

Adaptation and prolonged inhibition as a main cause of motion-induced blindness

Andrei Gorea

Laboratoire Psychologie de la Perception,
Université Paris Descartes and CNRS, Paris, France



Florent Caetta

Laboratoire Psychologie de la Perception,
Université Paris Descartes and CNRS, Paris, France



Motion-induced blindness (MIB) is one of the most enigmatic perceptual disappearance phenomena. Here we suggest that MIB may be caused by the combined effects of two distinct adaptation processes: one shared with two other non-MIB configurations and entailing a *response-gain* reduction, and a second, MIB-specific transient-to-sustained incremental inhibition causing a *contrast-gain* reduction. Response-gain reduction is evidenced by brightness-tracking experiment where the 1-minute brightness time course of an MIB target is compared to the time courses of the same target superimposed on a static mask (SM) and on no mask at all (absent mask; AM). MIB and SM yield about the same brightness time courses with a faster initial drop and reaching a lower plateau than AM. While the frequency of phenomenal suppressions and their duration are very much reduced under SM and AM conditions, they increase as for MIB within the first 5–15 s of inspection and level off thereafter. Contrast-gain reduction over time is evidenced in a detection experiment showing that MIB target thresholds are higher and increase more steeply with inspection time than AM or SM thresholds. The interplay between these noisy adaptation and prolonged inhibition processes may well account for MIB's specificity.

Keywords: motion-induced blindness, adaptation, brightness, luminance, thresholds, response-gain, contrast-gain

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Introduction

Motion-induced blindness (MIB) refers to the spontaneous disappearance and reappearance of highly salient, localized stimuli when superimposed on a global moving pattern (Bonneh, Cooperman, & Sagi, 2001). Several mechanisms underlying the perceptual suppression during MIB have been proposed such as attentional competition (Bonneh et al., 2001), interhemispheric competition (Funk & Pettigrew, 2003), filling-in (Hsu, Yeh, & Kramer, 2004, 2006), and/or surface completion (Graf, Adams, & Lages, 2002). Such processes endow MIB with some functional relevance inasmuch as they facilitate object selection and completion, may suppress orienting to scotomas (New & Scholl, 2008), and possibly enhance visibility (like in binocular rivalry; Arnold, Grove, & Wallis, 2007). In many such respects but also from a quantitative point of view (Carter & Pettigrew, 2003), MIB and binocular rivalry seem to be related phenomena.

Quite obviously and in contrast with the high-order processes above, a most intuitive account of MIB was to relate it, on the one hand, to the Troxler (1804) effect (known to have a retinal adaptation substratum; Clarke & Belcher, 1962; Krauskopf, 1963) and, on the other hand, to the masking of the MIB target by the moving background. Both processes were however discarded from the very beginning by Bonneh et al. (2001) on a number of

grounds. Early sensory adaptation was rejected because it does not fit these authors' observations that (slowly) moving targets (preventing retinal adaptation) still disappear and that perceptual grouping of MIB targets modulate the MIB effect (see also Mitroff & Scholl, 2005). While such observations do indeed discard the exclusive implication of retinal adaptation in MIB, they clearly do not exclude it under those (most numerous) MIB stimulating conditions where the MIB target is static. They definitely do not leave out the contribution of striate and/or extrastriate adaptation processes to MIB. In fact, following Ling and Carrasco's (2006) demonstration that sustained attention depletes sensitivity via an adaptation process, Carter, Luedeman, Mitroff, and Nakayama (2008) proposed that such attention-related adaptation may well be a critical MIB cause, a claim empirically supported by Schölvinck and Rees (2009). Local masking (a reputedly, low-level effect; e.g., Hermens, Luksys, Gerstner, Herzog, & Ernst, 2008) by the moving MIB background was thrust away because targets surrounded by a "protection zone" (where targets and mask do not overlap) persist disappearing (Bonneh et al., 2001). This argument is also debatable as lateral interactions do occur well beyond the classical receptive field (Allman, Miezin, & McGuinness, 1985) and as MIB eventually disappears for sufficiently large "protection zones." As, by construction, the MIB phenomenon requires the presence of a temporally modulated (not necessarily moving; e.g., Kawabe & Miura, 2007) back-

ground, it is most likely that such background exerts an inhibitory effect on the stationary (or slowly moving) MIB target (e.g., Breitmeyer, 1984; Breitmeyer & Ganz, 1976; Gorea & Fiorentini, 1982). If so, such prolonged inhibition may accumulate over time and contribute to the adaptation process (Dealy & Tolhurst, 1974).

