

DISPARATE TIME-COURSES OF ADAPTATION AND FACILITATION IN MULTI-STABLE PERCEPTION

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Far from being “memoryless”, the phenomenal appearance of an ambiguous display depends in complex ways on the recent history of similar perceptions. Given several possible appearances, the continued dominance of one appearance mitigates against its renewed dominance at a later time. This “negative priming” effect is likely caused by neural adaptation. At the same time, continued dominance of one appearance mitigates in favor of its renewed dominance when stimulation resumes after an interruption. This “positive priming” effect may reflect some kind of neural facilitation. We have used a multi-stable, kinetic depth display to disentangle these positive and negative priming effects. We report that negative priming builds up and decays in seconds, whereas positive priming builds up in seconds and decays in minutes. Moreover, unambiguous displays induce negative, but not positive, priming. This difference, together with their disparate time-courses of recovery, render the two effects cleanly dissociable.

Keywords: ambiguous perception, multi-stable displays, structure-from-motion, sensory memory, neural adaptation, neural fatigue

INTRODUCTION

Ambiguous displays often elicit seemingly spontaneous alternations of phenomenal appearance (“perceptual multi-stability”, “binocular rivalry”, for reviews see (Tong et al., 2006; Blake and Logothetis, 2002; Leopold and Logothetis, 1999)). The alternations are irregular and their average rate differs widely between observers (Aafjes et al., 1966; Medith, 1967), types of multi-stable displays (Sheppard and Pettigrew, 2006; van Ee, 2005), or presentation

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modes (Leopold et al., 2002; Pastukhov and Braun, 2007; Orbach et al., 1963; Adams, 1954); ranging from less than one to more than ten seconds.

The underlying cause or causes of perceptual multi-stability remain unclear. Observers are able to exercise some degree of voluntary control over perceptual alternations (Toppino, 2003; Meng and Tong, 2004; Leopold and Logothetis, 1999), either by means of eye blinks (Leopold et al., 2002), by executing eye movements (Ross and Ma-Wyatt, 2004), or by shifting focal attention (Chong et al., 2005; Meng and Tong, 2004; Mitchell et al., 2004). However, perceptual alternations seem to occur even when these factors are excluded (Blake et al., 1971). When observers orient attention away from a multi-stable display, perceptual alternations slow by approximately 50%, but do not cease altogether (Reisberg and O'Shaughnessy, 1984; Paffen et al., 2006). This remains true even when attention is controlled very carefully and even brief attention shifts to the multi-stable stimulus are precluded (Pastukhov and Braun, 2007). For these reasons, it seems likely that perceptual alternations are an intrinsic feature of perceptual processing.

Indeed, most current models assume that the neural representation of ambiguous displays is intrinsically unstable (Wilson, 2003; Blake, 1989; Laing and Chow, 2002; Tong et al., 2006). Three potential sources of instability have been proposed. Firstly, mutual inhibition between neural representations of alternative perceptual states, which ensures that exactly one representation dominates awareness at any moment (Laing and Chow, 2002; Wilson, 2003). Secondly, neural adaptation of the currently dominant representation (and recovery of currently suppressed representations), which curtails dominance durations and perpetuates fluctuations of awareness (Kohler and Wallach, 1944; van Ee, 2009; Alais et al., 2010). Thirdly, neural noise may trigger spontaneous transitions between alternative representations (Moreno-Bote et al., 2007; Shpiro et al., 2007; Brascamp et al., 2006; Kim et al., 2006).

However, the phenomenal appearance of ambiguous displays is also subject to stabilizing influences. The intermittent presentation of an ambiguous display tends to stabilize phenomenal appearance, provided the 'intermissions' are long enough (Adams, 1954; Orbach et al., 1963; Leopold et al., 2002). Apparently, whichever appearance dominates prior to the intermission leaves a persistent bias and ensures its renewed dominance once stimulation returns. Indeed, more detailed studies show that this persistent bias reflects not merely the most recent dominant appearance but the entire prior history of perceptual alternations on the order of minutes (Pastukhov and Braun, 2008; Brascamp et al., 2008), for a review see (Pearson and Brascamp, 2008). The persistent bias in question has also been called a "sensory memory" (Pearson and Brascamp, 2008), but here we will use the term "facilitation".

The apparent coexistence of adaptation and facilitation during multi-stable perception raises a number of questions. How can both effects be dissociated? How can their characteristic time-constants be determined? What is their respective contribution to perceptual alternations? How do both effects interact? Any attempt to answer these questions is complicated by the fact that both are comparatively weak and therefore not readily observed during normal multi-stable dynamics. For example, the presumed role of neural adaptation predicts that particularly long dominance phases of one percept should tend to follow particularly short dominance phases of the same percept, and *vice versa*. Although numerous studies have failed to confirm this prediction during continuous viewing of a multi-stable display (Fox and

Herrmann, 1967; Borsellino et al., 1972; Walker, 1975; Leopold and Logothetis, 1999), we have recently used a more sensitive statistical approach to show that this is indeed the case (Pastukhov and Braun, 2011, see also van Ee 2009). Furthermore, the role of adaptation in multi-stability is readily evident after extensive adaptation to non-ambiguous (Wolfe, 1984; Blake et al., 1990; Nawrot and Blake, 1989; Petersik, 2002). Similarly, the role of facilitation is revealed when ambiguous displays are presented intermittently (Adams, 1954; Orbach et al., 1963; Leopold et al., 2002).

We have investigated adaptive and facilitative effects on multi-stable appearance, aiming to dissociate the two and to establish their respective time-constants. To this end, we adapted priming paradigms of earlier studies (Wolfe, 1984; Petersik, 2002) such as to independently characterize the negative and positive priming effects of adaptation and facilitation, respectively. Specifically, we determined how the appearance of a probe display is affected by the appearance of a preceding prime display. We were able to monitor the build-up of both priming effects by varying the prime duration and to monitor their decay by varying the duration of the ‘intermission’ between prime and probe. For the most part, our ambiguous displays relied on the kinetic depth effect (Wallach and O’Connell, 1953).

