt and in subsequent replication studies (except for an example shown page 173 of David Leopold's thesis [1997], where Levelt's second proposition was validated for the fixed eye at intermediate contrast), its corresponding durations were indeed the ones mostly affected by changing the lower contrast to the other eye. But the durations corresponding to the manipulated eye were also slightly affected, as already emphasized by Bossink, Stalmeier, & De Weert (1993). Most notably, when the fixed eye was set to a low contrast, the main change was for the duration of the eye with the modified higher contrast. Accordingly, a new version of proposition II states that "largest change in percept durations tends to be associated with the eye that is presented with the strongest stimulus, regardless of which eye's stimulus strength is varied" (Brascamp, Klink, & Levelt, 2015), a result observed indeed for different sets of ambiguous stimuli (Riani et al., 1986; Moreno-Bote et al. 2010). Importantly, this new proposition did not make any reference to the possible independent manipulations of each competing percept, by considering only the relative strength of the percepts, thus abolishing the distinction between binocular rivalry and ambiguous stimuli.

Our data are roughly compatible with this modified version of Levelt's proposition II, since the largest change happened for the coherent percept, which was also the dominant one (Figure 5). However, we did not observe at all the slight increase of the nondominant percept reported for binocular rivalry. Also, for three subjects (S8, S10, and S15), both percepts were on average equally dominant. Yet the durations of the transparent percepts did not increase with increased speed, a result compatible with the original Levelt's proposition but not the modified one. A more systematic exploration of the effect of speed when the transparent percept is clearly dominant would be required to decide between both versions of proposition II. Unpublished data presented in Supplementary File S1, Appendix F3 do show, however, an example where the largest changes of percept durations were associated with the less dominant percept, in contradiction to the modified proposition. The question of which formulation of proposition II, if any, should be considered as the definitive law remains open (see also Platonov & Goossens, 2013).

The purpose of our study, however, was not to test the generality of Levelt's laws, modified or not, but to test their relationship to supposed mechanisms of inhibition. For us, the only important requisite was the existence of a range of parameters where the manipulation of one interpretation affected only the duration of the other interpretation. The touchstone of our study was therefore to be able to affect the strength of only one interpretation, an objective not addressed by Moreno-Bote et al. (2010) or Brascamp et al. (2015), who considered only the relative strength of both interpretations. Even in the original binocular rivalry paradigm, independent manipulation was in fact not guaranteed, because mechanisms of contrast gain control certainly affect the strength of the percept of the fixed eye, especially when a large range of luminance or contrast is used. To our knowledge, this issue has not been taken into account. Also for binocular rivalry, pure bistability is rarely achieved. As soon as the stimuli extend more than a fraction of a degree, piecemeal rivalry may happen. Kang (2009) showed convincingly that deviations from Levelt's original second proposition could be accounted for by the spatial integration of multiple zones of competition, while the original proposition applied strictly for very small patches of binocular rivalry. We could therefore consider that stimuli with clearly bistable states like plaids are in fact more suitable than binocular rivalry to test models of bistability as they never exhibit a piecemeal or "patchwork" of competing percepts.

The demonstration of inhibitory coupling mechanisms for protocols other than binocular rivalry suggests that the mechanisms of perceptual competition are similar for very different paradigms of bistability. This is consistent with a proposal by Leopold and Logothetis in 1999, yet with even more precise common rules than suggested by those authors. We further tested if common mechanisms across different bistable paradigms suggested a unique neural network dedicated to resolving perceptual conflicts, as proposed for example by Pettigrew and colleagues (Pettigrew, 2001; Carter & Pettigrew, 2003). Within our theoretical framework, this would suggest that the strength of coupling is similar for different competitions ($\beta_1 \approx \beta_2$ in our Figures 2 and 4) at the subject level. Since different subjects may have very different yet stable rates of perceptual alternations (Borsellino, De Marco, Allazetta, Rinesi, & Bartolini, 1972; Miller et al., 2010; Shannon, Patrick, Jiang, Bernat, & He, 2011), a unique mechanism should lead to correlations of switch rates across different kinds of bistable stimuli, a result observed previously in several studies (George, 1936; Lindauer & Baust, 1974; Carter & Pettigrew, 2003; Sheppard & Pettigrew, 2006; Hupé, Joffo, & Pressnitzer, 2008; Kondo et al., 2011; Shannon et al., 2011; Kashino & Kondo, 2012; Patel, Stuit, & Blake, 2014; Baker, Karapanagiotidis, Coggan, Wailes-Newson, & Smallwood, 2015). Shannon et al. (2011) further showed a moderate correlation of switch rates across monozygotic but not dizygotic twins, suggesting a genetic component. However, correlation was not observed (or not statistically significant) in other studies (Pressnitzer & Hupé, 2006; Carter et al., 2008; Gallagher & Arnold, 2014; Wernery et al., 2015; Brascamp, Becker, & Hambrick, 2018) or only across some sets of paradigms involving similar competition mechanisms (Cao, Wang, Sun, Engel, & He, 2018).