The modulation of early visual areas during MIB has been discarded based on the observation that orientation-selective adaptation (Montaser-Kouhsari, Moradi, Zandyakili, & Esteki, 2004) and negative afterimages (Hofstoetter, Koch, & Kiper, 2004) are preserved even for suppressed targets. The logic underlying this conclusion is that, had the known early processing of orientation (i.e., by V1 units) been the substrate of MIB, such suppressed units should not have been prone to adaptation. That suppressed units do not adapt remains however an unsupported premise, particularly so if adaptation itself is one cause of MIB. It remains that this type of argument has been used in many other binocular rivalry or crowding studies (e.g., Blake & Fox, 1974; He, Cavanagh, & Intriligator, 1996; Maruya, Watanabe, & Watanabe, 2008) including those that favor the early-stage substrate of such phenomena (Blake, Tadin, Sobel, Raissian, & Chong, 2006).

At the same time, several lines of evidence suggest that early retinotopic areas do participate in MIB. For example, pre-adaptation to an MIB target (actually a potentially related “flash suppression” paradigm; Wilke, Logothetis, & Leopold, 2003) or to its edges (Hsu et al., 2006) facilitates its subsequent MIB (or flash) suppression. It has also been suggested that MIB could result, at least partially, from a contrast-gain reduction due to sensory inhibition (Caetta, Gorea, & Bonneh, 2007). Evidence of such suppressive interaction occurring at early visual areas also comes from the observation that MIB is more effective when target and mask are on the same side of fixation (Libedinsky, Savage, & Livingstone, 2009) as this points to an interaction occurring before the optical chiasma. Libedinsky et al. (2009) also found that although unitary V1 recordings do not mimic the disappearance/reappearance MIB rate, they do show a target-related response reduction in the presence of a moving mask.

In conclusion, like for binocular rivalry (Blake & Logothetis, 2002), or any other visual instability phenomenon, the physiological substratum of MIB cannot be exclusively attributed to “low” or “high” processing stages. The present study does not bear, however, on the site of MIB’s neural substrate but rather on whether or not it could be accounted for in terms of the interplay between two basic neural processes, namely, neural adaptation and prolonged inhibition. Adaptation and prolonged inhibition, wherever they occur, are known to cause brightness (Troxler-like; e.g., Knau & Spillman, 1997), perceived contrast (e.g., Ross & Speed, 1996), and sensitivity drops (Blakemore & Campbell, 1969; Sekuler & Ganz, 1963) as well as a variety of aftereffects (of tilt, size, motion, etc.; e.g., Barlow & Hill, 1963; Blakemore & Sutton, 1969; Gibson & Radner, 1937). Is it possible that, after all, these

processes be also the main cause of MIB? In the affirmative, MIB would be just their by-product rather than the consequence of some higher-level functional processes such as filling-in or surface completion.

The present study investigates the adaptation time course of an MIB target (as evidenced by its brightness and detection threshold) and compares it with the adaptation time course of this same target when superimposed on a static (rather than moving) background as well as on no background at all. Adaptation time course was assessed in two experiments, one where target’s brightness was monitored over time (Experiment 1) and another where this target’s detection threshold was measured following different target exposure times (Experiment 2). A shorter adaptation time constant and/or a lower brightness adaptation plateau and/or a larger sensitivity depletion under the MIB configuration would point to the fact that this process, wherever its site, could be the main substrate of MIB’s specificity. More specifically, if the brightness and threshold functions of inspection time happen to abut against each other, it is to be expected that random variations in the system’s adaptation state will make these two functions to crisscross causing the transient invisibility of the target. This might be the case for the MIB but not for the static or absent background configurations.

