Perceptual reversals need no prompting by attention

Alexander Pastukhov Cognitive Biology Lab, University of Magdeburg, Leipziger, Germany

Jochen Braun Cognitive Biology Lab, University of Magdeburg, Leipziger, Germany

Many ambiguous patterns elicit spontaneous alternations of phenomenal appearance. Attention is known to influence these phenomenal reversals, as do several other factors. We asked whether a shift of attention individually prompts each reversal of phenomenal appearance. By combining intermittent presentation with a proven method of attention control, we monitored phenomenal alternations in the complete absence of attention shifts. We found that reversals become less frequent but continue even when observers neither report on nor shift attention to an ambiguous pattern. The statistical variability of reversals remains unaffected. We conclude that reversals of phenomenal appearance are not prompted externally by attention shifts, but internally by an intrinsic instability of the neural representation of ambiguous patterns.

Keywords: perceptual rivalry, divided attention, dual-task, ambiguous patterns, multistable perception

Introduction

The contents of visual awareness often shift spontaneously, without external cause. In ambiguous visual displays such as the Rubin vase, the Necker cube, or dichoptically presented patterns, phenomenal appearance switches back and forth between rivaling percepts (Blake & Logothetis, 2002; Leopold, Wilke, Maier, & Logothetis, 2002), even when there are no stimulus transients or eye movements (Blake, Fox, & McIntyre, 1971). During this so-called "multistable perception," neural activity in the visual thalamus and cortex fluctuates hand in hand with phenomenal reversals (Haynes, Deichmann, & Rees, 2005; Lee, Blake, & Heeger, 2005). Visual awareness of a static scene also changes with "visual attention," that is to say, with the selective enhancement of scene aspects that are relevant to current behavioral goals (Boynton, 2005; Itti & Koch, 2001; Reynolds & Chelazzi, 2004). Attentional selection is thought to result from dynamic interactions between multiple brain areas encoding visual and goal information (Deco & Rolls, 2002; Itti & Koch, 2001). Visual awareness of stimuli selected by attention improves both qualitatively and quantitatively (Braun, Koch, Lee, & Itti, 2001) and neural responses to such stimuli increase in visual thalamus and cortex (Kastner & Pinsk, 2004; Shulman, d'Avossa, Tansy, & Corbetta, 2002).

In spite of more than a century of research, we do not know why the phenomenal appearance of ambiguous patterns shifts and what neural events precede or prompt these reversals. One possibility is that the neural representation of an ambiguous pattern is intrinsically unstable. An unstable representation might result from neural adaptation (Blake, 1989; Kohler & Wallach, 1944), from competitive interactions between the neural activities associated with different perceptual states (Laing & Chow, 2002; Wilson, 2003), from random fluctuations in neural background activity (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Kim, Grabowecky, & Suzuki, 2006; Shpiro, Curtu, Rinzel, & Rubin, 2007), or from a combination of these and other factors. Computational models incorporating various combinations of these factors can account for many aspects of the dynamics of multistable perception, including the variability of dominance times and the dependence on stimulus intensity (Laing & Chow, 2002; Wilson, 2003).

An entirely different possibility is that phenomenal reversals are triggered top-down by visual attention (James, 1890; von Helmholtz, 1866/1925). In an influential review, Leopold and Logothetis (1999) compiled evidence to support this view, arguing in essence that spontaneous and involuntary shifts of visual attention, presumably reflecting exploratory behavior, prompt phenomenal reversals. More recently, several psychophysical studies have shown that phenomenal alternations can be influenced by exogenous (Meng & Tong, 2004; Toppino, 2003; van Ee, van Dam, & Brouwer, 2005) as well as endogenous attention (Chong, Tadin, & Blake, 2005; Mitchell, Stoner, & Reynolds, 2004). Moreover, functional imaging (Inui et al., 2000; Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998; Sterzer, Russ, Preibisch, & Kleinschmidt, 2002) and electrophysiological studies (Strüber, Basar-Eroglu, Hoff, & Stadler, 2000) have shown that phenomenal reversals are associated with transient activations of right frontoparietal

cortex, an area generally associated with attentional guidance and control (Desimone & Duncan, 1995; Nobre et al., 1997). Patients with lesions in this area have difficulties experiencing multiple aspects of complex ambiguous drawings (Meenan & Miller, 1994) and exhibit diminished voluntary control over phenomenal alternations (Windmann, Wehrmann, Calabrese, & Gunturkun, 2006).

The observations summarized above suggest that phenomenal reversals and attention shifts are linked or associated somehow, but they do not reveal to the precise nature of this apparent relationship. One possible causal relationship is that attention prompts phenomenal reversals. Attentional selection is known to enhance neural responses to the attended stimulus in visual cortex (Boynton, 2005; Reynolds & Chelazzi, 2004). Accordingly, attention could trigger a phenomenal reversal either by shifting to the currently suppressed aspect of an ambiguous stimulus, boosting the associated neural activity, by drawing away from the currently dominant aspect and lowering the associated activity, or by a combination of both. However, it seems equally possible that the causal relationship is inverted because a phenomenal reversal could well act like a "visual onset" and induce an involuntary shift of attention to the ambiguous stimulus and its newly changed phenomenal appearance. That a sudden image change tends to trigger an involuntary shift of attention to the changed location has been well documented for many years (Prinzmetal, Park, & Garrett, 2005; Remington, Johnston, & Yantis, 1992).

The goal of the present work was to investigate seemingly spontaneous phenomenal reversals and to ascertain whether (or not) they are in fact prompted by attention shifts. Due to a difference in time scales, a possible role of attention shifts in spontaneous reversals is not easy to prove or disprove: attention can shift as fast as several times per second (Duncan, Ward, & Shapiro, 1994; Egeth & Yantis, 1997), whereas the transition between rivaling percepts may take seconds or even tens of seconds to complete. To overcome this hurdle, we devised means to discourage attention shifts by combining a dual-task paradigm with intermittent stimulus presentation. In this way, we could monitor phenomenal reversals while tightly controlling the distribution of attention. One condition (Experiment 2) induced observers to divide attention highly unequally, allocating on average less than 10% of attention to an ambiguous display and more than 90% of attention to a concurrent task. In another condition (Experiment 3), the allocation of attention was even more lopsided in that observers neither reported on nor attended to an ambiguous display for certain periods. In both cases, withdrawing attention from an ambiguous display slowed phenomenal alternations significantly. However, phenomenal reversals continued to take place even in the latter condition, in which attention demonstrably did not shift to the ambiguous display.

Accordingly, we conclude that at least some phenomenal reversals take place spontaneously, without being prompted by attention.

Methods

Observers

Seven observers (four female, three male) including first author (A.P.) participated in the study. The three most experienced observers (one female, two male; A.P., K.M., and O.M.) carried out Experiment 2 (poor attention). Procedures were approved by the medical ethics board of the University of Magdeburg and informed consent was obtained from all observers. All observers had normal or corrected-to-normal vision. Apart from the first author, observers were naive as to the purpose of the experiment and were paid for participation.

Apparatus

Stimuli were generated by computer (video card Quattro FX 1100, NVidia, Santa Clara, CA) and displayed on a 19-in. screen with a refresh rate of 117 Hz and a resolution of 1280×1024 (Vision Master Pro 454, Iiyama corporation, Nagano, Japan). At an eye-screen distance of 95 cm, each pixel subtended approximately 0.015°. Screen luminance was calibrated with a luminance meter and color-bit stealing was used to create small luminance steps (Tyler, 1997). The background luminance of our displays was 19 cd/m^2. Small eye movements cannot be ruled out when viewing a moving stimulus, known to induce optokinetic nystagmus even for brief stimulus presentations (Kommerell & Thiele, 1970). To counteract this, observers were instructed to fixate on a stationary dot at the display center, a measure known to suppress optokinetic nystagmus and significantly reduce residual eye movements (Pola, Wyatt, & Lustgarten, 1995). Additionally, brief presentations of central targets (200 ms each) coupled with concentric layout of the display rendered voluntary eye movements to peripheral target counterproductive.