In our data, we found no correlation when comparing depth ordering and plaid bistability. This is consistent with the meta-analysis by Brascamp et al. (2018) showing that, overall, the published evidence for correlation is weak. In light of this, when correlations are observed they are possibly due to factors not related to the core mechanism of perceptual competition (such as the general level of attention). Moreover, the studies that did not observe any correlation had more careful methodological procedures: for example, Brascamp et al. (2018) computed the mean of the log duration of percepts (as we did; Wernery et al. [2015] also used meaningful indicators of the distribution), Gallagher and Arnold (2014) controlled for key-press behavior, and both studies (as with ours) allowed subjects to report mixed percepts rather than forcing a dichotomy on the perceptual reports. Our study, however, seems to be the only one where stimuli were adjusted for each subject to equidominance. Equidominance is required for percept duration to be related to hypothetical parameters. Since the distribution of percepts is highly asymmetrical, a strong imbalance in percept dominance leads to overall fewer switches within a fixed time (Ditzinger & Haken, 1989; Moreno-Bote et al., 2010).

We could argue that equidominance, if necessary, is not sufficient to test correlations across paradigms. Indeed, following Levelt's fourth proposition and as shown in our data, percept duration depends also on the strength of balanced inputs. Given the high level of idiosyncratic differences, we cannot be sure that the comparison between paradigms was performed at the same regime of equidominance across subjects, maybe all the more because we had to adjust the stimuli for each subject to find the equidominance regime. The problem is that we do not have any measure of the strength of the input at the level of the hypothetic neuronal populations involved. By pursuing this line of reasoning, we should conclude that, in fact, the comparison of switch rate across stimuli can never be a method to test for the presence or absence of a unique competition mechanism.

Given these considerations, we conclude that, if keeping within the way the question was framed in the literature, the lack of correlation for depth ordering and plaid bistability suggests that reciprocal inhibition governs both kinds of bistability but it is instantiated between different neural populations in each case, as proposed by Pressnitzer and Hupé (2006) and Hupé et al. (2008) when comparing bistability in vision and audition.

Conclusions

Our results show that perceptual competition in plaids is based on the coupling of neural populations or networks by reciprocal inhibition, with each population representing one of the competing percepts, similar to what was established for binocular rivalry (Alais et al., 2010). Our demonstration is important because coupling is implemented in most if not all formal models of bistable perception (listed in the Introduction). Those models are indeed powerful to mimic the precise dynamics of perceptual reports, even for tristable perception (Huguet et al., 2014). The lack of switch rate

correlation between two bistable paradigms, for the first time tested at equidominance, further suggests that there is no unique, high-level neural network dedicated to resolving perceptual conflicts. Instead, it suggests that the resolution of bistability through mutual inhibition is widespread and is instantiated among a variety of neural populations.

Keywords: ambiguous stimuli, *bistable perception*, *visual plaids*, *binocular rivalry*, *non-linear dynamics*

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References

Adelson, E. H., & Movshon, J. A. (1982, December 9). Phenomenal coherence of moving visual patterns. *Nature*, *300*(5892), 523–525.

Alais, D., & Blake, R. (2005). *Binocular rivalry*. Cambridge, MA: MIT Press.

Alais, D., Cass, J., O'Shea, R. P., & Blake, R. (2010). Visual sensitivity underlying changes in visual consciousness. *Current Biology*, *20*(15), 1362–1367, https://doi.org/10.1016/j.cub.2010.06.015.

Alais, D., Wenderoth, P., & Burke, D. (1994). The contribution of one-dimensional motion mechanisms to the perceived direction of drifting plaids and their after effects. *Vision Research*, *34*(14), 1823–1834.