It should be noted that such account of MIB also applies to the Troxler effect. The standard “Troxler” target is spatially low-pass (has blurred edges) so that microeye movements are less critical in entailing local temporal transients (Cui, Wilke, Logothetis, Leopold, & Liang, 2009; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; also see Hsieh & Tse, 2009). Given this low spatial frequency content and its sustained temporal presentation, a “Troxler” target should yield much higher detection thresholds than a sharp-edged, small target (Robson, 1966) as typically used in MIB and as presently experimented with in the absence of any background. It follows that an adaptation process (wherever its site) would entail a brightness drop steadily below the high detection threshold of the “Troxler” target but not below the lower detection threshold of a sharp edged, tiny stimulus.

Methods

General

Stimuli were presented on a 19-in. gamma corrected screen (Philips Brilliance 109P, 1024 × 768 pixels, 100 Hz refresh rate) and generated by a PC running Matlab software with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). They were presented on a uniform gray field ($L_0 = 10 \text{ cd/m}^2$). Subjects viewed the display binocularly from a distance of 50 cm in a dark room, with the head stabilized by a chin rest with a forehead bar.

Experiment 1: Time course of brightness perception

The aim of this experiment was to assess (1) mean rate (R ; mean number of suppressions per 10-s time bins) and duration (D ; mean duration per 10-s time bins) of a suppressive state as a function of the inspection time of a static target when presented alone and when superimposed on a static or moving background; (2) brightness time course for these same three stimulus configurations. The latter was achieved via an adjustment procedure where the observer monitored in real time the brightness of a probe stimulus so as to match the brightness of the target stimulus. The probe was slowly moving on a circular trajectory around fixation so as to prevent its own adaptation. A preliminary experiment was conducted to make sure that this was really the case. We first fiddled with the probe's angular speed to spot a velocity that was fast enough to prevent local adaptation and slow enough to not impede observers' brightness adjustment task. Once this speed was chosen ($0.09^\circ \cdot s^{-1}$), probe's brightness constancy over time was assessed with an adaptive procedure (see [Appendix A](#)).

Method

Observers

They were four volunteers (different from those used in the preliminary experiment; age range = 26–31 years) naive to the purpose of this study and the first author. They had normal or corrected-to-normal vision.

Stimuli

They were the same as in the preliminary experiment except for the following. This time the target was static, set 140 cd/m^2 , and always presented in the left hemifield. It was displayed either without (absent mask, AM, condition) or with a static (SM condition) or moving (MIB condition) $9.5^\circ \times 9.5^\circ$ “mask” composed of 64 (8×8) white crosses (20 cd/m^2 , $1^\circ \times 1^\circ$). The mask was centered at 9° from the fixation cross along the horizontal meridian of the left hemifield. In the MIB condition, the mask rotated clockwise about its center at 0.28 turns/s. The probe was always presented in the right hemifield and drifted to and fro at $0.09^\circ \cdot s^{-1}$ along 1/4th of a 7° radius virtual circle centered on fixation ([Figure 1](#)). Its initial motion direction was downward or upward depending on its starting location—respectively in the upper or lower right-hand quadrant of the virtual circle—randomly chosen across trials. Test, mask (if present), and probe were presented for a 1-minute period.

Procedure

While they maintained fixation on the central cross, observers were asked to adjust the luminance of the probe

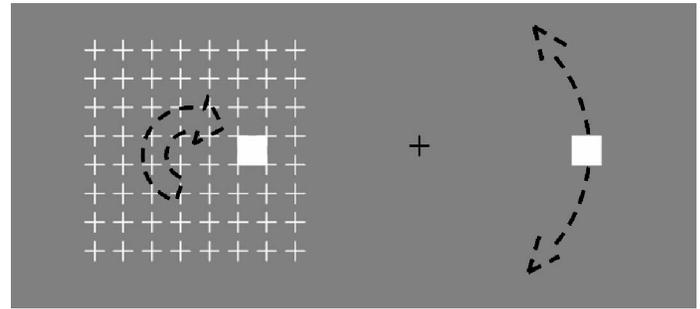


Figure 1. Spatial layout of the stimuli (not at scale) used in the brightness tracking experiment. Observer's task was to adjust the luminance of the probe (square in the right hemifield) so that it appeared of equal brightness to the target (square in the left hemifield). Dotted arrows indicate the rigid rotational movement of the mask (left hemifield; MIB condition) and the to-and-fro circular trajectory of the probe. In the SM condition, the mask did not move and was absent in the AM condition.