Moving plaids

Phenomenally, moving plaids appear either as two surfaces sliding across each other (transparent, Figure 1C bottom), or as a single surface translating rigidly (coherent, Figure 1C top). Observers reported whether the plaid appeared to move close to vertically (pressing "j" for "coherent"), close to horizontally (pressing "f" for "transparent"), or in some intermediate direction (pressing no
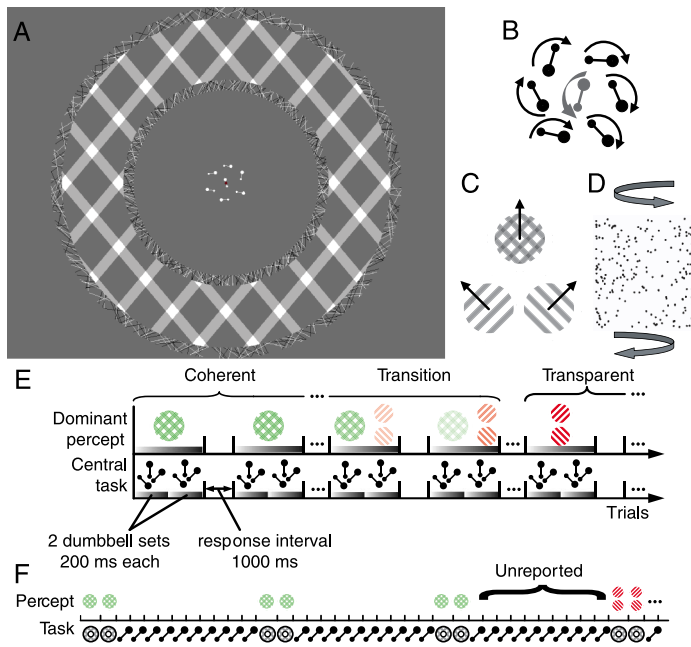
Figure 1. Moving plaid displays. (A) Display layout. Observers fixated at display center. Moving plaids appeared for 400 ms in an annular region (r_{inner} = 9°, r_{outer} = 14.5°) with a visible boundary to minimize terminator effects. Component gratings moved diagonally up or down. At the center (r_{center} = 1.5°), two target sets appeared for 200 ms each, without interval. (B) Central task (schematic). Each of the two target sets comprised seven "dumbbells" rotating clockwise and counterclockwise. Observers reported the rotation of most "dumbbells," separately for each target set. Task difficulty depended on the number of "dumbbells" rotating against the majority (here shown in grey). (C) Phenomenal appearance of moving plaids (schematic). In the peripheral task, observers reported the motion as either "coherent" (a single surface moving vertically), "transparent" (two surfaces sliding across each other, moving diagonally), or "unsure/transition." (D) Phenomenal appearance of depth-from-motion stimulus (schematic). Observers reported "front moves left," "front moves right," or "unsure/transition." (E) Presentation sequence for Experiments 1 and 2 (schematic). Moving plaids were presented for 400 ms, concurrently with two successive sets of central targets (200 ms each), and followed by a 1000-ms blank interval, during which responses were collected. Typically, the phenomenal appearance of moving plaids remained stable for many presentations. Consecutive presentations with reports of the same phenomenal appearance (or "unsure/transition") were counted as a single "dominant percept." Toward the end of each "dominant percept," frequent reports of "unsure/transition" revealed an extended transition period (see also Figures 2 and 3). (F) Trial sequence for Experiment 3 (schematic). For two trials, observers ignored the central task and reported on the ambiguous pattern. For the 10 following trials, observers reported on the central task and ignored the ambiguous pattern ("unreported period"). This sequence repeated up to 20 times. During "unreported periods," central task performance revealed how faithfully attention was kept away from the ambiguous pattern.

key for "unsure/transition"). For moving plaids, the appearance of transition phases is quite distinct and none of the observers reported difficulties in identifying such phases. Observers were instructed to report "unsure/transition" also when the appearance was uncertain during only part of the presentation time.

Moving plaids were presented in an annular region (inner radius 9°, outer radius 14.5°), with visible apertures (diameter 0.5°, 10% contrast) to minimize the visual impact of terminators (Figure 1A). Each plaid component grating was a square wave grating (2.2 cycles/deg spatial frequency, duty cycle 0.3, contrast 5.0%, 5.75%, 8.5%, or 50%). The contrast of intersections was computed with an additive transparency rule. The angle between component gratings was 110°, 115°, or 120°, chosen individually for each observer to balance coherent and transparent percepts. Grating speed was computed for a coherent speed of 6 deg/s from the intersection of constraints: $s_{component}$ = $s_{pattern} \cos(\theta/2)$. The direction (up or down) of plaid motion alternated between blocks (continuous presentation sequences). In the divided attention experiment, where blocks lasted up to 25 min, observers paused at least 10 min between blocks.

Depth-from-motion display

The phenomenal appearance of a rotating cylinder was created by projecting 200 random dots (diameter 0.045°) from the surface of a virtual cylinder (4.5° height and diameter, rotation period 1.0 s) orthographically onto the screen (Figure 1D). As there were no depth, size, or perspective cues differentiating front and rear surface, the depth perception was ambiguous and alternated between both senses of rotation (front left and front right). The rotating cylinder was presented at eccentricity of 12°, directly above fixation.

Observers reported whether the cylinder rotated one way (pressing "f" for "front left"), the other way (pressing "j" for "front right"), or whether the sense of rotation was unclear (pressing no key for "unsure/transition"). Observers report "unsure/transition" also when the appearance was unclear during only part of the presentation time.

Central task

Two sets of seven rotating dumbbells (set diameter 1.5°) were presented for 200 ms each, without interval (Figure 1B). Each dumbbell rotated with a frequency chosen randomly between 1.5 and 3.5 Hz. Dumbbells rotated both clockwise and counterclockwise, and the prevailing sense of rotation was chosen randomly for each set. For each set, observers reported the prevailing sense of rotation (pressing "right" for "mostly clock-wise" and "left" for "mostly anticlockwise"). The number of reversely rotating dumbbells was chosen for individual

observers to control task difficulty (range 1–3). Based on earlier findings (Lee, Itti, Koch, & Braun, 1999), we expected this task to create an exceptionally high attentional demand and we verified this expectation with control experiments described in Appendix A.

Full attention condition (Experiment 1)

In Experiment 1, a moving plaid stimulus was presented intermittently, alternating ON intervals of 400 ms and OFF intervals of 1000 ms (Figure 1E). In addition to the moving plaid, two sets of rotating central targets were presented during ON intervals, each lasting 200 ms. In the "full attention" condition, observers were instructed to attend and to report the phenomenal appearance of the moving plaid and to ignore the rotating central targets. Each block lasted for six consecutive periods of perceptual dominance and block length ranged from ~200 to ~1000 trials.

Poor attention condition (Experiment 2)

With the identical display, we altered instructions to induced observers to "poorly attended" the moving plaid (Figure 1E). Specifically, we instructed observers to give priority to the two sets of central targets and, with a first and second key-press, to report as accurately as possible on the rotational state of these two sets of targets. With a third key-press, we asked observers to report the phenomenal appearance of the moving plaid.

No attention condition (Experiment 3)

In a third experiment, we again presented ambiguous displays (either moving plaids or depth-from-motion displays) intermittently, alternating ON intervals of 400 ms and OFF intervals of 1000 ms in the case of moving plaids, or ON intervals of 400 ms and OFF intervals of 500 ms in the case of depth-from-motion displays. In addition, two sets of rotating central targets (200 ms each) were presented during 10 consecutive trials. In the two subsequent trials, however, central targets were omitted. The trial sequence is illustrated in Figure 1F. Observers were asked to attend fully to, and report only on, the central targets for 10 consecutive trials (whenever central targets were present), but to shift attention to, and report only on, the ambiguous display for the following 2 trials (whenever central targets were omitted). For the trials in which the ambiguous display remained unreported, we were able to infer the allocation of attention from the performance level of the central task (see Appendix A). As the observed performance was not consistent with attention having shifted away from the central task for even 1 out of 10 trials, we conclude that the ambiguous display remained unattended

during this period (see Results). Accordingly, we call this the "no attention" condition.

Dominance and transition times

The reported times of perceptual dominance and transition represent "cumulative presentation time" and do not include the intervals between stimulus presentations. Cumulative presentation time T in seconds is calculated as $T = N \cdot \Delta T$, where N is the number of trials and ΔT is the presentation time (0.4 s).

Trials with more than 25% of "unsure" reports were assigned to transition periods. All other trials were assigned to one or the other dominance period, depending on most reports.

Attentional lapses

If attention lapses, instead of focusing on the two sets of rotating central targets, central task performance will be at chance during the affected trial (50% performance, see Appendix A). Given a reference level for an observer's performance of the central task (P_{ref}, performance when the observer attends fully to, and reports only on, the central targets), we can infer the number of attention lapses N_{lapsed} that is consistent with an average level of performance during "unreported periods" (P_{test}, performance during 10 consecutive trials in which the observer was instructed to ignore the ambiguous stimulus):

$$N_{\text{lapsed}} = 10 - \frac{10 \cdot P_{\text{test}} - 5}{P_{\text{ref}} - 0.5}. \tag{1}$$

Statistical methods

Standard Matlab 7.0.4 and Statistical Toolbox 5.2 (The Mathworks, Inc., Natick, MA) routines were used for statistical analysis and fitting.

