Coupled dynamics of bistable distant motion displays

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This study explores the extent to which a display changing periodically in perceptual interpretation through smooth periodic physical changes—an inducer—is able to elicit perceptual switches in an intrinsically bistable distant probe display. Four experiments are designed to examine the coupling strength and bistable dynamics with displays of varying degree of ambiguity, similarity, and symmetry—in motion characteristics—as a function of their locations in visual space. The results show that periodic fluctuations of a remote inducer influence a bistable probe and regulate its dynamics through coupling. Coupling strength mainly depends on the relative locations of the probe display and the contextual inducer in the visual field, with stronger coupling when both displays are symmetrical around the vertical meridian and weaker coupling otherwise. Smaller effects of common fate and symmetry are also found. Altogether, the results suggest that long-range interhemispheric connections, presumably involving the corpus callosum, are able to synchronize perceptual transitions across the vertical meridian. If true, bistable dynamics may provide a behavioral method to probe interhemispheric connectivity in behaving human. Consequences of these findings for studies using stimuli symmetrical around the vertical meridian are evaluated.

Keywords: perceptual organization, motion—2D, spatial vision, temporal vision


Introduction

Changes in perception in the absence of physical stimulus modifications—perceptual multistability—have attracted the interest of researchers for centuries (Necker, 1832; Rubin, 1921). This phenomenon indeed raises a number of issues related to the processes underlying perception, explaining that numerous studies were conducted to identify the dynamics of bistability and the parameters that modulate this phenomenon in order to infer the underlying mechanisms and offer plausible models of its existence. Coupled with imaging techniques, bistability recently proved a powerful tool to investigate the neural architecture of conscious perception (Blake & Logothetis, 2002; Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998; Leopold & Logothetis, 1999) and provided meaningful ideas, concepts, and theories for the understanding of perceptual processes (Long & Toppino, 2004; Miller et al., 2000; Pettigrew, 2001; Pressnitzer & Hupé, 2006; Ramachandran & Anstis, 1985).

Most studies on bistable perception have used a single bistable stimulus—with the notable exception of binocular rivalry necessarily involving two stimuli. The first investigation of bistability with several bistable stimuli—two Necker cubes presented in the two hemifields—was conducted by Flugel (1913) who reports that observers can dissociate their perceptual alternations when asked to attend to a single stimulus. Studying the effects of a contextual stimulus on bistable perception can provide relevant evidence to disentangle and improve models of perception. For instance, whether contextual stimuli alter the dynamics of bistability may bring evidence that not only local processes—the limited neuronal assemblies activated in alternance by a focal stimulus in visual areas—but also long-range processes determine bistable perception dynamics. An effect of a context on bistability may involve lateral low-level interactions (Klink, Noest, Holten, van den Berg, & van Wezel, 2009; Ramachandran & Anstis, 1985), feedback from remote visual areas (Rock, Hall, & Davis, 1994; Strüber & Stadler, 1999; Toppino, 2003), more cognitive top-down processes, including decisional, attentional, inferential, or volitional effects (Kornmeier, Hein, & Bach, 2009; Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005; for a review, see Long & Toppino, 2004), or depend on a specific subcortical modulatory influences (Carter & Pettigrew, 2003; Miller et al., 2000; Ngo, Liu, Tilley, Pettigrew, & Miller, 2008; Pettigrew, 2001).

Studies using bistable stimuli presented in different perceptual modalities indicate that bistable dynamics was similar for vision and audition. However, perceptual
switches were not synchronized, suggesting that bistability is a modality-dependent phenomenon (Hupé, Joffo, & Pressnitzer, 2008; Pressnitzer & Hupé, 2006). Other studies of the effect of contextual stimuli, either bistable or not, have shown that a visual context can bias the dominant of two equally probable percepts (Alais & Blake, 1999; Long & Toppino, 2004; Ramachandran & Anstis, 1985; Sundareswara & Schrater, 2008).

Studies with three-dimensional structure-from-motion (SFM) stimuli yielding bistable direction of rotation have shown that an unambiguously rotating 3FM stimulus can alter the dynamics of perceptual alternations (Freeman & Driver, 2006; Grossmann & Dobbins, 2003; Sereno & Sereno, 1999). Recently, Klink et al. (2009) reported perceptual coupling between a bistable ambiguous 3D cylinder and an unambiguous, disparity-defined, cylinder when the far depth planes of both displays were collinear. To model their results, Klink et al. build upon the model of Noest, van Ee, Nijs, and van Wezel (2007) involving an adaptation, or fatigue, component and a competition between mutually inhibitory neural populations coding for one perceptual state. Adding a facilitatory long-range connectivity whose effect is to link the modeled units depending on depth and border alignments strengthens the perceptual coupling between both displays and allows simulating the observed behavior. Klink et al. argue that these facilitatory lateral connections may correspond to the long-range horizontal connections described in V1 (Gilbert & Wiesel, 1989) and MT (Ahmed et al., 2008). A striking feature of Klink et al.’s displays, also existing in many (e.g., Freeman & Driver, 2006; Gilroy & Blake, 2004), but not all (Grossmann & Dobbins, 2003) studies of contextual effects, is that the two bistable displays were presented left and right from fixation, thus eliciting activity in homotopic regions of both hemispheres. This specific configuration raises the possibility that long-range interhemispheric connections played a significant role in the coupling reported in these studies.

To determine the extent to which contextual effects depend on interhemispheric connections, we measured the influence of a physically changing unambiguous inducer presented in one hemifield on the bistable dynamics of a similar unchanging bistable probe display presented in the other hemifield. By modifying the relative locations of the two displays in the visual field and their relative motion characteristics, we probed and partially dissociated the respective influences of spatial location and common fate. To anticipate, the results indicate that contextual effects are strongly determined by the symmetrical arrangement of the displays across the vertical meridian, such that coupling strength is notably decreased whenever the stimuli are not located in homotopic locations, suggesting that contextual effects are, at least in part, driven by interhemispheric connections.

**Methods and stimuli**

### Apparatus

Stimuli were displayed on a 21” Iiyama CRT (1024 × 768, 75-Hz refresh rate). Observers used the right and left buttons of a mechanical mouse to signal their—rigid or non-rigid—perceptual states. Movements of the right eye were recorded (EyeLink II, SR Research) and analyzed offline to verify that observers maintained their eyes on a central fixation cross throughout trials.