by sliding the mouse forward or backward so that probe and target appeared of equal brightness. In cases of perceptual invisibility/suppression, they had to press the left mouse button for as long as the target remained invisible. The probe was physically removed during these periods and, on key release, reappeared at the position where it had been removed. One session consisted in 12 one-minute trials (AM, SM, and MIB conditions repeated four times each). Sessions were repeated eight times for each observer yielding a total of 32 repeats per condition and observer (with the exception of one observer who could be run through 12 repeats per condition only). The order of the three conditions was randomized across sessions and observers. Inter-trials breaks of at least 30 s were imposed to recover from adaptation.

Results

Target suppression rates (R) and duration (D) for the three background conditions

As expected, the MIB (i.e., rotating background) condition entailed significantly more target suppression states (16.95% of total duration, with an average of 10.36 suppression events per minute with $1.05 \pm 0.17 \text{ s}$ mean suppression duration¹) than either the SM (1.41%, 1.41, $0.63 \pm 0.06 \text{ s}$) or the AM (0.55%, 0.60, $0.55 \pm 0.05 \text{ s}$) background conditions. [Appendix B](#) provides more details on the distribution of the suppression periods for each of the three configurations.

Although much less frequent than under the MIB condition, the observed phenomenal suppressions under SM and AM conditions demonstrate that background motion is not their only cause: the adaptation state of the system is most likely one additional factor shared by all three conditions. The involvement of adaptation in target disappearance under each of the three background con-

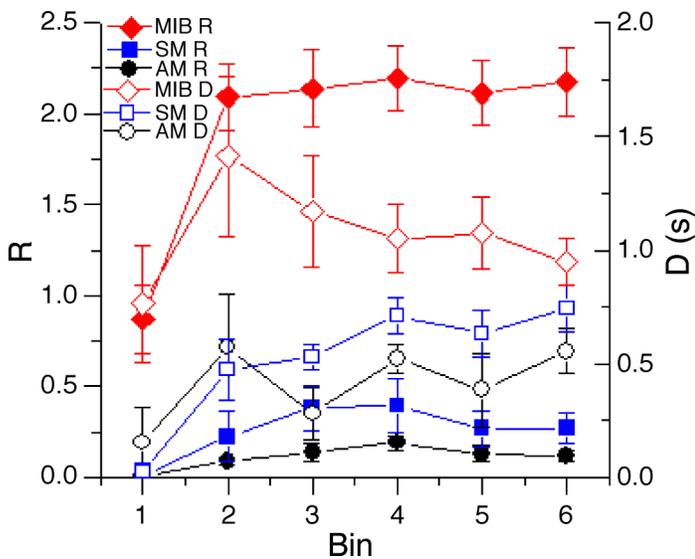


Figure 2. Mean suppression rate (R ; left ordinate, solid symbols) and mean duration of disappearance (D ; right ordinate, open symbols) per 10-s time bins as a function of the bin rank within the 1-minute inspection period, for conditions AM (circles), SM (squares), and MIB (diamonds). All datum points are averages over the five observers with the vertical bars showing ± 1 SE.

ditions is suggested by the analysis of the rates (R) and duration (D) suppression indices as a function of the inspection time. Both indices were computed per time bins of 10 s for each of the three background conditions and for six such bins spanning the 1-minute inspection period and are displayed in Figure 2. On visual inspection, both R and D indices increase for each of the three conditions up to the second bin (i.e., in-between 10 and 20 s) with the R index leveling off thereafter.² Within this time span (0–20 s), R increases by an average factor of 14.29, 31.00, and 2.41 for the AM, SM, and MIB conditions, respectively. The D index increases up to the second bin by an average factor of 3.76, 18.25, and 1.85 for the AM, SM, and MIB conditions. After the second bin, R remains constant for all three configurations suggesting a steady-state adaptation. At the same time, D appears to decrease monotonically for the MIB condition, which is to say that the total suppression period under MIB decreases with inspection time. This trend that could reflect an increase of eye movements (including microsaccades) over time in the presence of the moving background is, however, not sustained by the statistical analysis.³ This analysis does not support either the visible D increase with inspection time (after the second bin) for the SM condition.