RESULTS

Observers viewed dots in planar motion (some moving left, some moving right, see Methods), but due to the kinetic depth effect (Wallach and O’Connell, 1953) perceived an illusory sphere rotating about its vertical axis. This display was perfectly ambiguous, as two directions of illusory rotations were equally plausible. Either left- and right-moving dots were perceived to form, respectively, the front- and back-surface of the sphere, or the situation was reversed (*Figure 1*, see Supplementary Movie 1). An unambiguously rotating sphere can be created by moving all dots in the same direction and by adding perspective cues (so that only a front surface is perceived, see Supplementary Movie 2).

When the ambiguous display was viewed for 2 minutes, perception alternated continually between the two directions of rotation. Mean dominance durations $\langle T_{\text{dom}} \rangle$ ranged from 1.2 s to 13 s amongst the 9 observers. To facilitate comparison between observers, we normalized

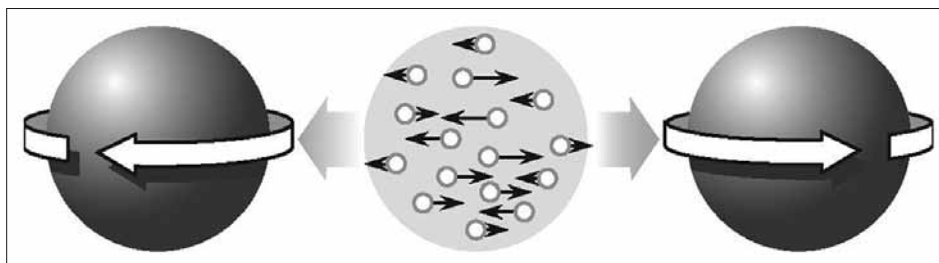


Figure 1. Ambiguous rotation in depth. Observers view dots in planar motion (center), but perceive an illusory volume rotating in one of two directions (left or right). Each dot is perceived to form part of either the front or the back surface of the volume.

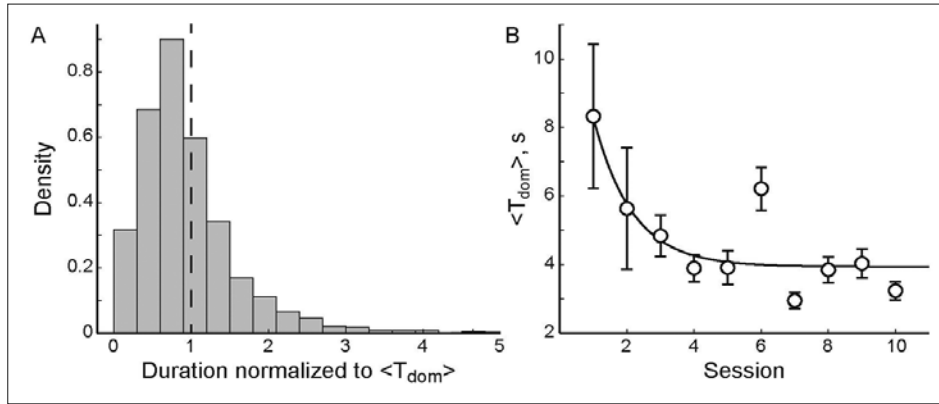


Figure 2. Mean dominance duration $\langle T_{\text{dom}} \rangle$. A) Distribution of dominance durations for nine observers, normalized to the mean dominance duration $\langle T_{\text{dom}} \rangle$. B) Representative decrease of $\langle T_{\text{dom}} \rangle$ over multiple sessions (observer JK).

all time intervals to the *mean dominance duration*, $\langle T_{\text{dom}} \rangle$, of each observer (Figure 2A). As dominance durations tended to decrease with practice (Suzuki and Grabowecky, 2007), we re-measured $\langle T_{\text{dom}} \rangle$ for every experimental session (Figure 2B). Over all observers and sessions, the average value of $\langle T_{\text{dom}} \rangle$ was 4.2 ± 4.1 seconds.

Experiment 1: build-up of adaptation

To monitor the build-up of adaptation, an unambiguous prime was followed immediately by an ambiguous probe (Figure 3A). Observers reported the perceived direction of the probe

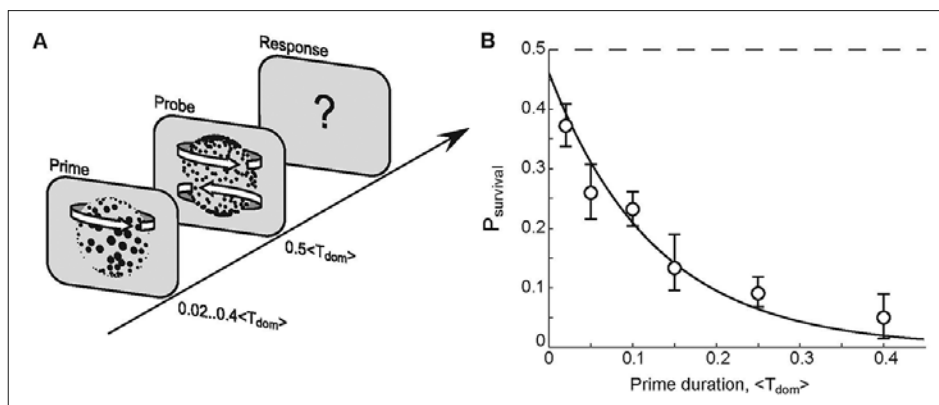


Figure 3. Build-up of adaptation A) Trial sequence (schematic). An unambiguous prime sphere was followed by an ambiguous probe sphere. Observers reported the perceived rotation of the probe. B) Probability P_{survival} that the rotation of the prime ‘survives’ and is perceived also in the probe. P_{survival} decreased from 0.5 (baseline) to 0 (maximal negative priming), revealing the build-up of adaptation to the prime.