Psychophysical performance of all objective tasks (central task, control tasks) was measured in terms of sensitivity d' and reported in terms of an unbiased nominal percentage correct. For the central task, we separately compute performance on the first and second sets of dumbbells and report the minimum. Blocks in which separate performances differed by more than 1 *SD* (computed over blocks) were discarded (~2%). Blocks with central performance more than 1 *SD* (computed over blocks) below reference central task performance were also discarded (~3%).

Mean dominance times were normalized to unity and their distribution fit by a Gamma function

$$P(t)\mathrm{d}t = \frac{\alpha^{\alpha} t^{\alpha-1} \exp(-\alpha t)}{\Gamma(\alpha)} \mathrm{d}t. \tag{2}$$

The mean, variance, and coefficient of variation of the distribution of dominance times are given by

$$\langle t \rangle = 1, \tag{3}$$

$$\langle t^2 \rangle - \langle t \rangle^2 = {}^1/_\alpha, \tag{4}$$

$$C_v = {}^1/\sqrt{\alpha}. \tag{5}$$

In Experiment 3, we used a Wilcoxon rank sum test to determine whether individual observers' distribution of block performances different significantly between test and reference blocks. The results of a control experiment in which only the central task was performed served as *reference performance* (P_{ref}). Ten-trial sequences of central task performance ("unreported periods") were assigned to *switch* and *no switch* categories as follows: if phenomenal appearance was reported differently before and after a 10-trial sequence, the sequence was classified as switch; otherwise, the sequence was classified as no switch. Average performance during switch and no switch sequences was termed P_{switch} and $P_{\text{no switch}}$, respectively.

Results

To control the allocation of attention across the display, we divided our display into distinct central and peripheral regions (Figures 1A–1D): the central region engaged the observer's attention while the periphery accommodated the ambiguous pattern. We instructed observers to perform separate visual tasks with reference to each region, which we termed central task and peripheral task, respectively. The central task concerned two sequentially presented sets of seven rotating shapes, shown for 200 ms each (Figure 1B, see Methods). For each set, the task required an independent response as to whether most shapes rotated clockwise or counterclockwise.

The *central task* was designed to ensure that attention is nearly absent whenever ambiguous patterns are physically present. We have shown previously how to control the allocation of attention with a concurrent task (Braun et al., 2001). The task used here was a particularly sensitive indicator of attention allocation (see Figure A1, Appendix A): its optimal performance focused at least 92% of attention ($p = .05$) and relaxing this focus by 6.2% of attention lowered performance significantly ($p = .05$). More important, the concurrent task required attention for two

successive periods of 200 ms. A complete lapse of attention during either one of these periods reduced performance to chance. Thus, the accurate performance of this concurrent task could effectively preclude a shift of attention to a rivalry-inducing pattern.

With the help of this central task, we were able to study phenomenal alternations under conditions of *full attention* (Experiment 1), *poor attention* (Experiment 2), and *no attention* (Experiment 3).

Experiment 1: Appearance reported and attended (full attention)

In a first experiment, we sought to establish the time course of phenomenal alternations under conditions of full attention, but with intermittent, rather than continuous, presentation. Intermittent presentation is known to slow alternations without necessarily disrupting them altogether (Leopold et al., 2002; Maier, Wilke, Logothetis, & Leopold, 2003; Orbach, Ehrlich, & Heath, 1963). In particular, we wanted to establish precisely how intermittent presentation changes the temporal and statistical characteristics of multistable perception, compared with continuous presentation.

As ambiguous pattern, we intermittently presented a moving plaid (Adelson & Movshon, 1982; von Grünau & Dubé, 1993) in an annular region in the periphery of the display (Figure 1A) and we instructed observers to classify the phenomenal appearance (*peripheral task*). The phenomenal appearance of this pattern alternated between a single surface moving vertically ("coherent") and two separate surfaces moving diagonally ("transparent"; Figure 1C, see Methods). The presentation was repeated until six phenomenal reversals had occurred.

To establish the time course of alternations with full attention, we instructed observers to perform only this peripheral task after each presentation. Observers reported phenomenal appearance as either "transparent," "coherent," or "unsure/transition" (see Methods). Each percept tended to dominate for numerous presentations before yielding to its rival. Dominant periods lasted between 5 and 448 presentations, with a mean value of 56.8 presentations (seven observers). The mean value for three selected observers (A.P., K.M., and O.M.), who performed also in Experiment 2, was 48.85 presentations. As is typical for multistable percepts, the distribution of dominance times approximated a Gamma function with a coefficient of variation of $C_v \sim .5$ (Figure 2B), and the dominance times of successive percepts were not correlated (Figure 2C). These data were based on five of six dominance periods in each continuous sequence of presentations. The initial dominance period of each sequence (almost always coherent) was not included, as it tended to last longer than the others (Hupé & Rubin, 2003).

The average trial histogram of the 15 presentations preceding a perceptual reversal (defined as the first report

of a different percept, Figure 2A) showed an interesting feature: the proportion of "unsure" reports increased in all but one of seven observers toward the end of a dominance period, indicating the transition between phenomenal percepts. Observers reported that, during this period, the annular plaid pattern appeared subjectively to move in intermediate directions (neither vertical/coherent nor diagonal/transparent). The average transition time (see Methods) varied between observers but correlated strongly (correlation coefficient .61, $p = .042$) with the average dominance time (i.e., whether the observer was a slow or fast "switcher"). This correlation suggests that the variance in transition lengths was genuine and not due to criterion differences between observers.

For the sake of comparison, we also established distributions of dominance times for continuous presentation of the same display. Consistent with earlier results (Leopold et al., 2002), both average dominance and transition periods were considerably shorter, but the statistical variability of dominance periods was virtually identical. This is evident from the normalized distribution of dominance times, which followed a Gamma function with a coefficient of variation of $C_v \sim .5$ (Figures 2B and 2C). The first percept, which remained dominant for an unusually long time also, was again excluded from the analysis. Except for the overall time scale, intermittent and continuous presentation therefore resulted in very similar sequences of dominance periods: an atypically long first period followed by periods of Gamma distributed duration. This close correspondence suggests that similar mechanisms govern phenomenal alternations in intermittently and continuously presented displays.

Experiment 2: Appearance reported, but largely unattended (poor attention)

Our second experiment characterized multistable perception under conditions of poor attention. As attention is not guaranteed to be completely withdrawn from the ambiguous
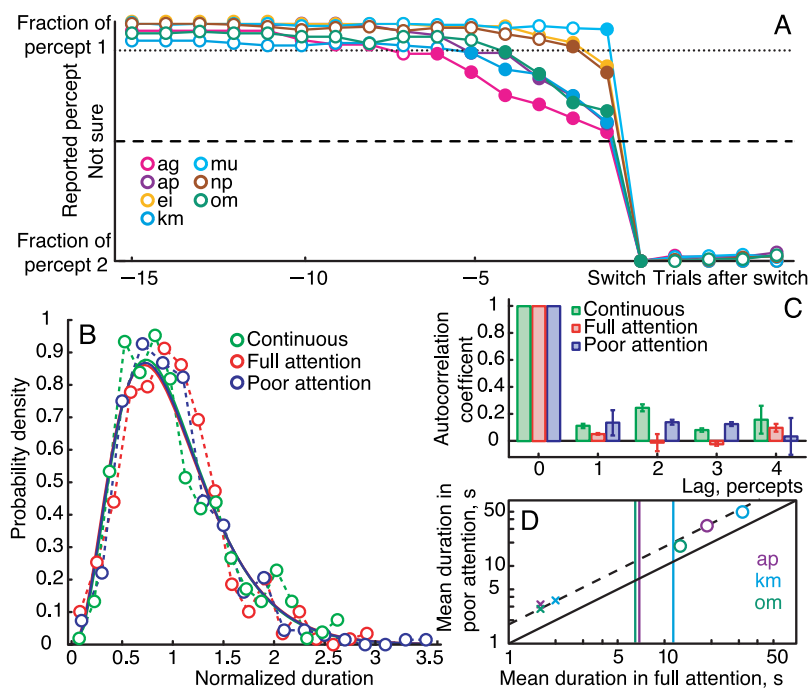

Figure 2. Stochastic rivalry of moving plaid. Time values in seconds are cumulative presentation times and do not include the intervals between stimulus presentations. (A) Phenomenal appearance in the trials preceding and following a perceptual reversal (full attention, 7 observers). Fraction of positive reports ("transparent" or "coherent") as a function of trial position relative to the switch. In trials preceding the switch, the fraction decreases ("unsure/transition" reports increase) for most observers, revealing a transition phase (less than 75% positive reports, dotted line, solid circles). (B) Distribution of dominance times for three selected observers for continuous presentation (green), intermittent presentation with full attention (red), and intermittent presentation with poor attention (see text, blue). Mean dominance times normalized to unity. Gamma distribution fits (solid lines) yielded $\alpha_{cont} = 3.8 \pm 0.3$, $\alpha_{full} = 3.6 \pm 0.3$, $\alpha_{poor} = 3.7$ (0.3 (see Methods). In absolute terms, mean dominance times were 4.9 and 11.4 s for continuous presentation (coherent and transparent percept, respectively), 10 and 25.9 s for intermittent presentation with full attention, and 17.2 and 37.4 s with poor attention. (C) Autocorrelation coefficient for time series of dominance times, as a function of lag in numbers of percepts. (D) Comparison of mean dominance times (circles) and transition times (crosses) with full and poor attention for three observers. For comparison, mean dominance times for continuous presentation (vertical lines). The dashed diagonal marks the average difference between full and poor attention.

pattern, this condition has also been described as "near absence of attention" (Li, VanRullen, Koch, & Perona, 2002; Reddy, Reddy, & Koch, 2006; Reddy, Wilken, & Koch, 2004).