The smaller R and D values for both the SM and the AM conditions during the first 10 s together with their larger increase within the next 10 s suggest that target disappearance under these conditions is caused by an adaptation process.⁴ If so, adaptation must also be a factor in MIB. On this premise, one may conclude that adaptation under MIB builds up more rapidly (i.e., within the first 10 s)

as the related R and D indices are by far larger than under SM and AM conditions. Alternatively, adaptation build-up may be equivalent across the three conditions with the MIB target detection threshold significantly higher than for the remaining two conditions. This tentative conclusion is based on the reasoning developed in the Introduction according to which phenomenal suppressions might reflect the fact that target brightness occasionally drops below the target detection threshold (see Experiment 2 and Discussion).

Brightness as a function of inspection time

Figure 3 displays the luminance of a probe matched to the brightness of the target over a 1-minute period (6,000 raster frames). Each jagged track (black, blue, and red for AM, SM, and MIB conditions, respectively) was obtained by first bootstrapping each observer's data for each condition,⁵ taking the frame-by-frame means of these bootstraps and averaging these means across observers. The shaded areas show ± 1 SE of these latter means. Each mean track was fit with an exponential decay function (smooth curves) of the form $y = y_0 + A \times e^{-kt}$, with y_0 as the asymptote (i.e., plateau) and k as the steepness of the adaptation process. The mean tracks for each observer were also fit with the exponential decay functions and their asymptotes and the half-lives, i.e., $t_{0.5} = (\ln 2) / k$, are given in Table 1.

The general three observations from Figure 3 and Table 1 are as follows:

- adaptation first follows a rapid phase (< 15 s) for all three conditions with the SM and MIB conditions

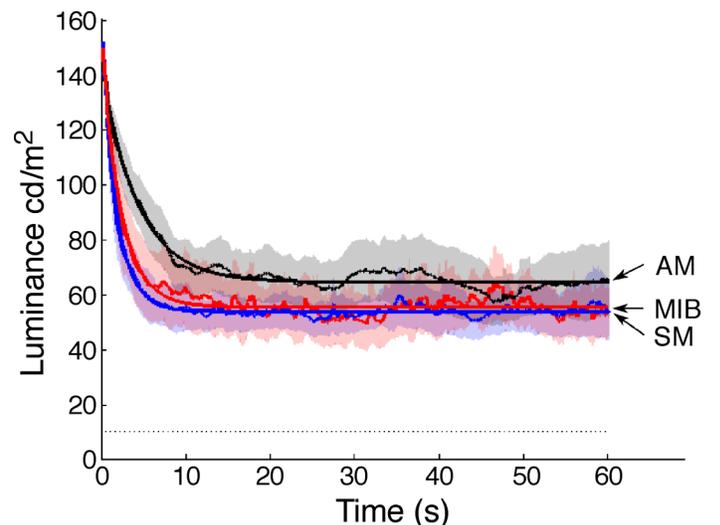


Figure 3. Brightness as a function of adaptation time for AM, SM, and MIB conditions (black, blue, and red tracks). Jagged tracks are frame-by-frame cross-observer means of their bootstrapped data (see text for details). Shaded areas show frame-by-frame ± 1 SE of these cross-observers means. Smooth curves are exponential decay fits of the mean tracks. The dotted horizontal line shows the background luminance.

- yielding faster brightness drops ($t_{0.5} = 1.99, 2.17$, respectively) than the AM condition ($t_{0.5} = 3.32$);
- ii. adaptation plateaus are also very similar for the SM and MIB conditions ($y_0 = 52.99, 54.70$) and clearly below the plateau for the AM condition ($y_0 = 63.07$);
 - iii. as a consequence of the above, the inflection points of the adaptation curves are about the same for the SM and MIB (≈ 5 s) conditions and clearly delayed for the AM condition (≈ 15 s).

Unexpectedly, none of these parameters seems to differ across the SM and MIB conditions.⁶ In order to further explore the link between adaptation state and phenomenal disappearance, we also investigated observers' adaptation (brightness) state immediately (i.e., 1 s) prior to the onset and subsequent to the offset a suppressive state. Brightness during these pre- and post-suppression periods did not differ significantly from the mean plateau level. This analysis and its logic are presented in [Appendix C](#).