sphere. Similar to earlier studies (Wolfe, 1984; Petersik, 2002), we measured the fraction of trials in which prime and probe spheres appeared to rotate in the same direction (P_{survival}), as a function of prime duration. The combined results of nine observers are shown in *Figure 3B*. Prime duration ranged from 0.01 to $0.4\langle T_{\text{dom}} \rangle$, and probe duration was $0.5\langle T_{\text{dom}} \rangle$. P_{survival} was typically below 0.5, revealing the negative priming effect due to adaptation to the unambiguous prime sphere.

As shown further below (Exp. 5), unambiguous prime spheres do not have a positive priming effect. Accordingly, these results reflect adaptation only and are not contaminated by facilitation.

In agreement with previous reports (Long et al., 1992; Petersik, 2002; Wolfe, 1984), longer prime durations increased negative priming (*Figure 3B*), reducing P_{survival} from 0.5 to almost 0. Fitting this decline with an exponential function, yielded a time-constant $\tau_{\text{rise}}^- = 0.13\langle T_{\text{dom}} \rangle$. Thus, the build-up of adaptation is rapid and essentially complete after $0.5\langle T_{\text{dom}} \rangle$.

Experiment 2: recovery from adaptation

To monitor the recovery from adaptation, we kept prime duration constant at $1\langle T_{\text{dom}} \rangle$ and inserted a blank period between prime and probe spheres (*Figure 4A*). The duration of the blank period ranged from 0.1 to $0.6\langle T_{\text{dom}} \rangle$. Observers once again reported the perceived rotation of the probe sphere.

The results from nine observers are shown in *Figure 4B*. Consistent with previous reports (Wolfe, 1984; Petersik, 2002), longer blank intervals decreased negative priming. This was reflected in an increase of P_{survival} from 0 (maximal negative priming) to 0.5 (no priming) and revealed the time-course of recovery from adaptation. Fitting an exponential function to this

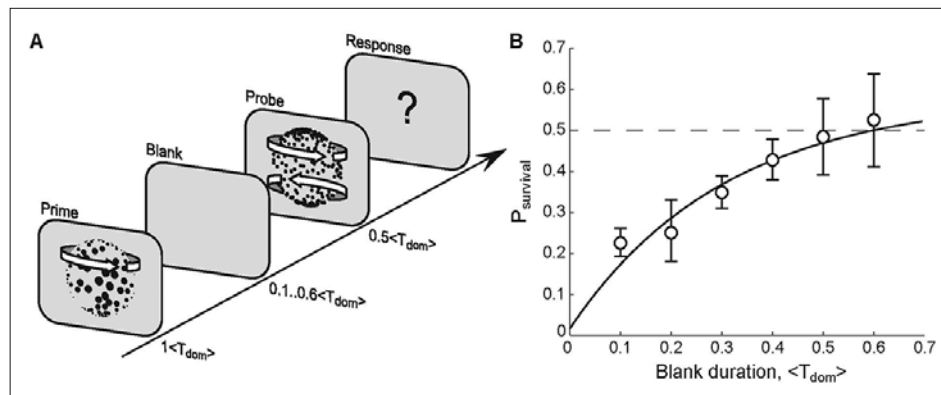


Figure 4. Recovery from adaptation A) Trial sequence (schematic). An unambiguous prime sphere was followed by a blank period and an ambiguous probe sphere. Observers reported the perceived rotation of the probe. B) Probability P_{survival} that the rotation of the prime ‘survives’ and is perceived also in the probe. P_{survival} increases from 0 (maximal negative priming) to 0.5 (baseline), revealing the recovery from adaptation to the prime.

time-course yielded a time-constant of $\tau_{\text{fall}}^- = 0.3\langle T_{\text{dom}} \rangle$. Accordingly, recovery from adaptation is also fast and essentially complete after $1\langle T_{\text{dom}} \rangle$.

Experiment 3: build-up of facilitation

To monitor the build-up of facilitation, we modified our procedure in several respects. Firstly, we used an ambiguous prime sphere, as all previous work on perceptual persistence has employed ambiguous displays. Secondly, we presented an unambiguous ‘pre-prime’ just prior to the prime proper, in order to control the latter’s phenomenal appearance. For, as shown in the previous experiment, negative priming from an unambiguous pre-prime virtually guarantees that the prime proper is perceived to rotate in the opposite direction ($P_{\text{survival}} \sim 0$). Thirdly, we introduced a blank interval of $2\langle T_{\text{dom}} \rangle$ between prime and probe spheres, in order to allow time for recovery from adaptation. As both prime and probe spheres were ambiguous, observers reported the apparent rotation of each sphere with a separate and independent response. P_{survival} was computed by comparing the reported appearances of prime and probe. This trial sequence is illustrated in *Figure 5A*.

If the phenomenal appearance of the prime induces a persistent bias, which subsequently facilitates an identical appearance of the probe, then P_{survival} should exhibit values above 0.5. The reader may ask why any facilitation from the prime should not be counteracted by an (opposite) facilitation from the pre-prime. However, because the pre-prime is unambiguous, it does not contribute any facilitation of its own (see Exp. 5 below).

The duration of the pre-prime was $1\langle T_{\text{dom}} \rangle$, prime duration ranged from 0.01 to $1\langle T_{\text{dom}} \rangle$, and probe duration was $0.5\langle T_{\text{dom}} \rangle$. The results from nine observers are shown in *Figure 5B*. P_{survival} was typically above 0.5, consistent with positive priming (facilitation) by the prime.