### Stimuli

In the four experiments presented thereafter, two displays were presented in different locations of the visual field against a gray background (23.6 cd/m²). Each display consisted of 4 light bars (length: 3.14 degrees of visual angle (dva thereafter), width: 0.11 dva) arranged in a diamond shape with invisible corners (Figure 1). Bars oriented at 45° oscillated up and down in phase, while bars oriented at 135° oscillated up and down 90° out of phase with the same amplitude (0.42 dva) and frequency (1 Hz). Under these conditions, each display could be seen as a single diamond-like shape translating along a circular trajectory—a rigid percept—or as four bars translating up and down independently—a non-rigid percept.

During long-lasting observations, these displays were bistable and seen alternately as rigid or non-rigid. These two percepts could occur spontaneously with an unchanging physical display—bistable display thereafter—or could be induced by periodic changes of the distribution of luminance along the bars (inducer display thereafter): bars with high line-end luminance and low center luminance were mostly seen as non-rigid, whereas bars with low line-end luminance and high center luminance were mostly seen as rigid (Lorenceau & Shiffrar, 1992). Smoothly shifting from one luminance distribution to the other with a period of 8 s was chosen so as to elicit perceptual alternations every 4 s, although the exact duration of rigid and non-rigid percepts can slightly differ from this value since different observers may have different sensitivities to low-contrast line end. Preliminary testing with a bistable display was conducted to determine the distribution of luminance along the bars yielding a rigid percept in approximately 50% of the time. In all dual configurations, the diamonds’ centers were positioned on a circle with a radius of 5.4 dva. Mean bar luminance is identical in all displays. Depending on the experiment, the motion of the two displays could be identical, opposite, or 90° out of phase; clockwise and counterclockwise rotations were also tested.

In Experiment 1, inducer and bistable displays were located in symmetrical positions relative to the vertical
Figure 1. (A–D) Spatial configurations used in the study. Each panel represents relevant dual display configurations used in Experiments 1, 2, 3, and 4. (A & C) The left, middle, and right columns show the bistable, direct inductive, and indirect inductive conditions, respectively, together with the probe and the inducer displays. (B & D) All conditions were indirect inductive. When perceptually integrated, the moving bars are seen as a rigid diamond moving clockwise or counterclockwise along a circular trajectory (rounded arrows; see method for details).
meridian and observers reported the perceptual alternations of the spontaneous bistable display in order to assess the existence and characteristics of a contextual effect. Several control conditions consisting of two bistable displays, two inducers, or combinations of static and moving displays were used for comparisons. Experiment 2 examined the effects of changing the relative motion of the bistable and inducer displays. In Experiment 3, coupling strength was compared for inter- and intra-hemifield configurations. Finally, Experiment 4 explored the effects of breaking vertical symmetry by changing the relative location of displays presented in each hemifield. Figure 1 summarizes the different configurations used in the four experiments.

Task

Previous studies with two bistable displays often used a dual task in which observers have to simultaneously report on the two displays. Although a dual task provides a straightforward measure of coupling strength (the percentage of the time where identical percepts are seen), we were concerned that it would yield uncontrolled shifts of attention or eye movement strategies that could bias the results; preliminary experiments using a dual task proved hard to perform with our displays; informal debriefing suggested that some observers attended to each display in alternation or made eye movements toward one of the two displays. During long-lasting presentations, the attentional load appeared unevenly distributed over time as observers were quickly tired or confused while tracking their internal state. We therefore decided to use a simpler task where observers had to report only on one of the two displays, defined as the probe thereafter.

Procedure

Observers were seated in a dark room with their head resting on a chin rest at 57 cm of the screen. Before the beginning of the experiment, the bistable diamond was shown for 20 s to check that observers experienced the two perceptual—rigid and non-rigid—interpretations. Observers were asked to keep their gaze on the central fixation cross and to avoid blinking as much as possible. Before each trial, observers were told to report their perception of one of the two displays by continuously pressing the right mouse button during rigid states and the left button during non-rigid states. A 10-min pause was given at halfway of each session.

Data analyses

As the same analyses on variables derived from the data were performed in the four experiments, we present them now in details.

Distributions of phase duration

The 8-s period of the luminance changes in the inducer display should entail perceptual alternations every 4 s. This notably differs from a chaotic, gamma-like, distribution of phase durations expected with a single, physically unchanging display (Borsellino, De Marco, Allazeta, Rinesi, & Bartolini, 1972; Brascamp, van Ee, Pestman, & van den Berg, 2005; Fox & Herrmann, 1967). With our settings, preliminary testing with a single bistable display showed that the mean phase duration was longer than 4 s (7–8 s on average). If a periodically changing inducer alters the dynamics of a distant bistable probe display, the observed distribution of phase durations should differ from a gamma-like or lognormal distribution and the mean phase duration should shift toward the 4-s period of the inducer. Moreover, the sign of the perceptual transitions—toward a bound or toward an unbound state—should be the same as that of the inducer changes. We evaluated the coupling strength between both the bistable probe and inducer displays by comparing (two-sampled Kolmogorov–Smirnov test) the distributions of phase duration and the mean phase durations across conditions. Since the distributions of phase duration are not necessarily Gaussian, we also performed statistical tests on the medians of phase durations. However, the results were globally similar for mean and median values and the distributions of interest did not significantly differ from normality (see Distribution of phase durations section in the Results section of Experiment 1). Thus, we report in details the results for the mean and median in Experiment 1 only. In the remaining experiments, we preferentially report tests on mean values.

Temporal delays

We analyzed the delays between the time of perceptual switches (rigid to non-rigid and non-rigid to rigid) and the maxima and minima of line-end luminance of the smoothly changing inductive diamond, using a temporal window ranging from −4 to +4 s. These delays were expected to be distributed around zero if perceptual transitions were triggered by the inducer’s periodic luminance modulations but should be distributed at random otherwise, using arbitrary maxima and minima of line-end luminance for a bistable display. Because of the limited number of transitions for each observer in each condition, it appeared unreasonable to attempt fitting the distributions of temporal delays, for instance, with a Gaussian function, so as to perform statistical analyses on its parameters. Instead, we used the variance of the temporal delays for each condition and observer as a relevant index. If the inducer is effective in imposing perceptual switches, phase distributions should be characterized by a low variance of temporal delays. If the inducer is absent or ineffective, phase distributions should
be scattered in the $-4$ to $4$-s interval resulting in a high variance. Statistical analyses were conducted on these variances to compare the distributions of temporal delays across conditions.