The fast brightness drops within the first 5–15 s of inspection followed by the steady plateaus for each of the three experimental conditions is globally congruent with the observed increase in suppression rate and duration within about the same time interval and with their leveling-off thereafter ([Figure 2](#)). Assessing the specific relationship between brightness adaptation and phenomenal suppression over time is a matter of modeling beyond the scope of the present study. Clearly, however, such modeling is doomed to fail if ignoring a process other than brightness adaptation. Indeed, the present SM and MIB brightness functions are practically indistinguishable, whereas the corresponding suppression rates and durations are very different. This other process is appraised in the next experiment.

Experiment 2: Time course of the detection threshold

The manifestation of an adaptation process is not limited to the suprathreshold appearance (brightness) of

the adapting stimulus; it should also affect its detection threshold. Adaptation does not necessarily entail identical stimulus appearance and sensitivity effects (e.g.: Klein, Stromeyer, & Ganz, 1974; Tolhurst & Thompson, 1975; Snowden & Hammett, 1998; Wilson & Humanski, 1993) presumably subtended by distinct physiological processes (response-gain vs. contrast-gain reduction effects, respectively; e.g., Albrecht, Farrar, & Hamilton, 1984; Albrecht & Hamilton, 1982; Kohn & Movshon, 2003). The purpose of this experiment is the assessment of adaptation effects on the detection threshold under the same three stimulus configurations as in [Experiment 1](#). While the brightness tracking functions have not discriminated between the MIB and the SM conditions, it may well be that the observed differences in total disappearance time, disappearance rate, and mean disappearance time between these two conditions be due to both higher thresholds and steeper threshold raise with inspection time for MIB than for the remaining two conditions (SM and AM). Following the logic exposed in the [Introduction](#), the more brightness and threshold functions abut against each other, the higher their crisscrossing probability (due to internal noise) with any such crisscross being equivalent to the onset/offset of a phenomenal suppression.

As threshold measurements with a standard 2AFC procedure for the whole 1-minute adaptation period is extremely time consuming, they have been limited to only three adaptation periods with the longest of 20 s.

Method

Subjects

This experiment was run with six observers (age range = 25–57 years, including the two authors), two of which (including the first author) also served in [Experiment 1](#).

Stimuli

They were two $0.70^\circ \times 0.70^\circ$ adapting white squares (140 cd/m^2) arranged at a radial distance of 0.7° from the fixation cross (80 cd/m^2) and alternatively presented

Observer	y_0			$t_{0.5}$		
	AM	SM	MIB	AM	SM	MIB
FC	34.37	31.78	33.61	2.04	1.04	0.93
PC	54.70	43.10	37.68	6.80	5.01	2.22
CT	52.39	55.24	48.39	5.00	1.20	1.50
EC	77.34	58.73	66.33	0.75	0.54	0.56
SG	96.53	76.09	87.48	2.01	2.13	5.63
Mean	63.07	52.99	54.70	3.32	1.99	2.17
SE	10.80	7.48	9.96	1.12	0.80	0.91

Table 1. Plateaus (y_0) and half-life times ($t_{0.5}$) of the fitted exponential decay brightness adaptation functions for each observer.

(across trials) at trigonometric angles of 10° and 350° in the right hemifield and of 170° and 190° in the left hemifield (Figure 4) on a 10 cd/m^2 background. As in Experiment 1, the two squares appeared in three conditions, AM, SM, and MIB, with the same mask characteristics as in Experiment 1. The luminance detection threshold was measured for a smaller test square ($0.50^\circ \times 0.50^\circ$) displayed at the location of one of the two adapting squares after an adaptation phase of 2, 10, and 20 s. The smaller size of the test square was chosen to ensure that neither part of it appeared outside the adapted zone given inevitable eye movements. The test square was displayed for a total of 300 ms with 100-ms onset and offset cosine ramps. Importantly, the 100-ms full luminance presentation period is beyond the visual system's temporal integration constant so that the measured luminance thresholds should be close to those that would have been assessed for longer displays (except for some probability summation over time; see Gorea & Tyler, 1986). As a consequence (given a few considerations to be presented in the Results section), these thresholds can be directly compared with the brightness functions of Experiment 1.⁷