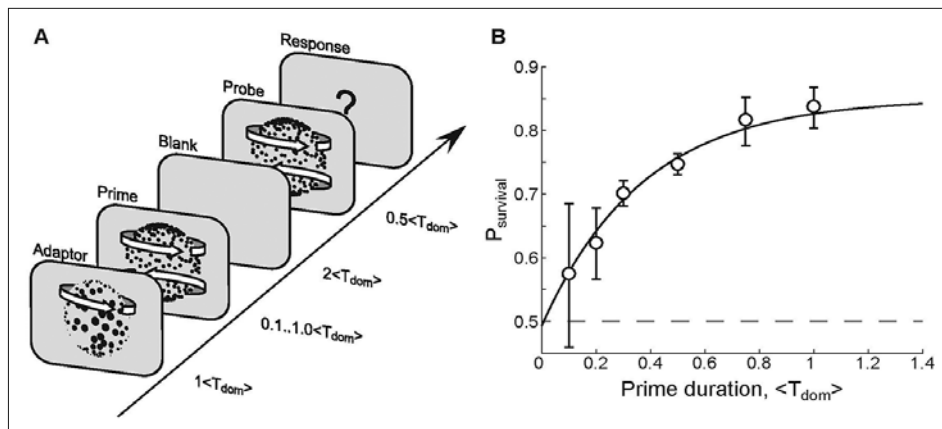


Figure 5. Build-up of facilitation A) Trial sequence (schematic). An unambiguous pre-prime sphere was followed by an ambiguous prime sphere, blank period and an ambiguous probe sphere. Observers reported the perceived rotation of prime and probe. B) Probability P_{survival} that the rotation of the prime ‘survives’ and is perceived also in the probe. P_{survival} increases from 0.5 (baseline) to 1 (maximal positive priming), revealing the build-up of facilitation to the prime..

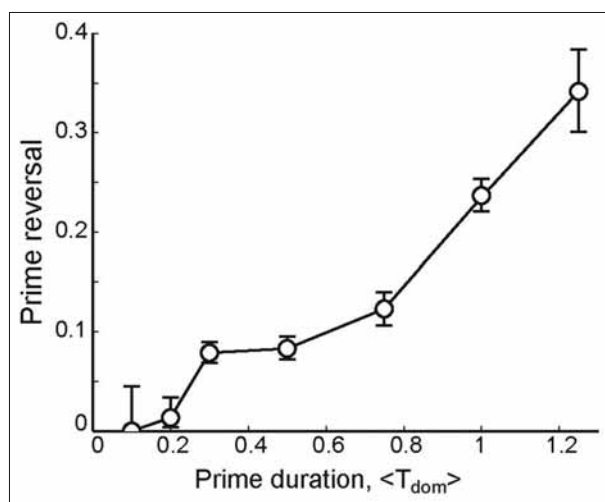


Figure 6. Spontaneous reversal of prime appearance (Exp. 3). Fraction of trials with a spontaneous reversal in the appearance of the ambiguous prime sphere and its dependence on the duration of prime presentation. Mean and standard error of nine observers.

sphere. Moreover, when the duration of the prime was increased, the value of P_{survival} also increased from 0.5 (baseline) to 1 (maximal positive priming), revealing the time-course of the build-up of facilitation. Fitting an exponential function to these results yielded a time-constant $\tau_{\text{rise}}^+ = 0.37\langle T_{\text{dom}} \rangle$.

When the presentation of an ambiguous prime approaches or exceeds $\langle T_{\text{dom}} \rangle$, there is a growing likelihood that the apparent rotation will reverse spontaneously (Figure 6). In this case, both appearances (before and after the spontaneous reversal) are expected to contribute to any facilitation. In general, facilitation from the initial appearance (before the reversal) should decrease as prime duration is further increased. Indeed, as prime duration lengthens from 1 to 1.25 $\langle T_{\text{dom}} \rangle$, P_{survival} decreased from 0.83 to 0.73 (data not shown in Figure 5B). To guard against contaminating our measurement of τ_{rise}^+ with this contravening trend, we limited our analysis to prime durations up to 1 $\langle T_{\text{dom}} \rangle$, discarding the approximately 14% of trials in which observers reported the ‘wrong’ prime rotation (i.e., same rotation as the pre-prime). Accordingly, we are confident that our measurements of τ_{rise}^+ are not compromised by spontaneous reversals of phenomenal appearance.

Experiment 4: recovery from facilitation

The previous experiment showed that ambiguous primes induce a facilitation, which persists for at least the duration of the blank period ($2\langle T_{\text{dom}} \rangle$). Indeed, significant positive priming has been reported after blank durations of up to 40 s (Leopold et al., 2002). Accordingly, we expected the recovery from a facilitated state to be a matter of minutes rather than seconds.

To monitor this recovery, we proceeded in analogy to previous experiments, but used longer blank intervals (Figure 7A). A trial consisted of an unambiguous pre-prime sphere (duration 1 $\langle T_{\text{dom}} \rangle$), an ambiguous prime sphere ($0.75\langle T_{\text{dom}} \rangle$), a blank interval ranging from 5 to 60 $\langle T_{\text{dom}} \rangle$ in duration and, finally, an ambiguous probe sphere ($0.5\langle T_{\text{dom}} \rangle$). An auditory cue alerted observers to the approaching end of the blank interval. Observers reported the