To establish the time course of phenomenal alternations with poor attention, we instructed observers to report on both parts of the display and to carry out central task and peripheral task concurrently. This necessitated three responses to each presentation (two for rotating shapes and one for the moving plaid) and imposed a considerable memory and decision load. A control experiment, in which the moving plaid changed its physical direction of motion, verified that three selected observers could combine all tasks without significant interference (Figure A2A, Appendix A). In the experiment proper, the moving plaid retained its direction and changed only in phenomenal appearance. As instructions stressed the preeminent importance of the central task (see Methods), we expected observers to focus attention primarily, but not necessarily exclusively, on the central task. We relied on diminished central task performance to flag any slackening in this focal allocation of attention. Only three most experienced observers (A.P., K.M., and O.M.) participated in this experiment.

Figure 3 shows average trial histograms of central task and peripheral task reports for 15 trials leading up to, and
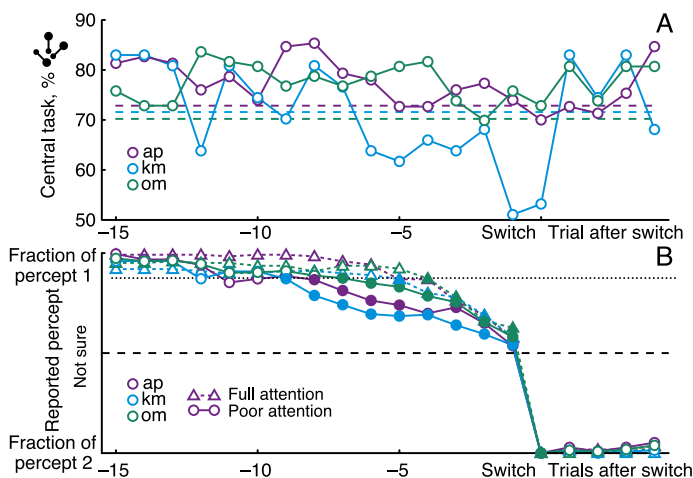

Figure 3. Rivalry reported but poorly attended. Observers divide attention unequally between central and peripheral task, giving priority to the central task. (A) Central task performance in trials preceding and following perceptual reversals, for three observers. For comparison, dashed lines indicate performance level one standard deviation below average. (B) Phenomenal appearance of moving plaid with poor attention (circles). For comparison, data from Figure 2A with full attention (triangles). Fraction of positive reports ("transparent" or "coherent") as a function of trial position relative to the reversal. Prior to reversals, the fraction decreases, revealing an extended transition phase (less than 75% positive reports, dotted line, solid circles).

4 trials following, perceptual reversals in three observers. Central task performance remained consistently high, staying within a $p = .05$ corridor around the reference perfor-mance of $P_{full} = 75\%$ in 98% of all presentations (Figure 3A, dashed lines). Only immediately prior to the reversal did central task performance dip significantly below P_{full} in two of three observers. Overall, however, the consistently high central task performance implied that attention to the peripheral task and the moving plaids remained scarce, justifying our characterization of the situation as one of poor attention. Trial histograms of peripheral reports revealed a high proportion of "unsure/ transition" responses prior to the reversal, indicating extended transition periods of intermediate phenomenal appearance (Figure 3B, circles). Compared to conditions of full attention (see above), poor attention prolonged transition times by approximately 58% (Figure 2D). The untypical aspects of central and peripheral reports in the transitional period leading up to a reversal would seem to be related. Either attention lapsed from the central task to initiate the phenomenal transition, or the intermediate phenomenal appearance of the transitional percept attracted the observers' attention and thereby interfered with central task performance.

Even under conditions of poor attention, the distribution of dominance times retained the typical characteristics of perceptual rivalry: it followed a Gamma distribution with $C_v \sim .5$ (Figure 2B) and it exhibited no correlation between successive periods (Figure 2C). However, mean dominance times were approximately 50% longer with poor than with full attention (73.3 trials for poor as compared to 48.8 trials for full attention, Figure 2D). The difference between the two distributions was highly significant ($p = 10^{-5}$, Wilcoxon rank sum test). Thus, attention had almost identical effects on transition times and dominance times. We conclude that poor attention stabilizes or, equivalently, that full attention destabilizes ambiguous phenomenal percepts.

It is interesting to analyze this top-down effect of attention more closely and to compare bottom-up effects of stimulus intensity and stimulus duration. To this end, we increased plaid contrast in three steps from 5% to 50% and plaid presentation times in three steps from 300 ms intermittent to continuous. We compiled mean dominance durations separately for coherent and transparent percepts (Figure 4A), excluding the first percept (almost always coherent) from the analysis, as it tended to be exceptionally stable. Full attention destabilized both coherent and transparent percepts to a comparable degree, reducing mean dominance times by approximately 42% and 31%, respectively. Increased contrast destabilized the coherent percept by ~16% but stabilized the transparent percept by ~80% (Figure 4B). Increased presentation time destabilized coherent and transparent percept by ~52% and ~60%, respectively (Figure 4C). Thus, effect attention on perceptual stability
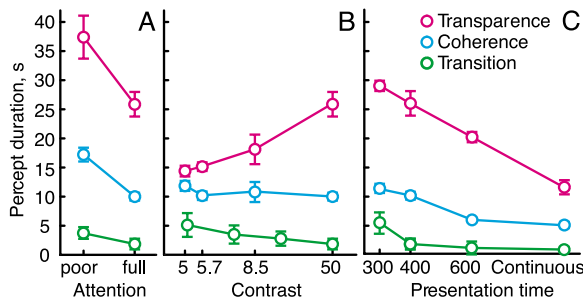
Figure 4. Effects of different manipulations on mean dominance time (cumulative presentation time) of coherent (cyan), transparent (magenta) and unsure/transition (green) percepts, average across all observers. (A) Poor attention (dual-task condition) and full attention (single-task condition). Contrast 50% and presentation time 400 ms. (B) Different stimulus contrasts (presentation time 400 ms). (C) Different presentation times (contrast 50%).

resembled the effect of longer presentation but not that of higher contrast.

Experiment 3: Appearance unreported and unattended (no attention)

The previous experiment showed that the restriction of attention does not stop phenomenal alternations: dominance periods become longer but their statistical variability remains the same. The transition phase between rivaling percepts, in which observers are "unsure" about the phenomenal appearance, also lasts longer (up to eight trials). However, the previous experiment did not completely remove attention from the ambiguous pattern. For at least some observers, attention tended to shift to the ambiguous pattern during its transition phase. This was evident from the fact that central task performance tended to be lower during the transition phase.

To discourage attention shifts even further and, if possible, to rule out attention shifts completely, we asked observers to ignore the ambiguous pattern and report only the central task for a number of consecutive presentations. As the phenomenal appearance of the peripheral pattern remained unreported during these presentations, we expected that it would be easier for observers to fully attend to the central task and to achieve a consistently high level of performance in this task.

One ambiguous pattern used in this experiment was the moving plaid described above (Figure 1C). To anticipate one aspect of the results, perceptual alternations were slow, each percept lasting 93 presentations or 130 s total time (37 s presentation time) on average (seven observer), or 80.5 trials or 32.2 s presentation time for three selected observers. For both observer groups, the distribution of dominance durations was significantly different from that obtained with full attention condition (seven observers:

$p = 10^{-10}$; 3 observers: $p = 10^{-8}$, Wilcoxon rank sum test). Mean dominance times were somewhat longer with no attention than with poor attention, but this difference did not reach significance (73 vs. 80.5 trials; $p = .085$, Wilcoxon rank sum test). As before, possible observer responses were "transparent," "coherent," and "unsure/ transition."