### Correlations

To characterize the dynamics of bistability across conditions, we used first return maps (Poincaré, 1885), equivalent to an autocorrelation matrix, in which the phase duration of a perceptual state, $N$, is plotted as a function of the phase duration of state $N + 1$. In first return maps, a periodic system is characterized by a single-point attractor of the system, while scattered phase durations are characteristics of a chaotic system. We then derived one-dimensional histograms from first return maps by counting the $[N, N + 1]$ events in cells of $500 \times 500$ ms covering the phase space and used these histograms to compute correlation coefficients ($R$ of Bravais–Pearson) across conditions. We expected a dense probability of events around $4$ s for the inducer and scattered values for the bistable display. High positive correlations between the bistable/inducer and the inducer/inducer conditions would provide evidence for an effect of the inducer.

### Experiment 1

This first experiment aimed at determining whether a remote display whose perception periodically changes over time through physical changes influenced the perception of a physically unchanging bistable display. Perceptual transition times were recorded for several dual configurations so as to compare the number of transitions and the distribution of phase durations across conditions. An influence of a remote inducer on a bistable probe should shift the phase duration of both rigid and non-rigid episodes toward $4$ s. Moreover, the temporal delays of perceptual transitions between $-4$ and $+4$ s should be centered around zero. Finally, we should observe a strong positive correlation between the perceptual dynamics of a probe inducer and a bistable probe in the presence of a contextual inducer and weak correlations otherwise.

### Methods and stimuli

Nine observers with normal or corrected-to-normal vision participated; two of them were aware of the purpose of the study. Different combinations of static, bistable, and inductive moving diamonds displayed $5.4$ dva left and right from a central fixation cross were tested. The spatial location, left or right from fixation, and the direction, clockwise or counterclockwise, were randomly chosen for each run. The circular motion of the two displays was identical. Observers were told which display was the probe (left or right) on each run. Overall, a session lasted $45$ min and comprised $8$, randomly mixed, runs of $4$ min each. The different conditions are detailed below.

### Spontaneous condition

One bistable probe diamond and one static diamond were displayed on each side of the central fixation cross (Figure 1A, left panel). In this condition, perceptual changes were spontaneous since the physical parameters of the probe stimulus were constant. These trials represented a reference baseline condition of bistability for each observer.

### Direct inductive condition

A static diamond and a moving inducer were presented on each side of the fixation cross (Figure 1A, middle panel). Perceptual switches were exogenously driven by smoothly changing the distribution of luminance along the bars (see Methods and stimuli section). These trials allowed to ensure observers’ perception change in phase with the physical modulations and provided a baseline for comparisons with the spontaneous and indirect inductive trials.

### Indirect inductive condition

A bistable probe and an inducer were presented on both sides of the central fixation cross. These trials were designed to evaluate the influence of the inducer acting as a dynamical visual context on the bistable probe.

### Control conditions

As we used a contextual static diamond in the spontaneous and direct inductive conditions, we also used a control bistable condition and an inducer condition with two identical displays. These conditions were designed to test whether the presence of two moving diamonds—as compared to a static and a moving diamond—had an effect on bistable dynamics.

### Results

Among the 9 observers, one almost never switched to a rigid percept and another never switched in the inductive conditions. The data of these observers were discarded from further analyses. Figures 2A–2D show the mean phase durations, the normalized phase durations, the distribution of temporal delays, and the first return maps, respectively.
**Phase durations**

Mean phase duration averaged across observers was 8.3 s (SD = 9.7) in the bistable condition (Mdn = 6.2 s), 4.5 s (SD = 3) in the direct inductive condition (Mdn = 4 s), and 5.3 s (SD = 4.7) in the indirect inductive condition (Mdn = 4.1 s). These differences are significant for both the mean (F(2, 12) = 9.4, p < 0.005) and median values (F(2, 12) = 11.38, p < 0.002). Post-hoc analyses indicate that mean phase durations are significantly longer for bistable than for direct inductive trials (t(6) = 3.7, p < 0.01) and indirect inductive trials (t(6) = 2.78, p < 0.025). Mean phase durations between the direct and indirect inductive conditions are marginally different (t(6) = 1.92, p = 0.051) in contrast to median values (t(6) = 1.08, p = 0.32). The mean phase durations for both direct and indirect inductive conditions are close to 4 s as expected if the smooth luminance changes drove perceptual alternations.

The effects of the spatial location of the probe—left or right—and the direction of motion—clockwise or counterclockwise—were not significant (F(1,6) = 2.63, p = 0.16 and F(1,6) < 1, respectively). The median durations were not significantly different between moving/static and moving/moving conditions (F(1,6) < 1), and the mean durations were only marginally different (F(1,6) = 5.37, p = 0.06).

**Distribution of phase durations**

To characterize the dynamics of perceptual transitions, we fitted the observed distributions of phase durations (excluding phase duration shorter than 500 ms) with a Gaussian, gamma, or lognormal distribution and compared the quality of the fits. The bistable condition was better fitted by a lognormal than by any other function (one-sampled Kolmogorov–Smirnov: D = 0.04, p > 0.2).

For the direct induction condition, the raw distribution is bimodal because on some trials observers skipped a transition (as it can be seen in Figure 2B). Taking all phase durations into account does not provide significant fits for any function (Gaussian, lognormal, or gamma). We therefore decided to use phase durations lower than 7000 ms (thus removing 8% of the phase durations). As a result, the direct condition is not different from a Gaussian distribution (one-sampled Kolmogorov–Smirnov: D = 0.03, p > 0.5) but differs from both gamma and lognormal distributions (both p < 0.01). Similarly, taking all phase durations into account, the indirect induction condition is different from Gaussian, lognormal, and gamma distributions. Fitting phase durations lower than 7000 ms, as for direct induction, indicates that the distribution is not significantly different from a Gaussian (one-sampled Kolmogorov–Smirnov: D = 0.03, p > 0.5) but significantly differs from both gamma and lognormal distributions (both p < 0.01).