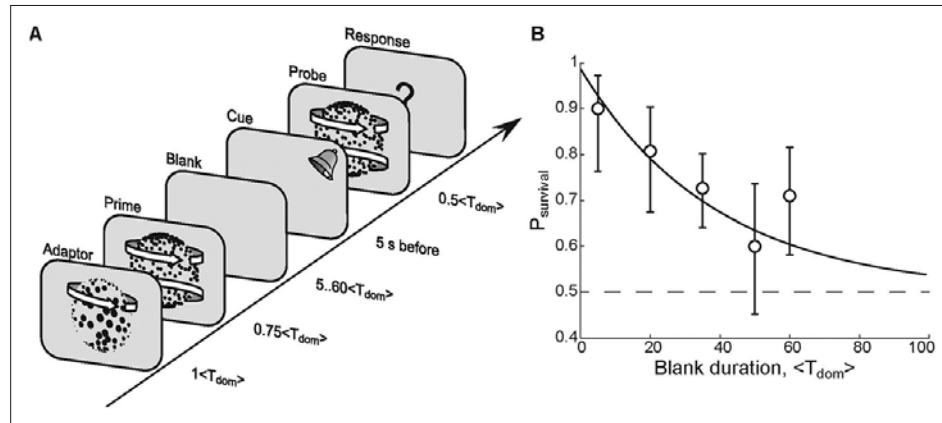


Figure 7. Recovery from facilitation A) Trial sequence (schematic). An unambiguous pre-prime sphere was followed by an ambiguous prime sphere, blank period (which could be as long as 4 min) with an auditory cue just before its end, and an ambiguous probe sphere. Observers reported the perceived rotation of prime and probe. B) Probability $P_{survival}$ that the rotation of the prime ‘survives’ and is perceived also in the probe. $P_{survival}$ decreases from 1 (maximal positive priming) to 0.5 (baseline), revealing the recovery from facilitation to the prime.

apparent rotation of prime and probe spheres. Trials in which the appearance of the prime reversed spontaneously were aborted (11.2% of total). As before, we measured by the probability $P_{survival}$ that prime and probe spheres exhibited the same appearance. The results of nine observers are shown in (Figure 7B). As expected, with increasing blank duration, $P_{survival}$ decreased gradually from initial values near 1 (maximal facilitation) to values near 0.5 (baseline). Fitting an exponential function to the observed time-course, yielded a time-constant of $\tau_{fall}^+ = 38.9 \langle T_{dom} \rangle$.

In view of the long blank durations, we were concerned that eye blinks or eye movements might have affected the facilitative state. For example, blinking is known to extend (rather than curtail) the persistence of a dominant percept (Leopold et al., 2002). Eye movements may have an opposite effect, as saccading during stimulus presentation reduces mean dominance times (Ross and Ma-Wyatt, 2004). To assess the potential for problems in this regard, we conducted a control experiment with a blank duration of $3 \langle T_{dom} \rangle$, in which observers were either required to move their eyes to a peripheral target or to maintain fixation during blank intervals. The value of $P_{survival}$ did not differ significantly between the two conditions (T-test, $p = 0.49$). This suggests that the conclusions of the main experiment are not compromised by eye movements during blank intervals.

Experiment 5: no facilitation by ambiguous primes

The design of the previous experiments was based on the assumption that unambiguous primes do not induce facilitation (i.e., a positive priming effect). To verify this assumption for our displays, we conducted additional experiments to compare directly facilitation by

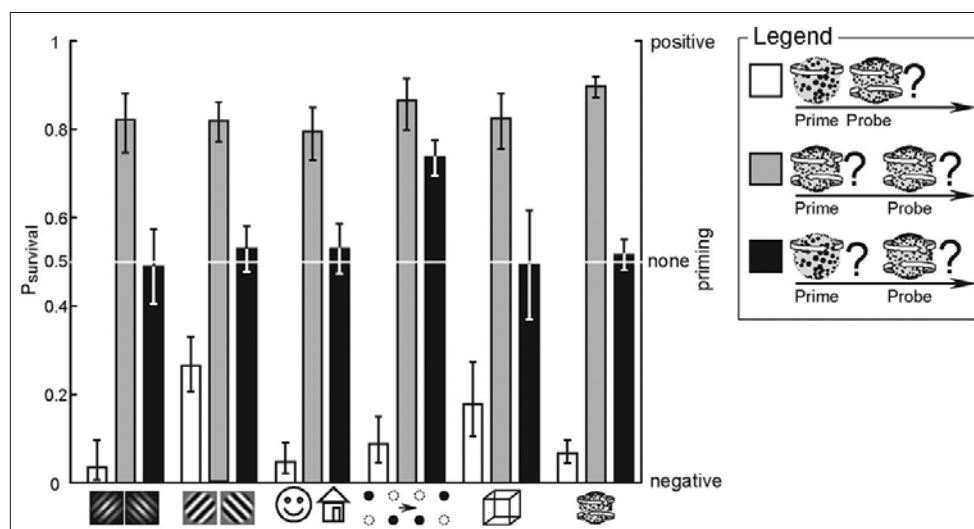


Figure 8. No facilitation by ambiguous primes. Comparison of *ambiguous facilitation* ($P_{\text{survival}} > 0.5$), *unambiguous adaptation* ($P_{\text{survival}} < 0.5$), and the failure of *unambiguous facilitation* ($P_{\text{survival}} \sim 0.5$). The inset illustrates the three conditions, with rotating spheres serving as an example. Several other types of displays were tested as well (3 types of binocular rivalry, jumping dots, Necker cube).

ambiguous and unambiguous primes. Three conditions were tested. In the critical condition (“unambiguous facilitation”), an unambiguous prime (duration $1\langle T_{\text{dom}} \rangle$) was followed by a blank period ($2\langle T_{\text{dom}} \rangle$) and an ambiguous probe ($0.5\langle T_{\text{dom}} \rangle$). A control condition (“ambiguous facilitation”) used an ambiguous prime and was expected to reveal facilitation (as in Exp. 3). A second control condition (“unambiguous adaptation”), which used unambiguous prime and omitted the blank period, was expected to reveal adaptation (as in Exps. 1 and 2).