Observers focused on one task at a time, performing the central task (only) for 10 consecutive presentations and then changed to the peripheral task (only) for two presentations, repeating this sequence up to 20 times (Figure 1F). Observers were prompted to switch tasks by the omission of central targets in the two peripheral task presentations. In other words, observers performed the central task when central targets were present (10 of 12 presentations) and carried out the peripheral task when central targets were absent (2 of 12 presentations). The aim of this design was to keep attention away from the ambiguous pattern during most presentations while still monitoring reversals of phenomenal appearance at regular intervals.

As reversals were rare, phenomenal appearance was unlikely to switch twice during a single 10-trial sequence in which it remained unreported ("unreported period"). Indeed, comparing peripheral reports before and after unreported periods, we found that the phenomenal appearance of moving plaids ("coherent" or "transparent") switched only in 13% of the unreported periods recorded (1.640 of 11.360 periods in seven observers).

Where did attention focus when phenomenal appearance switched during an unreported period? Did attention lapse at least once from the central task and swerve to the peripheral task? Or did attention adhere unwaveringly to the central task? To decide this crucial point, we analyzed central task performance in unreported periods for individual observers (Figure 5A), comparing unreported periods with and without a switch in phenomenal percept (observer average $P_{switch} = 80.63\%$ correct, $P_{no\ switch} = 80.15\%$ correct, respectively) and control blocks in which only the central task was being performed (observer average $P_{ref} = 80.05\%$ correct). The value of P_{switch} was not significantly below P_{ref} for any observer ($p = .43, .13, .54, .43, .72, .98$) and significantly above P_{ref} for one observer ($p = .017$).

Even more revealing is the maximally possible number of attention lapses; that is, the number of trials in which attention could have shifted away from the central task, given the observed level central task performance (see Methods). To calculate this number, we assume that n lapses (shifting attention for 200 ms to the moving plaid) would have resulted in n chance responses per 10-trial period, reducing average central task performance by $n * (P_{ref} - 50\%\ correct) / 10 \cong 3.0\% * n$. The value of n consistent with the observed values of P_{switch} and P_{ref} was $n = -0.24$ for the average observer and $-1.09, -0.51, 0.51, -0.19, -0.48, 0.12$, and -0.05 for individual observers (Figure 5A). Thus, if attention lapsed at all, it
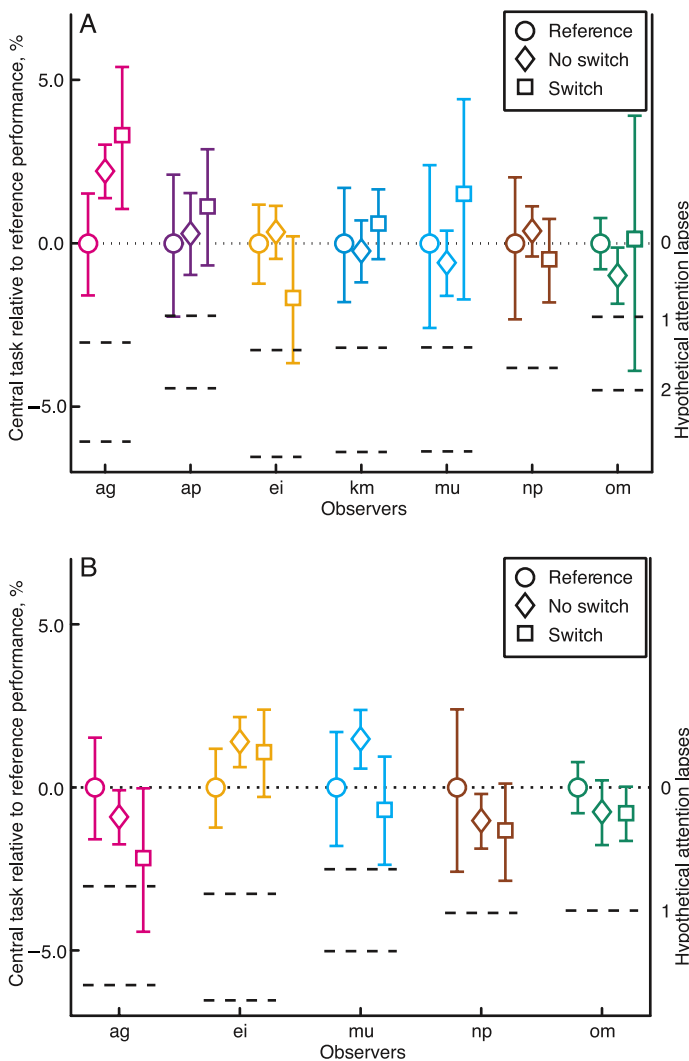
Figure 5. Rivalry unreported and unattended. (A) Results for moving plaids. Central task performance of individual observers and $p = .05$ intervals of confidence, comparing "unreported periods" with and without a phenomenal reversal ("switch" and "no switch," respectively), relative to performance in control blocks ("ref"). Dashed lines show expected performance if attention had lapsed in 1 or 2 trials during every 10-trial period (right abscissa). For every observer, the results show less than one lapse of attention per "unreported" period. (B) Results for depth-from-motion cylinders. Central task performance of individual observers and $p = .05$ intervals of confidence.

lapsed on average less often than once per unreported period with phenomenal reversal.

But did phenomenal reversals actually take place during unreported periods (i.e., with no attention), or did they perhaps occur mostly during the two-trial-long "reported periods" (i.e., *with* full attention)? To allay this concern, we compared the observed response proportions in "reported periods" with the response proportions expected based on Experiments 1 and 2. Under conditions of full attention (Experiment 1), the probability of initiating or

completing a phenomenal reversal on any given trial was $P_{full} = 0.030$, whereas under conditions of poor attention (Experiment 2), the probability was $P_{poor} = 0.017$. The average length of transition periods under conditions of poor attention was $N_{transition} = 6$. Assuming that transitions continue to be initiated during both "unreported" and "reported" periods in Experiment 3, and that the probabilities of initiation remain similar to Experiments 1 and 2, we may calculate the expected proportion of responses as follows:

$$P_{reversal} = (10 - N_{transition} + 1)P_{poor} = 0.085, \qquad (6)$$

$$P_{transition} = 2\,P_{full} + (N_{transition} + 1)P_{poor} = 0.145, \qquad (7)$$

where $P_{reversal}$ is the expected probability of a complete phenomenal switch occurring during 10 trials of unreported periods and $P_{transition}$ is the expected probability of transition being reported during two-trial-long "report periods." As the observed values for $P_{reversal}$ and $P_{transition}$ were 0.069 ± 0.034 (three observers) and 0.124 ± 0.051 (three observers), respectively, there is no indication that reversal probability increased during "reported periods." We conclude therefore that the phenomenal appearance of the moving plaid reversed in spite of the complete absence of attention shifts, in at least some unreported periods.

An analysis of reaction times confirmed that, even during phenomenal reversals, attention remained fully focused on the central task. Average reaction times were virtually identical in unreported periods with a reversal (611 ± 21 ms), unreported periods without a reversal (612 ± 20 ms), and in control blocks (611 ± 19 ms). None of the observed differences was significant ($p = .4, p = .78$).

To replicate this result with another kind of ambiguous pattern, we conducted a separate experiment with a depth-from-motion stimulus (Figure 1D). The orthographic projection of a rotating surface created an illusory depth, the phenomenal appearance of which alternated between the two possible senses of rotation in depth (Wallach & O'Connell, 1953). For this pattern, possible responses were "front surface moves left," "front surface moves right," and "unsure/transition." The intermittent presentation of this pattern followed a slightly different schedule (400 ms present, 500 ms absent), and each sense of rotation persisted for 70.5 presentations or 63 s total time (28 s presentation time) on average. Depth-from-motion stimulus, unlike moving plaids, exhibited very brief transitions, which were never reported to take longer than a single trial.

Under no attention condition, perceptual alternations were again slow—121 presentations (48.4 s presentation time), 72% longer than in full attention condition for the same pattern. The phenomenal appearance ("front surface moves left" or "front surface moves right") changed in

10% of the unreported periods recorded (1.179 of 11.800 periods total in five observers).

Central task performance (Figure 5B) in periods with a switch (P_{switch} = 82.1% correct), periods without a switch ($P_{no switch}$ = 83.2% correct), and in control blocks (P_{ref} = 83.03% correct) did not differ significantly for any observer (p = .1, .25, .58, .36, .58). The number of attentional lapses per unreported period with phenomenal switch consistent with these values was n = 0.217 in the observer average and 0.72, −0.33, 0.27, 0.34, and 0.085 for individual observers.