As expected, in the bistable condition, the distribution of phase durations was lognormal and significantly different from the direct (Figure 2B, two-sampled Kolmogorov–Smirnov: D = 0.46, p < 0.0001) and indirect inductive conditions (two-sampled Kolmogorov–Smirnov: D = 0.31, p < 0.0001). Furthermore, the distributions of the direct and indirect inductive conditions were also significantly different (two-sampled Kolmogorov–Smirnov: D = 0.15, p < 0.0001), but both were well fitted by a Gaussian.

**Temporal delays**

We further analyzed the temporal delays between the perceptual switches and the maxima and minima of the luminance changes in the inducer (see Methods and Stimuli section; Figure 2C). Separate analyses were conducted for the non-rigid to rigid transitions and vice versa. The obtained values ranged between −4000 ms and 4000 ms, with 0 corresponding to the time when inducer line end reaches a maximum (non-rigid induction) or a minimum luminance (rigid induction). If perceptual transitions were locked to luminance extrema in the direct and indirect inductive conditions, the temporal delays should be distributed around zero. Transitions toward rigid (blue) or non-rigid (red) states (Figure 2C) mostly occurred with short temporal delays in the direct and indirect inductive conditions, while delays spanned the −4 to +4 interval in the bistable condition, with a flat distribution.

Figure 2. Results of Experiment 1. (A) Left: Mean phase percept duration of the first seventh phases of the bistable, direct inductive, and indirect inductive conditions averaged across observers. Bistable condition (light grey) yields longer mean phase duration than both inductive conditions (black: direct inductive; grey: indirect inductive) for which mean phase durations are around 4 s, in agreement with the periodic change of inducer luminance. Right: Mean phase duration averaged over time and across observers (error bars represent the SD). (B) Normalized distribution of phase durations for the bistable, direct and indirect inductive conditions with their respective best fit (lognormal, Gaussian, and Gaussian, respectively). (C) Histogram of temporal delays between luminance extrema of the inducer (T1 = maximum luminance of inducer end line, T2 = minimum luminance of inducer end line) and perceptual switches for rigid to non-rigid (red) and non-rigid to rigid transitions (blue). The x-axis (range −4000 ms and 4000 ms) corresponds to a period of luminance changes. The probability of switching around the luminance extrema is large for both inductive conditions and weak for the bistable condition. (D) First return maps for the three conditions: phase duration N (y-axis) is plotted against phase duration N + 1 (x-axis) for all subjects. The grid (bottom left) illustrates a portion of the 500 ms × 500 ms matrix used to quantify perceptual dynamics (see text for details); a different color is used for each subject.
Using the variance of these distributions as a dependent variable, we found no significant effect of spatial location, motion direction, or number of moving displays whatever the sign of the transitions (all \( p > 0.05 \)). The variance of the temporal delays is significantly higher in the bistable than in the indirect inductive condition for both types of transitions (rigid to non-rigid: \( t(6) = 11.4, p < 0.0001 \), one-tailed; non-rigid to rigid: \( t(6) = 12.4, p < 0.0001 \), one-tailed). These results suggest that observers tended to switch in phase with the luminance changes in both the direct and indirect conditions. Analyzing further the median of the temporal delays indicated that perceptual switches occurred significantly later in the indirect inductive condition (\( \sim 350 \) ms) than in the direct inductive condition (\(-113 \) ms vs. 236 ms: \( t(6) = 3.16, p < 0.025 \)).

**Correlations**

To gain further insights into the dynamics of perceptual transitions, we constructed first return maps (FRMs) where the duration of a percept \( N \), is plotted against the duration of the following percept \( N + 1 \). As shown in Figure 2D, FRMs pooled across observers yield scattered plots in the bistable condition and highly centered plots in the direct inductive condition. In the indirect inductive condition, the distribution resembles that of the direct inductive condition. In order to compare these distributions, we derived one-dimensional histograms from the FRMs (small squares in Figure 2D; see Methods and stimuli section). We then calculated global correlation coefficients between conditions (all subject data points in one go). The correlation coefficient was 0.20 between the bistable and direct inductive conditions, 0.30 between the bistable and indirect inductive conditions, and 0.76 between the direct inductive and indirect inductive conditions, suggesting that these later conditions share similar perceptual dynamics.

We also conducted an ANOVA on individual correlation coefficients. Overall, correlation coefficients were highly dependent on the number of perceptual transitions and, for that reason, varied widely across individuals. In addition, deriving histograms from first return maps introduces a large number of null values—cells where no transition occurred. Thus, coefficient correlations were small, as compared to the fixed-effect analysis. However, this analysis confirmed the main findings: correlation coefficients between direct and indirect induction were significantly larger than between spontaneous and indirect induction (\( t(6) = 2.8, p < 0.03 \)).

**Experiment 2**

At this point, several explanations of the remote influence of the inducer on the perception of a bistable display are plausible. For instance, the motion parameters of both displays, being identical, shared “common fate” (Kohler, 1940, or symmetry (Royer, 1981) may explain the perceptual coupling in Experiment 1. To test this possibility, we designed a second experiment in which the motion similarity of both displays was broken by shifting the relative motion phase (90° out of phase) or by using opposite motion directions. Note, that in this latter condition, the positions of the stimuli in the visual field are symmetrical around vertical at all times. The resulting dynamic “mirror symmetry” could enhance the induction effect, whereas it should decrease with the out-of-phase displays. In addition to low-level factors, decisional and attentional factors could account for the observed coupling in Experiment 1. For instance, observers may have responded whenever they saw a change in the inducer independently of their veridical percept of a bistable probe display. Note, however, that if different perceptual coupling was found in the different conditions of Experiment 2, this would weaken the hypothesis that attentional or decisional factors account for the influence of the inducer in Experiment 1, as there is no a priori reason that these factors depend on motion similarity.

**Methods and stimuli**

Eight observers with normal or corrected-to-normal vision participated; one was aware of the goal of the study and two participated in Experiment 1.