Baker, D. H., Karapanagiotidis, T., Coggan, D. D., Wailes-Newson, K., & Smallwood, J. (2015). Brain networks underlying bistable perception. *NeuroImage*, *119*, 229–234, https://doi.org/10.1016/j.neuroimage.2015.06.053.

Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, *96*(1), 145–167.

Blake, R., & Fox, R. (1974, May 31). Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature*, *249*(456), 488–490.

Blake, R., Sobel, K. V., & Gilroy, L. A. (2003). Visual motion retards alternations between conflicting perceptual interpretations. *Neuron*, *39*(5), 869–878.

Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001, June 14). Motion-induced blindness in normal observers. *Nature*, *411*, 798–801.

Bonneh, Y. S., Donner, T. H., Cooperman, A., Heeger, D. J., & Sagi, D. (2014). Motion-induced blindness and Troxler fading: Common and different mechanisms. *PLoS One*, *9*(3), e92894, https://doi.org/10.1371/journal.pone.0092894.

Borsellino, A., De Marco, A., Allazetta, A., Rinesi, S., & Bartolini, B. (1972). Reversal time distributions in the perception of visual ambiguous stimuli. *Kybernetic*, *10*, 139–144.

Bossink, C. J., Stalmeier, P. F., & De Weert, C. M. (1993). A test of Levelt's second proposition for binocular rivalry. *Vision Research*, *33*(10), 1413–1419.

Brascamp, J. W., Becker, M. W., & Hambrick, D. Z. (2018). Revisiting individual differences in the time course of binocular rivalry. *Journal of Vision*, *18*(7): 3, 1–20, https://doi.org/10.1167/18.7.3. [PubMed] [Article].

Brascamp, J. W., Klink, P. C., & Levelt, W. J. M. (2015). The 'laws' of binocular rivalry: 50 years of Levelt's propositions. *Vision Research*, *109, Part A*, 20–37, https://doi.org/10.1016/j.visres.2015.02.019.

Brascamp, J. W., van Ee, R., Noest, A. J., Jacobs, R. H., & van den Berg, A. V. (2006). The time course of binocular rivalry reveals a fundamental role of noise. *Journal of Vision*, *6*(11):8, 1244–1256, https://doi.org/10.1167/6.11.8. [PubMed] [Article].

Breese, B. B. (1899). On inhibition. *The Psychological Review: Monograph Supplements*, *3*(1), i–65, doi: http://doi.org/10.1037/h0092990.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer-Verlag.

Cao, T., Wang, L., Sun, Z., Engel, S. A., & He, S. (2018). The independent and shared mechanisms of intrinsic brain dynamics: Insights from bistable perception. *Frontiers in Psychology*, *9*, 589, http://doi.org/10.3389/fpsyg.2018.00589.

Carter, O., Konkle, T., Wang, Q., Hayward, V., & Moore, C. (2008). Tactile rivalry demonstrated with an ambiguous apparent-motion quartet. *Current Biology*, *18*(14), 1050–1054.

Carter, O., & Pettigrew, J. D. (2003). A common oscillator for perceptual rivalries? *Perception*, *32*(3), 295–305.

Diaz-Caneja, E. (1928). Sur l'alternance binoculaire. *Annales d'Oculistique*, *165*, 721–731.

Ditzinger, T., & Haken, H. (1989). Oscillations in the perception of ambiguous patterns. A model based on synergetics. *Biological Cybernetics*, *61*(4), 279–287.

Fisher, G. H. (1967). Measuring ambiguity. *The American Journal of Psychology*, *80*(4), 541–557.

Fox, R., & Check, R. (1968). Detection of motion during binocular rivalry suppression. *Journal of Experimental Psychology*, *78*(3), 388–395.

Gallagher, R. M., & Arnold, D. H. (2014). Interpreting the temporal dynamics of perceptual rivalries. *Perception*, *43*(11), 1239–1248, https://doi.org/10.1068/p7648.

George, R. W. (1936). The significance of the fluctuations experienced in observing ambiguous figures and in binocular rivalry. *The Journal of General Psychology*, *15*(1), 39–61, https://doi.org/10.1080/00221309.1936.9917904.

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton, Mifflin and Company.

Gregory, R. L. (1970). *The intelligent eye*. New York: McGraw-Hill.