As we did not establish P_{poor} for the depth-from-motion stimulus, we cannot compute the expected probability of switch occurring during 10 no-attention trials ($P_{reversal}$). Fortunately, the KDE stimulus yielded exceptionally short transitions, lasting one trial at most (not shown). Thus, transitions initiated during the "unreported period" were less likely to "spill over" into the "reported period." From full attention measurements (see above), we expected the probability of transition reports in the "reported period" to be $P_{transition}$ = 0.028. The observed value of 0.031 ± 0.016 (five observers) was slightly but not significantly higher. The probability of reversal reports $P_{reversal}$ = 0.068 ± 0.035 (five observers) was substantially higher, reinforcing our conclusion that the depth-from-motion stimulus, too, reversed its phenomenal appearance in the complete absence of attention shifts.

An analysis of reaction times also failed to reveal any tendency for attention to lapse from the central task during phenomenal reversals. Average reaction times were 501 ± 11 ms unreported periods with a reversal, 502 ± 11 ms in unreported periods without a reversal, and 509 ± 9 ms in control blocks. None of the observed differences reached significance (p = .5; p = .33).

Finally, to avoid misunderstandings, we note that an absence of attention shifts does not necessarily imply lack of awareness (Braun et al., 2001): observers mentioned consistently that they tended to notice when phenomenal appearance switched during unreported trials and that the transition tended to occur slowly, over several trials. In this detail, their subjective reports were consistent with objective evidence from the first experiment.

Discussion

It has long been hypothesized that attention shifts might contribute in some way to the alternations of phenomenal awareness that are characteristic for ambiguous or rivalrous stimulus patterns (von Helmholtz, 1866/1925). By selecting a stimulus aspect other than the currently dominant one, attention could alter the associated neural activities, thereby tipping the balance and prompting a switch of phenomenal awareness. Consistent with this possibility, shifts of attention have been found to influence dominance (Meng & Tong, 2004; Mitchell et al., 2004) and to modulate overall reversal rates (van Ee et al., 2005), although the degree of attentional influence varied between studies. Moreover, several studies have found neural activity in areas associated with attentional control to transiently increase during phenomenal reversals (Inui et al., 2000; Kleinschmidt et al., 1998; Lumer et al., 1998; Sterzer et al., 2002; Struber et al., 2000).

However, the present results suggest that, at least under the present conditions, phenomenal reversals occur spontaneously, without any involvement of attention. Accordingly, it would appear that attention does not play a necessary causal role in prompting phenomenal reversals. But does the evidence presented here really compel this negative conclusion?

Reversals not prompted by attention

There is little doubt that Experiment 3 prevented attention from shifting to the ambiguous pattern for a number of consecutive presentations ("unreported periods"). Central task performance was a sufficiently sensitive indicator of attentional allocation to ensure this point (see Appendix A). Some questions remain, however, as to how phenomenal appearance of the ambiguous pattern developed while the latter remained unattended and unreported. The most important of these is whether phenomenal reversals indeed did occur during "unreported periods," that is, under conditions of no attention, or whether phenomenal reversals remained suspended during the 10-trial "unreported periods," only to accelerate and proceed precipitously during the two-trial "reported periods." A closely related question is whether phenomenal reversals proceeded gradually, with transition periods lasting several trials.

Introspectively, observers reported extended transition periods stretching into both "reported" and "unreported periods" during Experiment 3. Consistent with these subjective reports, the average duration of dominance period exhibited comparable values of 73.3 ± 6 in Experiment 2 (poor attention) and 80.5 ± 10 trials in Experiment 3 (no attention) and the difference did not reach significance (p = .085, Wilcoxon rank sum test). Moreover, as detailed in Results, the proportion of reports from the two-trial "reported periods" indicating either a "completed reversal" or a "transition phase" corresponded closely to the proportions obtained in Experiment 2 under conditions of poor attention. Finally, the comparison with Experiment 1 (full attention) leaves no doubt that removing attention from ambiguous patterns tends to lengthen rather than shorten transition periods, adding a further argument against precipitous transitions during "reported periods." Accordingly, both subjective and objective evidence suggest that the time course of phenomenal reversals was fundamentally similar under conditions of no attention and poor attention. We are thus

compelled to conclude that, at least under the conditions investigated here, phenomenal reversals did occur without attention ever shifting to the ambiguous pattern.

Alternative causes of reversals

What other process, if not attention, could limit the stability of phenomenal appearance in ambiguous visual scenes? One possible source of instability is spike-frequency adaptation, that is, the decrease in responsiveness that occurs during prolonged stimulation of visual cortical neurons (Laing & Chow, 2002; Wilson, 2003). Due to spike-frequency adaptation, the neural activity associated with a dominant percept is expected to diminish over time, eventually allowing a competing percept to dominate phenomenal awareness. Spike-frequency adaptation is mediated by active cellular mechanisms such as, for example, a slow hyperpolarization of neurons ($\tau = 1$–10 s) by Ca^{2+}-activated K^+ conductances (Sanchez-Vives, Nowak, & McCormick, 2000). Consistent with this hypothesis, presenting ambiguous stimuli in ways that minimize adaptation considerably slows perceptual rivalry (Blake, Sobel, & Gilroy, 2003). Another possible source of instability for visual representations is neural noise (Horsthemke & Lefever, 1984; Kim et al., 2006). If the neural activity associated with a dominant percept represents one of several possible attractor states in a competitive network, activity fluctuations will cause probabilistic transitions between attractor states, placing a statistical limit on dominance times (Brunel & Hakim, 1999; Shpiro et al., 2007; Wong & Wang, 2006).

Comparison of top-down and bottom-up effects

A number of studies have characterized the effect of attention on multistable perception or binocular rivalry. To control attention, these studies used an intermittent concurrent tasks [self-paced mental arithmetic (Reisberg & O'Shaughnessy, 1984); odd-color search spaced 3 s apart (Leopold, Fitzgibbons, & Logothetis, 1995); and motion discriminations spaced 6 s apart (Paffen, Alais, & Verstraten, 2006)], whereas the ambiguous pattern was presented continuously. Evidently, the intermittent nature of the concurrent tasks employed could not guarantee the complete withdrawal of attention from ambiguous patterns. Perhaps due to the less-than-complete control over attention, the results were not entirely consistent: reduced attention increased the perceptual stability of ambiguous patterns in two cases (Paffen et al., 2006; Reisberg & O'Shaughnessy, 1984) and decreased stability in one case (Leopold et al., 1995). Differential effectiveness of attention control may also account for quantitative differences in the results: when Paffen et al. (2006) withdrew

attention from the ambiguous stimulus with their "hard" secondary task, they observed a 25% increase in dominance times. In contrast, we observed 64% (moving plaid) and 72% (kinetic-depth-effect) longer dominance times in our Experiment 3.

Another relevant type of study induced observers to attend selectively to one of two rivaling patterns (Chong & Blake, 2006; Mitchell et al., 2004). This manipulation significantly increased both the dominance probability and the dominance duration of the attended pattern.

As attention is known to enhance neural responses to visual stimulation (Boynton, 2005; Reynolds & Chelazzi, 2004), the outcomes of both types of studies are readily understood by in terms of attention increasing effective stimulus contrast. Phenomenal alternations may be slowed down either by lowering the contrast of an ambiguous stimulus (Levelt, 1965) or by removing attention from that stimulus (Paffen et al., 2006; Reisberg & O'Shaughnessy, 1984; Experiment 2 of this study). The degree of dominance of one pattern over another may be increased either by increasing its contrast (Levelt, 1965; Mamassian & Goutcher, 2005) or by selectively attending to that pattern (Chong & Blake, 2006; Mitchell et al., 2004).

Presumably, phenomenal alternations in ambiguous patterns reflect competing activations at various levels of the visual thalamus and cortex (Kim et al., 2006; Laing & Chow, 2002; Wilson, 2003). It is thus not surprising that any modulation of these neural levels, whether caused bottom-up by stimulus parameters or top-down by selective attention, should alter the time course of perceptual alternations.

A closer analysis of our results (Figure 4) suggests, however, that the similarities between top-down and bottom-up effects are more qualitative than quantitative. The presumed dependence of dominance times on neural activity is summarized by the approximate formula

$$T_1 = \propto \frac{A_1^\alpha}{A_2^\beta}, \alpha < \beta, \tag{8}$$

$$T_2 = \propto \frac{A_2^\alpha}{A_1^\beta}, \tag{9}$$

where T_1 and T_2 are the mean dominance times and A_1 and A_2 are the activities associated with, respectively, percepts 1 and 2. This formula captures both the fact that a balanced increase of activity destabilizes both dominant and nondominant percepts (i.e., accelerates phenomenal alternations) and the fact that an unbalanced increase destabilizes the nondominant percept while stabilizing the dominant percept (Levelt's second proposition; Levelt, 1967).