The procedure, task, apparatus, and stimuli are identical to those of Experiment 1, except for the motion parameters (Figure 1B). Only indirect inductive trials were tested and observers were asked to report their perception (rigid/non-rigid) of the bistable probe that always moved clockwise. To control for left/right asymmetries, the probe display was presented right or left from fixation. Three types of relative motion conditions were tested: strictly identical motion (S: Similar), opposite directions of rotation (O: Opposite; clockwise rotation for the bistable probe vs. anticlockwise for the inducer), and 90° phase shift between the probe and the inducer (P: Phase condition). The S condition, identical to the indirect inductive condition of Experiment 1, was taken as a control baseline condition. Conditions were presented twice in a session in a Latin square order. One session consisted of 6 trials of 3 min each with a 10-min rest at halfway.

**Results**

One observer never saw perceptual transitions and his data were discarded from further analyses. Figures 3A–3D present the mean phase duration, the normalized phase durations, the temporal delays, and the first return maps, respectively, for the S, O, and P conditions.
Phase durations and distributions

Mean phase duration (Figure 3A) was 5.6 s (SD = 1.25) in the S condition, 5.9 s (SD = 1.7) in the O condition, and 7.4 s (SD = 2.3) in the P condition. An ANOVA performed on mean phase durations indicated that these differences are significant ($F(2, 12) = 6.1$, $p < 0.05$). Comparing the average phase durations of the S and O conditions yielded no significant differences ($t(13) < 1$). Average phase durations in the O condition were significantly higher than in the S condition ($t(13) = 3.8$, $p < 0.005$). The spatial location, left or right, of the probe display has no significant effect ($F(1.6) < 1$).

The same results were found with the phase distributions: Phase distributions (Figure 3B) were not significantly different in the S and O conditions (two-sampled Kolmogorov–Smirnov: $D = 0.09$, $p = 0.084$) but differed significantly in the S and P conditions (two-sampled Kolmogorov–Smirnov: $D = 0.12$, $p < 0.01$).

Temporal delays

As expected for indirect inductive conditions, the distributions of temporal delays (Figure 3C) were similar in all conditions and distributed around zero independently of the type of transitions (toward a rigid or toward a non-rigid percept). Further analyzing the variances of phase distributions (see Methods and stimuli section) indicates that variances were larger in the P as compared to the S and O conditions. The differences between conditions were not significant for non-rigid to rigid transitions ($F(2, 12) < 1$) and only marginally significant for rigid to non-rigid ($F(2, 12) = 3.3$, $p = 0.07$).

Correlations

Computing first return maps and calculating correlation coefficients as in Experiment 1, we found a correlation of 0.56 between the S and O conditions, 0.54 between the S and P conditions, and 0.58 between the P and O conditions (Figure 3D). ANOVA on individual correlation coefficients showed the same result as no significant effect was found for any comparison (all $F$ and $t$ values <1).

Overall, the results of Experiment 2 suggest that common fate is not a prerequisite to observe a coupling effect that therefore does not appear to strictly depend on motion similarity. The observation that the coupling effect was reduced (but not canceled) in the out-of-phase (P) condition, in agreement with previous results (Eby, Loomis, & Solomon, 1989; Gillam, 1972), could be accounted for by a break of vertical symmetry. However, it is worth noting that even in the P condition, the displays still occupy symmetrical positions on both sides of the fixation cross.

Experiment 3

If vertical symmetry is an important determinant of perceptual coupling, manipulating more directly this factor may more clearly reveal its impact on coupling strength. To that aim, Experiment 3 compared the bistable dynamics of dual displays presented on both sides of the vertical meridian, as before, with displays presented in a single hemifield, up and down relative to the fixation cross. Stimuli moved either with the same motion with the same phase (common motion as in Experiment 2) or in opposite directions. In this way, one aimed at disentangling the effect of vertical symmetry and common fate, in order to better estimate their respective influence. If vertical symmetry matters, stronger coupling should be found with bilateral as compared to unilateral configurations. Again, note that different coupling strengths in these different conditions would suggest that attentional and decisional factors are not the main determinant of coupling strength.

Methods and stimuli

Among the 14 observers who participated, 5 of them also participated in Experiment 1 or 2 and one was aware of the goal of the study. Two participants almost never switched between percepts and were discarded from further analyses. The apparatus, stimuli, procedure, and task were identical to the previous experiments. All trials lasted 3 min during which observers were required to continuously report their percept of a single probe display: rigid or non-rigid. The probe display was always located in the upper left quadrant and always moved clockwise. In half the trials, both displays were located in the left hemifield, symmetrical around the horizontal meridian. They were presented in both hemifields, symmetrical around the vertical meridian in the remaining trials (Figure 1C, Experiment 3). Two control conditions, consisting of two bistable displays and two inducers (left two panels in Figure 1C), were used to provide a baseline for comparison with the indirect inductive conditions.
(right two panels in Figure 1C) in which a probe bistable display was presented in conjunction with an inducer. In these two control conditions, the direction of motion was either the same or opposite. The diamond centers were located on a virtual circle (radius: 5.4 dva) centered on the fixation cross. The centers of the displays were separated by 7.8 dva in all conditions.

Results

One subject never switched between rigid and non-rigid percepts and his data were removed from further analyses. Results were first analyzed to compare bistable, direct, and indirect inductive conditions with the two displays moving in opposite directions. A separate analysis of the indirect inductive condition was conducted to assess the effect of motion direction per se.

Figures 4A–4C present the mean phase durations, the distribution of the temporal delays for the different conditions, and the correlation coefficients between conditions, respectively.

Analyses of conditions with opposite motion directions

Phase durations

As before, the mean phase durations were calculated for each condition separately (Figure 4A). An ANOVA performed on this variable indicated that mean phase durations in the bistable, direct, and indirect inductive conditions were significantly different ($F(2, 22) = 16.5, \ p < 0.0001$). In this global analysis, neither the location of displays in the visual field nor the interaction between condition and location had a significant effect ($F(1, 11) < 1$ for location; $F(2, 22) = 1.02, \ p < 0.38$ for the interaction).