To establish generality, we also performed analogous experiments with several additional multi-stable displays, including a Necker cube (Necker, 1832), jumping dots (Ramachandran and Anstis, 1983), binocular rivalry between gratings (Wheatstone, 1838; von Helmholtz, 2000), and binocular rivalry between faces and houses (Tong et al., 1998). The results are summarized in Figure 8 and are largely consistent across all types of multi-stable displays: unambiguous primes consistently induce negative priming ($P_{\text{survival}} < 0.5$), if no blank period separates prime and probe displays (“unambiguous adaptation” condition, Figure 8, white bars). However, when a blank period is included to allow recovery from adaptation, the same unambiguous primes do not induce positive priming (“unambiguous facilitation” condition, $P_{\text{survival}} \sim 0.5$, Figure 8, black bars). A possible exception are jumping dots, which exhibit a $P_{\text{survival}} \sim 0.75$. In contrast, positive priming ($P_{\text{survival}} > 0.5$) is induced consistently by ambiguous primes (“ambiguous facilitation” condition, Figure 8, gray bars).

DISCUSSION

Isolating negative and positive priming effects

Ambiguous stimuli are subject to both negative and positive priming effects (Kohler and Wallach, 1944; van Ee, 2009; Alais et al., 2010; Wolfe, 1984; Blake et al., 1990; Nawrot and Blake, 1989; Petersik, 2002; Adams, 1954; Orbach et al., 1963; Leopold et al., 2002; Pastukhov and Braun, 2008; Brascamp et al., 2008). When such stimuli are presented continuously, the two effects will contend for control over phenomenal appearance and will be difficult to disentangle. Here we sought to isolate the two priming effects with short sequences of discrete presentations, typically comprising a prime stimulus, a pause, and a probe stimulus. We took several steps to minimize interference between the two kinds of priming.

To isolate negative priming, we generated a completely unambiguous kinetic-depth display (“solid sphere”, see Methods), which failed to induce positive priming (Exp. 5). In Experiments 1 and 2, we exploited this property of unambiguous displays in order to characterize negative priming without interference from positive priming. In Experiments 3 and 4, we applied the same reasoning to the (unambiguous) pre-prime stimulus, which controlled the appearance of the (ambiguous) prime stimulus proper. In this case, we were interested in positive priming by the prime proper, and in avoiding positive priming by the pre-prime.

To isolate positive priming, we took advantage of the fast decay of negative priming. Specifically, we chose a blank duration long enough to allow essentially complete recovery from adaptation, based on the recovery time-constant measured for each observer. This did not interfere with characterizing positive priming, as its recovery time-constant is almost an order magnitude larger.

Finally, we took advantage of the retinotopic specificity of positive and negative priming (Blake et al., 2003; Knapen et al., 2009; Chen and He, 2004) in order to minimize priming effects across trials. Specifically, we presented trial sequences in four visual quadrants and never presented successive sequences in the same quadrant (see Methods). Without this precaution, priming between successive trials would have compromised our results.

Negative priming of ambiguous patterns

It is well known that the phenomenal appearance of an ambiguous pattern can be controlled by prior exposure to an unambiguous version of that pattern (e.g., patterns eliciting binocular rivalry, (Wolfe, 1984; Alais et al., 2010; Kang and Blake, 2010); patterns evoking a kinetic-depth effect, (Fang and He, 2004; Nawrot and Blake, 1989; Petersik, 2002); Schröder’s staircase, (Harris, 1980)). As prior exposure to one configuration favors perceiving the opposite configuration later on, this is an instance of negative priming. Interestingly, the priming seems to involve early levels of visual representation, for priming effects are specific to retinal location (Blake et al., 2003), to the stimulated eye (Wolfe, 1984), and to direction of stimulus motion (kinetic-depth effect, (Nawrot and Blake, 1989)). However,

incidental stimulus attributes, which do not contribute to perceptual ambiguity, may be altered without loss to priming. The favored explanation for this negative priming is that local neural adaptation, possibly due to spike-frequency adaptation (Sanchez-Vives et al., 2000), selectively reduces the responsiveness of primed neural populations (Blake et al., 2003; Alais et al., 2010).

The same mechanisms of local neural adaptation have long been thought to destabilize the phenomenal appearance of ambiguous stimuli. In this view, adaptation progressively weakens the neural activity that sustains the currently dominant appearance, until a competing neural population gains ascendance and phenomenal appearance reverses (Blake, 1989; Kohler and Wallach, 1944; Laing and Chow, 2002; Wilson, 2003; Noest et al., 2007). Indeed, there is compelling evidence that neural adaptation of the phenomenal appearance tips the scales on perceptual reversals (Pastukhov and Braun, 2011; Brascamp et al., 2008; Alais et al., 2010; van Ee, 2009; Blake et al., 1990; Kang and Blake, 2010). When adaptation is exacerbated, for instance by stabilizing perception artificially in one particular state, subsequent periods in which perception is dominated by another state are also exceptionally long (Blake et al., 1990; Alais et al., 2010). Conversely, reducing or avoiding adaptation slows down alternations of phenomenal appearance. For instance, moving an ambiguous pattern continuously to new, unadapted retinal locations, stabilizes phenomenal appearance (Blake et al., 2003). Similarly, presenting an ambiguous pattern intermittently, so that neural populations may recover from adaptation during the periodic absence of stimulation, lowers the rate of phenomenal reversals substantially (Adams, 1954; Leopold et al., 2002; Orbach et al., 1963).