In our experiment on moving plaids (Experiments 1 and 2), both the effect of attention and the effect of increased

presentation time conformed to this formula, in that increased activity destabilizes (reduces dominance times) for both dominant (coherent) and nondominant (transparent) percepts (Figures 4A and 4C). However, the effect of increased contrast differed from expectations in that it stabilized the dominant (coherent) percept but destabilized the nondominant (transparent) percept (Figure 4B). In other words, increased contrast mimicked an *unbalanced* increase in the activity of the dominant percept! Perhaps the impact of higher contrast was filtered by a winner-take-all competition at earlier levels of processing (Cook & Maunsell, 2004), so that it added mostly to the activity associated with the dominant percept.

These results suggest that all three manipulations—heightened attention, longer presentation time, and higher stimulus contrast—modulate the activity of competing representations. However, attention appears to act on these representations more directly than contrast does, as its impact does not seem to be distorted by earlier levels of processing.

Transient cortical activations

As mentioned, there is evidence from several functional imaging (Inui et al., 2000; Kleinschmidt et al., 1998; Lumer et al., 1998; Sterzer et al., 2002) and electrophysiological studies (Struber et al., 2000) that phenomenal reversals are associated with transient activations in frontoparietal cortex. However, due to the slow time course of hemodynamic signals and the variability of observer's reaction times, the precise timing of this activation relative to the phenomenal reversal remains unclear (Sterzer et al., 2002; Struber et al., 2000). In the light of the present results, it seems possible that these transient activations reflect attention capture by changed phenomenal appearance. Accordingly, we predict that a careful analysis of relative timing will show that transient activations follow, rather than lead, phenomenal reversals.

Conclusions

We have studied the time course of multistable perception while tightly controlling the allocation of attention. By combining intermittent presentation of an ambiguous stimulus with a synchronized concurrent task, we were able to either continuously withdraw more than 90% of attention (Experiment 2) or to completely withdraw attention for 10 successive presentations (Experiment 3). Our results confirm earlier reports that the effect of attention is qualitatively similar to the effect of increased stimulus contrast, in that both manipulations accelerate the phenomenal alternations that characterize multistable perception. However, in quantitative terms, the effects of

attention and increased contrast are not interchangeable, at least not for the type of ambiguous stimulus studied here (moving plaids). Our results rule out an additional, causal role of attention in phenomenal reversals and in particular demonstrate that spontaneous phenomenal reversals occur even when attention is prevented from shifting to the ambiguous pattern. In short, no attention shift is needed to prompt a phenomenal reversal. We do not rule out, and indeed think it likely, that voluntary shifts of attention do sometimes trigger phenomenal reversals. However, our findings would seem to suggest that most phenomenal reversals occur spontaneously, without the involvement of attention or other mechanisms of voluntary control.

Appendix A

Attention is an elusive concept and no operational definition commands general agreement across all branches of psychophysics and cognitive psychology. Thirty years ago, Sperling et al. have proposed the limited, but divisible, capacity of visual attention as a suitable operational definition (Sperling & Dosher, 1986; Sperling & Melchner, 1978). This approach provides a useful way to control the division of attention between concurrent visual tasks (Braun, 1998a; Braun et al., 2001). Importantly, we have shown that the results of this approach are self-consistent, in that the attention demand of Task A measured in combination with Task B is identical to the demand measured in combination with Task C (Lee, Koch, & Braun, 1999).

When two concurrent visual tasks compete for visual attention, their respective demands on attention are revealed by the way in which observers can trade performance on one task against performance on the other. By instructing observers either to give priority to one task or to the other task or equal priority to both, the trade-off function, which is usually termed the "attention-operating characteristic" or AOC (Sperling & Melchner, 1978), can be established. Assuming that each task possesses a "performance resource function" (PRF), which describes its level of performance as a function of the fraction of attention allocated to it, the PRFs of two concurrent tasks will uniquely determines the AOC of this particular task combination. In many cases, an empirically measured AOC will constrain the two underlying PRFs sufficiently well, so that the PRFs can be reconstructed (Lee et al., 1999). Of particular interest are tasks with an approximately linear PRF, as their performance increases approximately proportionally with the amount of attention allocated. The level to which such a task is performed by a particular observer in a particular situation measures the average fraction of attention allocated to the task.

This dual-task approach has been used extensively to investigate visual performance under conditions of poor attention (Braun, 1994, 1998b; Braun & Julesz, 1998;

Braun & Sagi, 1990; Lee et al., 1999; Li et al., 2002; Reddy et al., 2006; Reddy et al., 2004; Tsuchiya & Braun, 2007). Although many attributes of poorly attended stimuli remain discriminable to practiced observers, the almost complete absence of attention is nevertheless evident in significantly raised thresholds (Lee et al., 1999; Tsuchiya & Braun, 2007). Particularly relevant to the present context is that fact that dual-task situations prevents even involuntary shifts of attention to visual onsets at unexpected locations (Braun, 1998b).

Attention demand of the central task

This study combines an attention-demanding central task with subjective reports on an ambiguous pattern presented in the periphery of the display. We measured performance levels of the central task and inferred the fraction of attention allocated to that task, reasoning that the remaining fraction of attention constitutes the maximal amount of attention available to the ambiguous pattern. To infer fraction of attention from task performance, we had to establish the "performance resource function" of the central task.

To this end, we paired the central task with an alternative peripheral task, chosen for its attention demand (as we wished to create a severe competition for the limited attentional resources). Although numerous peripheral tasks would have been suitable, we chose the discrimination of a slowly rotating shape, as it requires a comparatively long presentation time (400 ms). Observers were required to concurrently discriminate the rotation of an ellipse (major and minor axis 2.7° and 2.4°, respectively), which appeared for 400 ms at random locations of 6° eccentricity and rotated either clockwise or counterclockwise. Rotation speed determined difficulty task (observer average of 0.6 cps). Observers reported ellipse rotation after reporting on the central task, pressing "j" for clockwise or "f" for counterclockwise rotation. In separate blocks of trials, observers were instructed to either give priority to the central task, the *ellipse task,* or equal priority to both tasks (*dual-task performance*). In yet further blocks of trials, observers performed only one task and ignored the other (*single-task performance*). Each block consisted of 50 trials.

The results scattered along a nearly linear trade-off in the respective performances of central and peripheral task (Figure A1A). This AOC shows for both tasks that maximal performance can be attained only with full attention. Using a maximum likelihood procedure (see Methods), we inferred performance resource functions for both tasks (Figures A1B and A1D). Due to the large amount of data (105 single-task and 239 dual-task blocks), confidence intervals were rather narrow. The central task reached its maximal performance level (single-task performance) when 92–100% of attention were allocated to it (Figure A1C). More important, its performance fell significantly short of this level when as little as 6.2% of

attention was withdrawn (e.g., allocated to the peripheral task; Figure A1B). This established central task performance as a sensitive measure of attentional allocation.