Figure 4. Results of Experiment 3. (A) Mean phase duration averaged across observers for each condition (error bars represent 1 SD). (B) Histogram of temporal delays between the maximum inducer luminance and perceptual switches (rigid to non-rigid: red; non-rigid to rigid: blue). The x-axis ranges between –4000 ms and 4000 ms corresponding to a period of the inducer luminance changes. (C) Correlations between indirect and direct inductive conditions.
Specific analysis of the indirect inductive conditions indicated that the mean phase duration in the bilateral configurations was shorter than in the unilateral configuration (one-tailed $t$-test: $t(11) = -1.8, p = 0.05$). Mean phase duration in the indirect inductive condition was significantly shorter than in the bistable condition for bilateral presentation (one-tailed $t$-test: $t(11) = -2.5, p < 0.025$). This was not the case for unilateral presentation (one-tailed $t$-test: $t(11) = -1.35, p = 0.10$).

Moreover, the lack of a significant main effect of spatial location ($F(1, 11) = 2, p = 0.18$) and the significant effect of the type of induction ($F(1, 11) = 28.24, p < 0.005$) indicate that phase durations were significantly longer in the indirect inductive condition, but only with unilateral displays, suggesting that the inducer was less influential in this condition. Furthermore, we found a significant interaction effect between display location and the type of induction (Direct/Indirect: $F(1, 11) = 5.8, p < 0.05$), which corroborates the observation than coupling is reduced in unilateral displays with stimuli in opposite motion direction (Figure 4A).

Kolmogorov–Smirnov tests confirmed that the distributions of phase duration were not significantly different between unilateral and bilateral presentations in the bistable ($D = 0.08, p = 0.34$) and direct inductive conditions ($D = 0.07, p = 0.28$), while differences were significant in the indirect inductive condition ($D = 0.14, p < 0.005$).

Additional analyses of indirect inductive conditions indicated that mean phase durations were not dependent upon left/right positions in unilateral configurations (one-tailed $t$-test: $t(11) < 1$) or up/down positions in bilateral configurations (one-tailed $t$-test: $t(11) < 1$). This is also true for the distributions of phase durations (Kolmogorov–Smirnov tests; Left/Right: $D = 0.06, p = 0.79$; Up/Down: $D = 0.09, p = 0.15$) and for the mean variance of temporal delays (one-tailed $t$-test: all $p > 0.025$).

**Temporal delays**

The distribution of temporal delays (Figure 4B) was flat in the bistable condition, whereas a peak around zero was observed in the direct and indirect inductive conditions. An ANOVA performed on the variance of the distributions calculated for each observer and condition (see Methods and stimuli section) indicates a significant effect of the conditions for both kinds of transition (rigid to non-rigid: $F(2, 22) = 51, p < 0.0001$; non-rigid to rigid: $F(2, 22) = 25.5, p < 0.0001$). In contrast to phase duration analysis, neither the location effect (one or two hemispheres) nor the interaction between location and condition was significant, whatever the type of transitions (all $p > 0.09$).

In the indirect inductive condition, the variance of the temporal delays is significantly lower than in the spontaneous condition for bilateral presentation (one-tailed $t$-test: non-rigid to rigid: $t(11) = -4, p < 0.001$; rigid to non-rigid: $t(11) = -4.6, p < 0.0005$). This effect was also found in unilateral presentation for rigid to non-rigid transition (one-tailed $t$-test: $t(11) = -3.5, p < 0.005$) but not for non-rigid to rigid transition (one-tailed $t$-test: $t(11) = -1, p = 0.16$). Overall, these results suggest that coupling strength is reduced only when stimuli moving in opposite directions are displayed in one hemifield.

**Influence of motion direction (opposite or same)**

**Phase durations**

ANOVA performed on the mean phase durations and the variances of the temporal delays do not show any significant effect of motion direction (same or opposite), stimulus location (one or two hemifields), or interaction (all $p > 0.3$). However, contrary to all other analyses, median values of phase durations do not yield to the same observation as the mean values, as significant effects, reported below, show up. In unilateral configurations, median phase durations were significantly shorter in the indirect inductive condition compared to bistable conditions when displays have the same direction (one-tailed $t$-test: $t(11) = -2.45, p < 0.025$) but were not different with opposite directions (one-tailed $t$-test: $t(11) = -0.7, p = 0.24$). Furthermore, Kolmogorov–Smirnov tests on phase duration distribution showed the same differences (same direction: $D = 0.15, p < 0.01$; opposite direction: $D = 0.10, p = 0.2$). Overall, these results indicate that motion similarity influenced perceptual coupling more in unilateral displays than in bilateral ones.

**Correlations**

The correlation between direct and indirect inductive conditions (Figure 4C) is large in bilateral configurations with opposite motion directions ($R = 0.66$) compared to unilateral configurations ($R = 0.33$). Similar differences were found with displays presented in the lower bilateral quadrants ($R = 0.61$) or in the unilateral right hemifield ($R = 0.4$). With identical motion direction, the correlations in bilateral ($R = 0.60$) and unilateral configurations ($R = 0.52$) remain high.

Group statistics on correlation values revealed a main effect of display location (two-tailed $T$-test: $F(1,12) = 5.3, p < 0.05$). No significant interaction was found ($F(1,12) < 1$). However, comparisons between unilateral and bilateral displays showed a significant difference for stimuli moving in opposite directions ($t(11) = -2.5, p < 0.03$) but not for displays moving in the same direction ($t(11) < 1$).

Overall, the results of this experiment indicated that, on average, bilateral configurations elicited a tighter coupling
between an inducer and a bistable probe display than in unilateral configurations. In this latter situation, a slight effect of motion similarity was observed.

**Experiment 4**

The comparisons between unilaterally and bilaterally presented dual displays in Experiment 3 revealed an advantage for bilateral configurations. However, it remains unclear whether the observed differences result from differences in the distribution of attention within or across hemifields (Alvarez & Cavanagh, 2005) or are accounted for by the pregnant vertical symmetry existing in bilateral configurations. If the observed effects are accounted for by heterogeneous allocation of spatial attention, using bilateral configurations should yield strong coupling independently of the relative positions of the displays in each hemifield. If, on the contrary, mirror symmetry is important for coupling, the influence of the inducer should decrease when vertical symmetry is disrupted. In order to test this prediction, Experiment 4 used dual configurations with displays positioned so as to break vertical symmetry (Figure 1D, Experiment 4).