Gregory, R. L. (2009). *Seeing through illusions*. Oxford, UK: Oxford University Press.

Huguet, G., Rinzel, J., & Hupé, J. M. (2014). Noise and adaptation in multistable perception: Noise drives when to switch, adaptation determines percept choice. *Journal of Vision*, *14*(3):19, 11–24, https://doi.org/10.1167/14.3.19. [PubMed] [Article].

Hupé, J. M., Joffo, L. M., & Pressnitzer, D. (2008). Bistability for audiovisual stimuli: Perceptual decision is modality specific. *Journal of Vision*, *8*(7):1 1–15, https://doi.org/10.1167/8.7.1. [PubMed] [Article].

Hupé, J. M., & Pressnitzer, D. (2012). The initial phase of auditory and visual scene analysis. *Philosophical Transactions of the Royal Society of London B. Biological Sciences*, *367*(1591), 942–953.

Hupé, J. M., & Rubin, N. (2000). Perceived motion transparency can override luminance / color cues which are inconsistent with transparency [Abstract]. *Investigative Ophthalmology and Visual Science*, *41*(Suppl.), 721.

Hupé, J. M., & Rubin, N. (2003). The dynamics of bi-stable alternation in ambiguous motion displays: A fresh look at plaids. *Vision Research*, *43*, 531–548.

Hupé, J. M., & Rubin, N. (2004). The oblique plaid effect. *Vision Research*, *44*(5), 489–500.

Kang, M.-S. (2009). Size matters: A study of binocular rivalry dynamics. *Journal of Vision*, *9*(1):17, 1–11, https://doi.org/10.1167/9.1.17. [PubMed] [Article].

Kashino, M., & Kondo, H. M. (2012). Functional brain networks underlying perceptual switching: Auditory streaming and verbal transformations. *Philosophical Transactions of the Royal Society of London. B. Biological Sciences*, *367*(1591), 977–987. https://doi.org/10.1098/rstb.2011.0370.

Kersten, D., Mamassian, P., & Yuille, A. (2004). Object perception as Bayesian inference. *Annual Review of Psychology*, *55*, 271–304, https://doi.org/10.1146/annurev.psych.55.090902.142005.

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception*, *36*, ECVP Abstract Supplement, 14.

Klink, P. C., van Ee, R., & van Wezel, R. J. (2008). General validity of Levelt's propositions reveals common computational mechanisms for visual rivalry. *PLoS One*, *3*(10), e3473, https://doi.org/10.1371/journal.pone.0003473.

Kondo, H. M., Kitagawa, N., Kitamura, M. S., Koizumi, A., Nomura, M., & Kashino, M. (2011). Separability and commonality of auditory and visual bistable perception. *Cerebral Cortex*, *22*(8), 1915–1922, https://doi.org/10.1093/cercor/bhr266.

Kovacs, I., Papathomas, T. V., Yang, M., & Feher, A. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences, USA*, *93*(26), 15508–15511.

Kruschke, J. K. (2015). *Doing Bayesian data analysis, Second Edition: A tutorial with R, JAGS, and Stan*. Burlington, MA: Academic Press/Elsevier.

Lack, L. (1978). *Selective attention and the control of binocular rivalry*. The Hague, the Netherlands: Mouton.

Lehky, S. R. (1988). An astable multivibrator model of binocular rivalry. *Perception*, *17*(2), 215–228.

Leopold, D. A. (1997). *Brain mechanisms of visual awareness. Using perceptual ambiguity to investigate the neural basis of image segmentation and grouping* (Doctoral dissertation). Baylor College of Medicine, Houston, TX.

Leopold, D. A., & Logothetis, N. K. (1996, February 8). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*, *379*, 549–553.

Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, *3*(7), 254–264.

Levelt, W. J. M. (1968). *On binocular rivalry*. The Hague, Paris: Mouton.

Liaci, E., Bach, M., Tebartz van Elst, L., Heinrich, S. P., & Kornmeier, J. (2016). Ambiguity in tactile apparent motion perception. *PLoS One*, *11*(5), e0152736, https://doi.org/10.1371/journal.pone.0152736.

Lindauer, M. S., & Baust, R. F. (1974). Comparisons between 25 reversible and ambiguous figures on measures of latency, duration, and fluctuation. *Behavior Research Methods & Instrumentation*, *6*(1), 1–9.