Our results concerning the time-course of negative priming are broadly consistent with the observations of several earlier studies. However, the comparison of different studies is complicated, as much depends on the nature and duration of the prime stimulus. The most systematic study of negative priming of binocular rivalry was conducted by Wolfe (Wolfe, 1984), who found that negative priming saturates for priming (adaptation) periods in excess of one second, and that recovery from adaptation is complete after comparable periods of time. For an ambiguous motion display, recovery from adaptation has been reported to require approximately 5 seconds (Kanai and Verstraten, 2005). Finally, recovery from prolonged (approximately one minute) adaptation to rotation is complete after approximately 40 seconds (Petersik, 2002).

Positive priming of ambiguous patterns

When an ambiguous pattern disappears for several seconds and is then restored, its phenomenal appearance typically remains unchanged. This finding was reported originally for Necker cubes (Adams, 1954; Orbach et al., 1963), but was recently extended to a variety of ambiguous situations, including kinetic-depth patterns and binocular rivalry (Pastukhov and Braun, 2008; Pearson and Brascamp, 2008; Leopold et al., 2002). The observation implies the existence of a visual short-term memory for phenomenal appearance, which persists over a gap in stimulation and which biases perception towards the same appearance once stimulation is resumed.

Remarkably, this positive priming or ‘facilitation’ shares many of the characteristics of negative priming or ‘adaptation’. Like adaptation, facilitation is specific to retinal location (Chen and He, 2004; Knapen et al., 2009) and to the stimulus attribute that causes the perceptual conflict (e.g., eye of origin, color, orientation, direction of motion, (Chen and He, 2004; Maier et al., 2003; Pearson and Clifford, 2004). Therefore, facilitation appears to involve early levels of visual representation, just as adaptation does.

The neural basis of positive priming is unclear, although functional imaging evidence points to an involvement of dorsolateral prefrontal cortex (Sterzer and Rees, 2008). In terms of its time constants and its robustness to interference, positive priming shares some of the characteristics of visual short-term memory (Maier et al., 2003). Several neural mechanisms of positive priming are conceivable, including a persistent neuronal or synaptic facilitation.

A puzzling aspect of positive priming, and a clear difference to negative priming, is that it is induced exclusively by ambiguous patterns. This categorical conclusion is based on the present experiments with kinetic depth displays, binocular rivalry displays, and two further types of ambiguous displays, as well as on earlier findings with binocular rivalry displays (Sterzer and Rees, 2008). In fact, we know of only two instances in which multi-stable appearance is positively primed by an unambiguous version of the display: ambiguous figurative drawings (e.g., man-rat figure, (Bugelski and Alampay, 1961)) and counter-phase gratings (Kanai and Verstraten, 2005). Both cases are arguably untypical as phenomenal reversals seem to require voluntary attention (Bugelski and Alampay, 1961; Kanai and Verstraten, 2005).

Our measurements of the time-course of positive priming were consistent with prior results (Leopold et al., 2002; Pastukhov and Braun, 2008; Brascamp et al., 2008). In these studies, positive priming saturated after a comparatively brief exposure (1 to 4 seconds) and remained strong after a blank period of 40 seconds. In our hands, positive priming accumulated with a time-constant of approximately 2 seconds and decayed with a time-constant of approximately 150 seconds.

CONCLUSION

Although multi-stable perception has long been considered a “memoryless” process (Fox and Herrmann, 1967; Levelt, 1965; Blake et al., 1971; Walker, 1975; Borsellino et al., 1972; Leopold and Logothetis, 1999), but see (Pastukhov and Braun, 2011; van Ee, 2009), this is true only to a first approximation. Indeed, memory effects have proven difficult to observe during the continual fluctuations of phenomenal appearance that characterize multi-stable perception. However, more sensitive psychophysical assays reveal a dual dependence on prior perceptual history: continued dominance of one appearance biases future perception both *against* and *in favor* of renewed dominance of the same appearance. Whereas the negative priming effect presumably reflects neural adaptation and builds in seconds and decays in seconds, the positive priming effect builds slightly more slowly and decays in minutes and its underlying mechanism is unknown. Both priming mechanisms may contribute causally to the intrinsic stability or instability of multi-stable perception.

METHODS

Observers

Nine observers (4 female, 5 male, including the first author) participated in experiments. Procedures were approved by the medical ethics board of the Otto-von-Guericke-Universität, Magdeburg and informed consent was obtained from all observers. All observers had normal or corrected-to-normal vision. Apart from first author, observers were naive as to the purpose of the experiment and were paid for participation.

Apparatus

Stimuli were generated by computer (HP xw8000 PC, HP Invent, Palo Alto, CA; video card Quattro FX 1100, NVidia, Santa Clara, CA) and displayed on a 19 CRT screen (Vision Master Pro 454, Iiyama, Nagano, Japan), with spatial resolution 1600×1200 pixels and refresh rate of 85 Hz. Eye-screen distance was 95 cm, so that each pixel subtended approximately 0.011° . Background luminance was 30 cd/m^2 . Screen luminance was calibrated (LS-110, Konica Minolta Business Technologies, Inc., Tokyo, Japan).

Rotating sphere

The perception of an ambiguously rotating sphere (also referred to as kinetic-depth effect (Wallach and O'Connell, 1953)) was evoked by an orthographic projection of 100 dots uniformly covering a virtual sphere of diameter 5.5° with a period of rotation of 4 seconds (0.25 Hz). When all dots assumed the same diameter and luminance (0.3° and 64 cd/m^2 , respectively), the sphere was ambiguous and equally likely to be perceived in clock-wise and in counter-clock-wise rotation. When presented continuously, the ambiguous sphere is perceived alternatively as rotating in both directions (see Supplementary Movie 1).