**Methods and stimuli**

The apparatus, stimuli, procedure, and task were identical to the previous experiments. All trials lasted 4 min during which observers were required to continuously report their percept of a single probe display: rigid or non-rigid. Ten observers with normal or corrected-to-normal vision participated in the experiment. One observer was aware of the goal of the study.

As before, spontaneous, direct, and indirect inductive conditions were tested. Diamonds’ motions were either identical or opposite. Critically, the two displays were always in different hemifields but displaced vertically up and down relative to horizontal so as to break vertical symmetry. These deviations could be zero (control condition with vertical symmetry), half a diamond’s height, or equal to a full diamond height (Figure 1D). Overall, ten conditions presented in a Latin square order were tested: 2 spontaneous and 2 direct inductive trials with the same or opposite directions presented with zero, half, or full deviations and 6 indirect inductive trials (same and opposite directions combined with 3 vertical offsets: symmetrical, half-size deviation, and full size deviation).

**Results**

Figures 5A and 5B presents the mean phase durations and the correlation coefficient between first return maps, respectively.

**Mean phase duration**

In indirect inductive conditions, the mean phase durations (Figure 5A) were significantly longer for larger spatial deviations ($F(2,18) = 4.67, p < 0.05$). A main effect of motion direction was also found ($F(1,9) = 10.23, p < 0.05$). The interaction between position and direction was

![Figure 5](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932800/)

Figure 5. Results of Experiment 4. (A) Average of mean phase duration across observers for each condition (error bars represent 1 SD). (B) Correlations between indirect and direct inductive conditions as a function of the spatial deviation between displays.
not significant \((F(2,18) = 1.2, p = 0.32)\). The effects of location were more important for a large vertical offset and opposite motion directions, as confirmed by post-hoc pairwise comparisons: Mean phase durations were significantly longer for a full as compared to no vertical offset \((F(1,9) = 5.37, p < 0.05)\). For this comparison, the effect of motion direction is also significant \((F(1,9) = 9.43, p < 0.05)\). Mean phase durations were not significantly different for half and zero vertical offsets \((F(1,9) < 1)\) and only marginally different for motion direction \((F(1,9) = 4.37, p = 0.07)\).

In summary, mean phase duration was longer when stimuli were offset from the horizontal meridian, e.g., when vertical symmetry was broken, and this effect was stronger when stimuli moved in opposite directions.

**Correlations**

As before, we constructed first return maps and calculated correlation coefficients between indirect and direct inductive conditions. The obtained correlations decreased with increasing deviations (Figure 5B). The lowest correlation was observed for fully deviated displays moving in opposite directions \((R = 0.23)\) and increased up to 0.5 for symmetrical configurations.

Group statistics on correlation coefficients on all indirect induction conditions revealed a main effect of deviation \((F(2,18) = 4, p < 0.05)\). When comparing only the full deviation to the no deviation condition, an effect of motion direction emerged \((F(1,9) = 14.8, p < 0.005)\), with a remaining effect of the deviation \((F(1,9) = 14.5, p < 0.005)\). Another specific finding showed that there is a significant difference between half-deviation and full deviation when stimuli are moving in opposite directions \((t(9) = 2.6, p < 0.03)\) but not when they are moving in the same direction \((t(9) < 1)\).

The overall distribution of correlation coefficients suggested that coupling strength is reduced when symmetry is broken and specific comparisons support the hypothesis of a stronger coupling strength reduction when stimuli move in opposite directions in keeping with Experiment 3.
exception to this statement is the case of unilateral versus bilateral configurations, as it was previously shown that attentional resources are differently allocated within a single hemifield or across the two hemispheres (Alvarez & Cavanagh, 2005). However, the finding of different coupling strength as a function of motion similarity in unilateral presentations again pleads against a pure attentional account. Although one cannot exclude that engaging attentional resources, for instance, by using a demanding task in parallel to perceptual reports, would influence coupling strength, it seems difficult that changes in attention allocation can account for the results found in the different experiments and conditions of the present study.

Decision and coupling

Another possible account of the present results considers decisional biases. Indeed, one cannot exclude that, while having to report on the probe, observers periodically noticed a change in the peripheral inducer, which could have either induced a false alarm or influenced their decision to press a key. If this would have been the case, one would expect these decisional biases to occur independently of the actual experimental condition. The findings of significant effects of location or motion direction argue against this possibility.

Eye movements and coupling

The same line of reasoning applies when considering a possible influence of eye movements on coupling strength. Back and forth saccades between the probe and the inducer may have elicited switches in perception, as it has been reported that perceptual transitions can be coupled to transient events (blinks, saccades, and microsaccades, for instance; see, e.g., Hupé et al., 2008; van Dam & van Ee, 2006; van Ee et al., 2005), but it is unclear why oculomotor behavior would systematically differ between experimental conditions. If the inducer elicited different eye movement behavior during bound and unbound states, this should occur whatever the motion or spatial configuration and therefore cannot explain the effects of these factors. We however decided to check more precisely whether observers had different oculomotor behavior during the bound and unbound states in the indirect inductive condition of Experiment 1. Two analyses were conducted. One tests the possibility that observers involuntary tracked the inducer in bound states, which could entail a transition toward a bound state in the probe display. If it were the case, small pursuit eye movements locked to the stimulus oscillation should differentiate bound and unbound states. We therefore segregated eye movements performed during bound and unbound states, performed a Fourier transform on both set of traces, and conducted an ANOVA on the power signal at the stimulus oscillation frequency (1.052 Hz) for both vertical and horizontal eye movements. Statistical analysis indicate no significant difference in power at frequency of interest between bound and unbound states for both vertical and horizontal eye movements ($t(6) = 1.56, p = 0.17$ and $t(6) = 1, p = 0.35$, respectively). A similar analysis was conducted on the number of saccadic eye movements with similar results ($p > 0.07$ for both horizontal and vertical saccades).

Overall, for attention, decision, or eye movements to influence coupling strength would require that observers behave very differently in the different conditions tested herein. In the absence of obvious reasons for a dependence of behavior on experimental condition differences, we conclude that other processes must explain the observed differences in coupling strength across conditions.