Liu, L., Tyler, C. W., & Schor, C. M. (1992). Failure of rivalry at low contrast: Evidence of a suprathreshold binocular summation process. *Vision Research*, *32*(8), 1471–1479.

Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996, April 18). What is rivalling during binocular rivalry? *Nature*, *380*(6575), 621–624.

Logothetis, N. K., & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science*, *245*(18 August), 761–763.

Long, G. M., & Toppino, T. C. (2004). Enduring interest in perceptual ambiguity: Alternating views of reversible figures. *Psychological Bulletin*, *130*(5), 748–768.

Mamassian, P., & Wallace, J. M. (2010). Sustained directional biases in motion transparency. *Journal of Vision*, *10*(13):23, 1–12, https://doi.org/10.1167/10.13.23. [PubMed] [Article].

Miller, S. M., Hansell, N. K., Ngo, T. T., Liu, G. B., Pettigrew, J. D., Martin, N. G., & Wright, M. J. (2010). Genetic contribution to individual variation in binocular rivalry rate. *Proceedings of the National Academy of Sciences, USA*, *107*(6), 2664–2668.

Moreno-Bote, R., Rinzel, J., & Rubin, N. (2007). Noise-induced alternations in an attractor network model of perceptual bistability. *Journal of Neurophysiology*, *98*(3), 1125–1139.

Moreno-Bote, R., Shpiro, A., Rinzel, J., & Rubin, N. (2008). Bi-stable depth ordering of superimposed moving gratings. *Journal of Vision*, *8*(7):20, 21–13, https://doi.org/10.1167/8.7.20. [PubMed] [Article].

Moreno-Bote, R., Shpiro, A., Rinzel, J., & Rubin, N. (2010). Alternation rate in perceptual bistability is maximal at and symmetric around equi-dominance. *Journal of Vision*, *10*(11):1, 1–18, https://doi.org/10.1167/10.11.1. [PubMed] [Article].

Mueller, T. J., & Blake, R. (1989). A fresh look at the temporal dynamics of binocular rivalry. *Biological Cybernetics*, *61*(3), 223–232.

Necker, L. A. (1832). Observations on some remarkable optical phaenomena seen in Switzerland; and on an optical phaenomenon which occurs on viewing a figure of a crystal or geometrical solid. *London and Edinburgh Philosophical Magazine and Journal of Science*, *1*(5), 329–337.

Noest, A. J., van Ee, R., Nijs, M. M., & van Wezel, R. J. (2007). Percept-choice sequences driven by interrupted ambiguous stimuli: A low-level neural model. *Journal of Vision*, *7*(8):10, 11–14, https://doi.org/10.1167/7.8.10. [PubMed] [Article].

Pastukhov, A., & Braun, J. (2011). Cumulative history quantifies the role of neural adaptation in multistable perception. *Journal of Vision*, *11*(10):12, 1–10, https://doi.org/10.1167/11.10.12. [PubMed] [Article].

Pastukhov, A., García-Rodríguez, P. E., Haenicke, J., Guillamon, A., Deco, G., & Braun, J. (2013). Multi-stable perception balances stability and sensitivity. *Frontiers in Computational Neuroscience*, *7*:17, https://doi.org/10.3389/fncom.2013.00017.

Patel, V., Stuit, S., & Blake, R. (2014). Individual differences in the temporal dynamics of binocular rivalry and stimulus rivalry. *Psychonomic Bulletin & Review*, *22*(2), 476–482, https://doi.org/10.3758/s13423-014-0695-1.

Pettigrew, J. D. (2001). Searching for the switch: Neural bases for perceptual rivalry alternations. *Brain and Mind*, *2*, 85–118.

Platonov, A., & Goossens, J. (2013). Influence of contrast and coherence on the temporal dynamics of binocular motion rivalry. *PLoS One*, *8*(8), e71931, https://doi.org/10.1371/journal.pone.0071931.

Pressnitzer, D., & Hupé, J. M. (2006). Temporal dynamics of auditory and visual bistability reveal common principles of perceptual organization. *Current Biology*, *16*(13), 1351–1357.

Riani, M., Tuccio, M. T., Borsellino, A., Radilova, J., & Radil, T. (1986). Perceptual ambiguity and stability of reversible figures. *Perceptual and Motor Skills*, *63*(1), 191–205.