To evoke the perception of a solid (unambiguous) sphere, dot diameter and luminance were adjusted dynamically so that “closer” dots were both larger and brighter than “farther” dots (Braunstein et al., 1982), see Supplementary Movie 2. Specifically, dot diameter was chosen as

$$D_i = Z_i \cdot (D_{\max} - D_{\min}) + D_{\text{mid}}, \quad (1)$$

with dot depth $Z_i \in [-1, 1]$, maximal dot size $D_{\max} = 0.22^\circ$, and mean dot size $D_{\text{mid}} = 0.11^\circ$. A similar formula determined dot luminance as

$$L_i = Z_i \cdot (L_{\max} - L_{\min}) + L_{\text{mid}}, \quad (2)$$

with maximal luminance $L_{\max} = 99 \text{ cd/m}^2$ and mean luminance $L_{\text{mid}} = 64 \text{ cd/m}^2$. For each observer, we confirmed that the phenomenal appearance of this stimulus remained stable for 3 minutes of continuous viewing.

Procedure

General procedure

Spheres appeared at varying peripheral locations, the center lying always 4° of visual eccentricity. To minimize priming from previous trials, the spheres in successive trials were separated by at least 90° of polar angle. In addition, the direction of the priming sphere (clock-wise or anti-clock-wise) alternated from trial to trial. Pre-prime and ambiguous prime spheres presentation time depended on particular experimental set up and individual observer spontaneous alternation rate (see main text and figures for details on timing). Probe spheres always lasted $0.5\langle T_{\text{dom}} \rangle$, where $\langle T_{\text{dom}} \rangle$ is the average dominance time (see below).

To characterize the build-up and decay of priming effects (positive or negative), we measured survival probability P_i for different stimulus (or pause) durations t_i , and fitted the resulting value pairs with a (rising or falling) exponential function, routinely used for fitting for these cases (Hoffmann et al., 1999; Petersik, 2002)

$$P_i = A \exp(-t_i/\tau) + B, \quad (3)$$

where A and B are (positive or negative) constants and τ is a (positive or negative) time constant. We were interested mainly in the value of time constants τ .

For each observer, we measured the mean dominance time, $\langle T_{\text{dom}} \rangle$, of the direction of apparent rotation of continuously presented, ambiguous spheres. As clock-wise and anti-clock-wise rotations dominate appearance, on average, equally long, we combined the dominance times of both rotations into a single value.

To establish positive and negative priming effects, we measured the probability that prime and probe spheres were perceived with the same apparent rotation (P_{survival}). A value above 0.5 indicated a positive correlation in the respective appearances of prime and probe (“positive priming”). A value below 0.5 indicated a negative correlation (“negative priming”).

Experiment 1: build-up of adaptation

An unambiguously rotating prime, presented for $[0.02 \ 0.05 \ 0.1 \ 0.15 \ 0.25 \ 0.4]\langle T_{\text{dom}} \rangle$, was followed by an ambiguous probe ($0.5\langle T_{\text{dom}} \rangle$) and a response interval (Figure 3A). Observers reported on the rotation direction of the ambiguous probe using key presses.

Experiment 2: recovery from adaptation

An unambiguously rotating prime, presented for $1\langle T_{\text{dom}} \rangle$, was followed by a blank interval ($[0.1 \ 0.2 \ 0.3 \ 0.4 \ 0.5 \ 0.6]\langle T_{\text{dom}} \rangle$), ambiguous probe ($0.5\langle T_{\text{dom}} \rangle$) and a response interval (Figure 4A). Observers reported on the rotation direction of the ambiguous probe using key presses.

Experiment 3: build-up of facilitation

An unambiguously rotating pre-prime ($1\langle T_{\text{dom}} \rangle$) preceded an ambiguous prime ($[0.1 \ 0.2 \ 0.3 \ 0.5 \ 0.75 \ 1.0]\langle T_{\text{dom}} \rangle$) to ensure that it rotates in predefined direction. It was followed by a long blank interval ($2\langle T_{\text{dom}} \rangle$) to minimize adaptation after-effect, ambiguous probe ($0.5\langle T_{\text{dom}} \rangle$) and response interval (Figure 5A). Observers reported on direction of rotation of both ambiguo-

ous prime and probe. Trials with prime not rotating in a predefined direction were discarded (14%).

Experiment 4: recovery from facilitation

An unambiguously rotating pre-prime ($2\langle T_{\text{dom}} \rangle$) preceded an ambiguous prime ($1\langle T_{\text{dom}} \rangle$), which was followed by a long blank interval ($[5\ 20\ 35\ 50\ 60]\langle T_{\text{dom}} \rangle$), ambiguous probe ($0.5\langle T_{\text{dom}} \rangle$) and response interval (Figure 7A). To ensure observers were alert to the reappearance of the stimulus after the long interval, they were prompted 5 seconds before by an auditory signal. Observers reported on direction of rotation of both ambiguous prime and probe. Trials with prime not rotating in a predefined direction were aborted (11.2%).

Control measurement: the effect of saccades. An ambiguously rotating sphere was presented intermittently: On interval $0.2\langle T_{\text{dom}} \rangle$, Off interval $3\langle T_{\text{dom}} \rangle$. Observers were instructed to either fixate during the blank interval or saccade to a peripheral target and back. Saccade target (red, radius 0.5°) appeared at random location at 5° eccentricity for 2 seconds in the middle of the blank interval.

Experiment 5: no facilitation by ambiguous primes

An ambiguous or an unambiguous version of the multi-stable display was presented for $0.5\langle T_{\text{dom}} \rangle$. It was either followed first by a long blank interval ($2\langle T_{\text{dom}} \rangle$) or directly by an ambiguous probe ($0.5\langle T_{\text{dom}} \rangle$) and response interval. Observers reported on direction of rotation of both prime and probe.

Binocular rivalry was disambiguated by presenting predefined stimulus only to one eye. For jumping dots an apparent motion was substituted by an actual motion in either horizontal or vertical direction. Necker cube was disambiguated via stereoscopic depth.

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