The callosal hypothesis

One possible account of the present results relies on the observation that coupling strength is more important whenever the displays are symmetrical around the vertical meridian and weaker otherwise. Moreover, symmetrical configurations seem to be relatively immune to differences in motion direction, whereas other configurations, as, for instance, unilateral configurations, are not (Experiment 3). Visual symmetry has been studied by many researchers who investigated how the different types of symmetry may impact perception (Machilsen, Pauwels, & Wagemans, 2009; Tyler, 1996; Wagemans, 1997). Mirror symmetry has been argued to be a particular case of symmetry as it was found to yield overall better detection performance (Herbert & Humphrey, 1996; Julesz, 1971; Royer, 1981; Tyler, 1996; Wagemans, 1993, 1997). Tyler (1996) suggested that detecting symmetry is a preattentive process and psychophysical experiments support the view that long-range connection through the corpus callosum could underlie symmetry detection (Herbert & Humphrey, 1996; Julesz, 1971; Mach, 1897; Tanaka, Miyaiuchi, & Misaki, 2007). In support of this “callosal hypothesis,” Herbert and Humphrey (1996) have shown that detecting symmetry is degraded when observers are born without a corpus callosum (also see Fagard et al., 2008).

In this context, a possible account of the present findings is that homotopic neurons recruited by displays symmetrical around the vertical meridian interact, so as to link their activities. In support of this idea, electrophysiological recordings in cat and monkey (Engel, König, Kreiter, & Singer, 1991; Nowak, Munk, Nelson, James, & Bullier, 1995) indicate that homotopic neurons in the two hemispheres tend to synchronize. Measures of cross-correlations between the firing rates of neurons from
the two hemispheres further indicate that different modes of synchronization coexist, some being mediated by feedback connections, as assessed by lesion studies (Nowak et al., 1995), and others being more specifically related to interhemispheric callosal connectivity. In the study by Engel et al. (1991), synchronized activity disappears after a section of the corpus callosum. It is therefore possible that the dynamic coupling of bistable stimuli depends on interhemispheric neuronal synchronization, whether it relies on feedback from remote cortical areas or more directly on the information transfer through the corpus callosum. Although psychophysical experiments in normal humans do not permit to determine whether remote influences on bistable perception are specifically carried out by callosal connections, the present results nevertheless suggest that bistable stimuli presented in symmetric locations relative to the vertical meridian interact.

Nowak et al. (1995) further distinguished synchronized activity in three classes and proposed that tight synchronization between neurons depends on the corpus callosum, while loose synchronization was more likely to involve feedback connections from higher areas. One possibility is that coupled perceptual dynamics in the present symmetrical configurations could reflect the existence of long-range connections possibly involving the corpus callosum. In this regard, coupled activity of homotopic neurons could result in synchronous changes in perception and explain the effect of a contextual inducer on a bistable display. Several characteristics of the results presented herein would fit with this scheme given that callosal connections connect neurons in the vicinity of the vertical meridian with similar orientation preferences. The observation of a delay of about 350 ms when comparing direct and indirect inductive conditions (Experiment 1) is intriguing. One tentative explanation is that the effect of the inducer on a distant bistable display may require some time. It is unlikely that this delay reflects the conduction times between hemispheres as the speed of propagation through callosal fibers is high, but it could reflect the time needed to force an attractor into a new state.

The detrimental effect of out-of-phase and opposite motion directions found in Experiments 2, 3, and 4, although weak on average, may temper the idea of an exclusive involvement of callosal connections between low-level areas (e.g., V1 and V2). Indeed, the integration of the moving bars into a moving diamond shape is likely to occur in high-level areas where receptive fields are large (MT/MST, LOC, for instance; Fang et al., 2008; Lorenceau et al., 2008). One therefore cannot exclude that feedback from these areas also contributes to coupling. One can, for instance, speculate that displays with identical motion recruit neurons with large receptive fields whose feedback tends to increase coupling. With dissimilar motion, these neurons may not be optimally recruited such that coupling would not benefit from their inputs.

Relations to previous studies

In a recent study, Klink et al. (2009) present evidence that the dynamics of bistability of two rotating cylinders defined by 3D dots can be coupled depending on the perceived depth planes. From their results, the authors argue that long-range horizontal connections (in V1 and/or MT) may underlie perceptual coupling. The model developed with this assumption accurately simulates the behavioral results. The present study complements this view as, here too, perceptual coupling between distant displays is observed. However, the displays used herein lack several of the characteristics that were modeled: they were always perceived in the same depth plane and the bars composing the stimuli were never collinear. It thus seems difficult to account for the present results within the framework modeled by Klink et al. because long-range horizontal connections between cells with similar orientations would be ineffective in our case. One way to reconcile both studies could be to take long-range interhemispheric connectivity into consideration instead. One prediction would then be that, with the stimuli used by Klink et al., coupling disappears if vertical offsets between stimuli break vertical symmetry. Moreover, and if the callosal hypothesis is correct, the result of Klink et al. would suggest that interhemispheric connections selectively link neurons tuned to similar disparity.

Open issues

Questions that arise are related to the possibility that a bistable contextual display influences perceptual alternations in a physically changing inducer. In Experiment 1, we did not find significant differences between a condition where two inducers were displayed and a condition where the probe inducer was presented together with a bistable display. As is possible that our analyses were not powerful enough to reveal such differences, one cannot yet conclude on this point.

If neuronal interactions through the corpus callosum underlie the perceptual coupling reported here, several predictions arise. First, coupling should depend on the distance to the vertical midline, as anatomical studies showed that the number and strength of connections of homotopic neurons decrease with increasing eccentricity (Kennedy, Dehay, & Bullier, 1986), a factor that could not be tested here because in eccentric viewing condition motion coherence dominates over motion segmentation (Lorenceau & Shiffrar, 1992). Second, coupling strength should decrease as a function of the relative orientation of the two diamonds, as the corpus callosum connects neurons with similar orientations (Rochefort et al., 2009; Schmidt, Lomber, & Innocenti, 2010).

Finally, the finding of long-range interaction between an inducer and a bistable display arranged in symmetrical
configurations raises the more general question of the influence of symmetry on a number of findings assessed with such configurations. A very large number of psychophysical studies employed a two-alternative forced-choice procedure with stimuli presented on each side of a central fixation point to investigate sensitivity, discrimination, recognition attention, etc. Whether the results obtained in these circumstances are biased by or reflect the contribution of long-range interhemispheric connections remains to be investigated.

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References


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