Rock, I., Hall, S., & Davis, J. (1994). Why do ambiguous figures reverse? *Acta Psychologica*, *87*(1), 33–59.

Rubin, E. (1921). *Visuell wahrgenommene Figuren*. Copenhagen, Denmark: Gyldendals.

Rubin, N., & Hupé, J. M. (2005). Dynamics of perceptual bi-stability: Plaids and binocular rivalry compared. In A. Alais & R. Blake (Eds.), *Binocular rivalry* (pp. 137–154). Cambridge, MA: MIT Press.

Schröder, H. (1858). Ueber eine optische Inversion bei Betrachtung verkehrter, durch optische Vorrichtung entworfener, physischer Bilder. *Annalen der Physik*, *181*(10), 298–311.

Schwartz, J. L., Grimault, N., Hupé, J. M., Moore, B. C., & Pressnitzer, D. (2012). Multistability in perception: Binding sensory modalities, an overview. *Philosophical Transactions of the Royal Society of London. B. Biological Science*, *367*(1591), 896–905.

Seely, J., & Chow, C. C. (2011). Role of mutual inhibition in binocular rivalry. *Journal of Neurophysiology*, *106*(5), 2136–2150, https://doi.org/10.1152/jn.00228.2011.

Shannon, R. W., Patrick, C. J., Jiang, Y., Bernat, E., & He, S. (2011). Genes contribute to the switching dynamics of bistable perception. *Journal of Vision*, *11*(3):8, 1–7, https://doi.org/10.1167/11.3.8. [PubMed] [Article].

Sheppard, B. M., & Pettigrew, J. D. (2006). Plaid motion rivalry: Correlates with binocular rivalry and positive mood state. *Perception*, *35*(2), 157–169.

Shpiro, A., Moreno-Bote, R., Rubin, N., & Rinzel, J. (2009). Balance between noise and adaptation in competition models of perceptual bistability. *Journal of Computational Neuroscience*, *27*(1), 37–54.

Stoner, G. R., & Albright, T. D. (1993). Image segmentation cues in motion processing: Implications for modularity in vision. *Journal of Cognitive Neuroscience*, *5*(2), 129–149.

Suzuki, S., & Grabowecky, M. (2002). Evidence for perceptual "trapping" and adaptation in multistable binocular rivalry. *Neuron*, *36*(1), 143–157.

Van Noorden, L. P. A. S. (1975). *Temporal coherence in the perception of tone sequences* [Doctoral dissertation], Eindhoven University of Technology, Netherlands.

Von Helmholtz, H. & Southall, J. P. C. (1967/1924–1925). *Treatise on physiological optics*. Rochester, NY: The Optical Society of America. Originally published as *Handbuch der Physiologischen Optik* in 1866, Leipzig, Germany: Leopold Voss.

Walker, P. (1975). Stochastic properties of binocular rivalry alternations. *Perception and Psychophysics*, *18*, 467–473.

Wallach, H. (1935). Uber visuell wahrgenommene Bewegungsrichtung. *Psychologische Forschung*, *20*, 325–380, *trans*. S., Wuerger, R., Shapley, & N. Rubin, (1996). "On the visually perceived direction of motion" by Hans Wallach: 60 years later. *Perception*, *25*(11), 1317–1367.

Wallach, H., & O'Connell, D. N. (1953). The kinetic depth effect. *Journal of Experimental Psychology*, *45*(4), 205–217.

Warren, R. M., & Gregory, R. L. (1958). An auditory analogue of the visual reversible figure. *American Journal of Psychology*, *71*(3), 612–613.

Wernery, J., Atmanspacher, H., Kornmeier, J., Candia, V., Folkers, G., & Wittmann, M. (2015). Temporal processing in bistable perception of the Necker cube. *Perception*, *44*(2), 157–168, https://doi.org/10.1068/p7780.

Wexler, M., Duyck, M., & Mamassian, P. (2015). Persistent states in vision break universality and time invariance. *Proceedings of the National Academy of Sciences, USA*, *112*(48), 14990–14995, https://doi.org/10.1073/pnas.1508847112.

Wheatstone, C. (1838). On some remarkable, and hitherto unobserved, phaenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, *128*, 371–394.

Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences, USA*, *100*(24), 14499–14503.