Task load experiment

Even when attending fully to one task, practiced observers can discriminate many attributes of salient
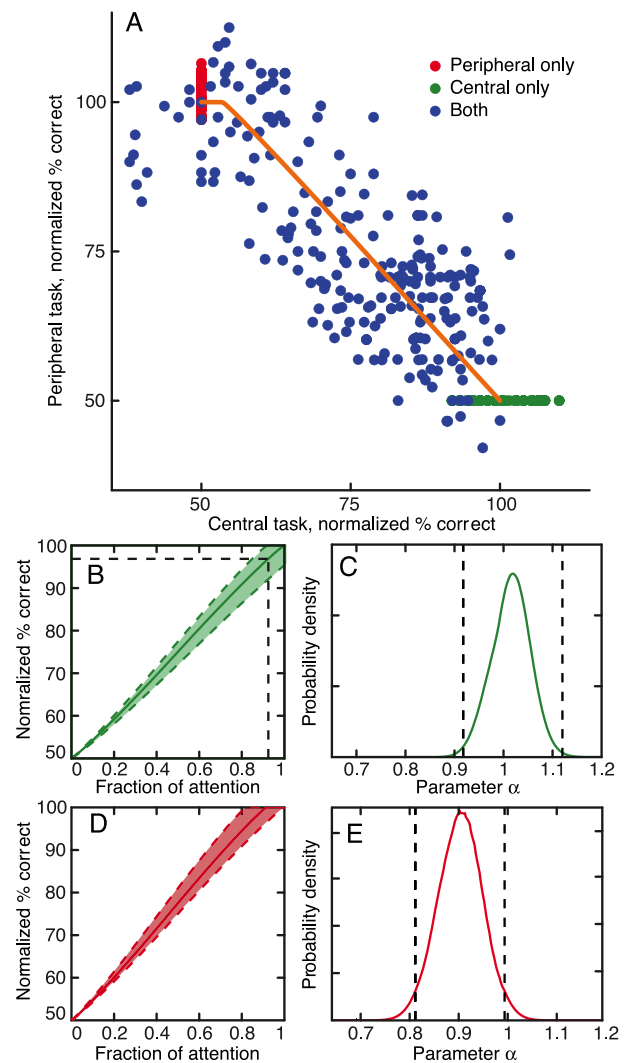
Figure A1. Experiment to establish the attention demand of the central task (3 observers). In the peripheral task, observers discriminate ellipse rotation. (A) Results from 69 blocks central task only (single-task, green), 36 blocks peripheral task only (single-task, red), and 238 blocks of both tasks together (dual-task, blue). Dual-task results are fitted with an attention-operating characteristic (sold line). (B) Family of well-fitting performance resource functions for central task ($p = .05$). A statistically significant ($p = .05$) performance drop corresponds to a decrement of 6.2% of attention (dashed lines). (C) Likelihood distribution of parameter $\alpha_{central}$. (D) Family of well-fitting performance resource functions for peripheral task ($p = .05$). (E) Likelihood distribution of parameter $\alpha_{peripheral}$.

stimuli elsewhere in the display (Braun, 1998a). This "vision outside the focus of attention" forms the basis of our approach. In the present context, we wished to establish that this "vision outside" extends also to the phenomenal appearance of an annular moving plaid. To this end, we devised a discrimination task concerning the direction of motion of an annular moving plaid (similar to the moving plaids used in the main experiment). Specifically we used two types of plaids, one coherent (40° angle between components) and one transparent (175°
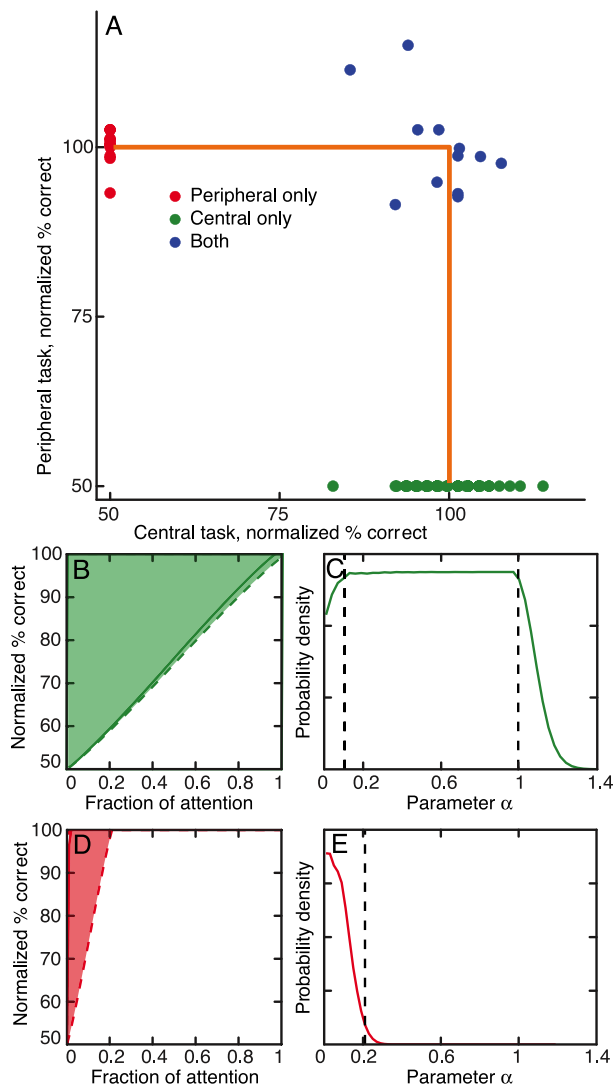

Figure A2. Task demand experiment (3 observers). In the peripheral task, observers discriminate the physical direction of plaid motion. (A) Results from 40 blocks central task only (single-task, green), 10 blocks peripheral task only (single-task, red), and 12 blocks of both tasks together (dual-task, blue). Dual-task results are fitted with an attention-operating characteristic (sold line). (B) Family of well-fitting performance resource functions for central task ($p = .05$). (C) Likelihood distribution of parameter $\alpha_{central}$. (D) Family of well-fitting performance resource functions for peripheral task ($p = .05$). (E) Likelihood distribution of parameter $\alpha_{peripheral}$.

angle). Both plaids were unambiguous in that no spontaneous reversals occurred. The further increase the similarity between this control situation and our main experiment, the order of appearance of the two pattern types duplicated the responses ("coherent" or "transparent") in a sequence of trials of the main experiment. Observers reported first on central task and then indicated whether physical plaid motion was closer to vertical (pressing "j") or closer to horizontal (pressing "f"; dual-task performance). In separate blocks of trials, observers reported only on one task and ignored the other (single-task performance). The number of trials per block varied between observers (200–600).

The results showed dual-task performance to be little different from single-task performances for either task (Figure A2A). Observers had no problem identifying direction of plaid motion while allocating all of their attention to the central task. In principle, such a lack of task interference is an ambiguous result, as it is consistent with a low attention demand on the part of either one task, or the other task, or both. In our case, the maximum likelihood analysis of the results yields a narrow range of PFCs for the peripheral task (Figure A2D). Specifically, it reaches its maximal performance level (single-task performance) when just 0–20% of attention is allocated to it, implying that it requires little or no attention. Maximal likelihood estimation for central task show that maximal performance is reached when 12–100% of attention is allocated to it, reflecting the inherent ambiguity of the situation.

The lack of interference in the task load experiment shows that no resource limitations other than attention (such as, for example, short-term memory or response planning) prevent practiced observers from carrying out central and peripheral tasks concurrently in the main experiment. Therefore, any interference in the main experiment can be attributed to competition for attentional resources.

Methods

To analyze dual-task results, we postulated for each task a monotonically increasing PRF, of the form

$$
p(r) = \begin{cases} \dfrac{p(1)}{2}\left(\dfrac{2r}{\alpha}\right)^{\beta} & \text{if } 0 \le r \le \dfrac{\alpha}{2} \\[2ex] p(1) - \dfrac{p(1)}{2}\left(\dfrac{2(\alpha - r)}{\alpha}\right)^{\beta} & \text{if } \dfrac{\alpha}{2} < r \le \alpha, \\[2ex] p(1) & \text{if } \alpha < r \le 1 \end{cases}
$$

(10)

where $p(r) \in [0,1]$ is the performance as a fraction of the interval between chance (defined as 0) performance and

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single-task performance (defined as 1); $r \in [0,1]$ is the fraction of attention allocated to the task; and $p(1)$ is the maximal performance (single-task performance or performance with full attention). The parameter α determines the fraction of attention that suffices for maximal performance. The parameter β ($\beta \geq 1$) determines the linearity of the monotonic relation between attention and performance ($\beta = 1$—linear, $\beta = 2$—quadratic, etc.). For further details, see (Lee et al., 1999). The AOC is the curve ($p_{central}(r)$, $p_{peripheral}(1-r)$). To fit a given set of observations, we choose the AOC that maximizes the a posteriori likelihood of these observations.

For each set of parameters $\alpha_{central}$, $\beta_{central}$, $\alpha_{peripheral}$, $\beta_{peripheral}$, we calculated the likelihood of a given observation ($p_{central}$, $p_{peripheral}$), from normal distributions with means given by the closest AOC point ($p_{central}(r)$, $p_{peripheral}(1-r)$), and variances given by the empirical single-task variance ($\sigma_{central}$, $\sigma_{peripheral}$). The most likely parameter set was $\alpha_{central} = 1.00$, $\beta_{central} = 1.1$, $\alpha_{periphery} = 0.92$, and $\beta_{peripheral} = 1.1$ for the attention demand experiment, and $\alpha_{central} = 0.97$, $\beta_{central} = 1.1$, $\alpha_{peripheral} = 0.01$, and $\beta_{peripheral} = 1.1$ for the task load experiment. Likelihood distributions for $\alpha_{central}$ and $\alpha_{peripheral}$ were computed by fixing the other three parameters at their optimal values.

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Corresponding author: Alexander Pastukhov.
E-mail: alexander.pastukhov@nat.uni-magdeburg.de.
Address: Leipziger Str 44, 39120 Magdeburg, Germany.

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