Procedure

At the beginning of a trial, initiated by observers' space bar press, the two adapting squares appeared either in the left or right hemifield. Observers were asked to maintain fixation on the central cross. Auditory beeps delivered 1, 9, or 19 s after the beginning of the trial prompted observers to initiate the offset of the adaptors and the

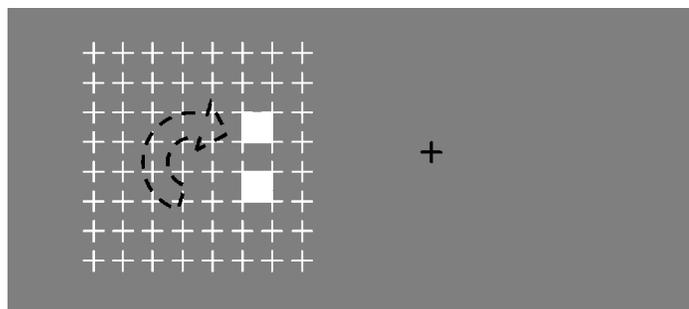


Figure 4. Spatial layout of the stimuli (not at scale) used in the 2AFC detection experiment. Observers adapted to the two large squares (here in the left hemifield) that were turned off at 2 ± 1 , 10 ± 1 , and 20 ± 1 s after the beginning of an adaptation period and a smaller test square was displayed for 100 ms (plus 100 ms onset and offset cosine ramps) at one of the two locations previously occupied by the adapting squares. The adapting squares reappeared 500 ms after the offset of the test square. Observers had 6 s to indicate the location of the test square. The dotted arrow indicates the rigid rotational movement of the mask in the MIB condition. In the SM condition, the mask did not move and was absent in the AM condition.

onset of the test square by pressing once more the space bar on the condition that both adapting squares were visible (i.e., not phenomenally suppressed). Observers had 2 s after the beep to press the space bar. If they did not comply (for any reason), a second, lower frequency beep indicated abortion of the trial. The two adapting squares were turned off 50 ms after a valid key press and, the test square was displayed 100 ms after at one of the two locations previously occupied by the adapting squares. The two adapting squares reappeared 500 ms after the offset of the test square. Observers were then given 6 s to decide whether the test square was presented at the location of the upper or lower adapting square (two alternative forced procedure, 2AFC); the lower frequency beep indicated then the end of the valid trial. Given this procedure and assuming no abortion, detection thresholds were measured in sequence after adaptation periods of $\approx 2 \pm 1$, 10 ± 1 , and 20 ± 1 s in each trial. Once a 20-s adaptation period was completed, the adapting squares were presented in the opposite hemifield so that adaptation started anew. Two interleaved, one-up-two-down staircases monitored target's luminance for each adaptation interval independently of the adapted hemifield. Target's luminance was increased/decreased by steps of 2, 1.58, and 1.26 dB for the first 2, 6, and subsequent reversals, respectively. One session was ended when all the six staircases (2 staircases \times 3 temporal windows) reached a minimum of eight reversals and the luminance detection threshold was measured as the mean test luminance over the last six reversals. AM, SM, and MIB sessions were repeated twice (i.e., four thresholds per time interval and condition) with the exception of two observers who could be run through one session per condition only. Sessions order was randomized across conditions and observers.

Results

Figure 5A shows the luminance detection thresholds under AM (black circles), SM (blue squares), and MIB (red diamonds) averaged across observers as a function of the adaptation period. Vertical bars show the corresponding ± 1 SE. While the use of only three adaptation durations does not allow the reliable assessment of the three threshold-versus-inspection time functions, the general observation is that MIB thresholds are significantly higher than AM and SM thresholds throughout the tested period and that they increase more rapidly with inspection time (a slope of .18) than the latter two (slopes of .06 and .04 for AM and SM, respectively) with no sign of saturation.⁸ This behavior differs from the brightness tracking functions of Experiment 1 (Figure 3) that showed steeper drops for MIB and SM than for AM within the first 5–15 s of adaptation and stabilized thereafter at about equivalent levels for AM and SM, higher than for MIB (see Table 1). The difference between the brightness and

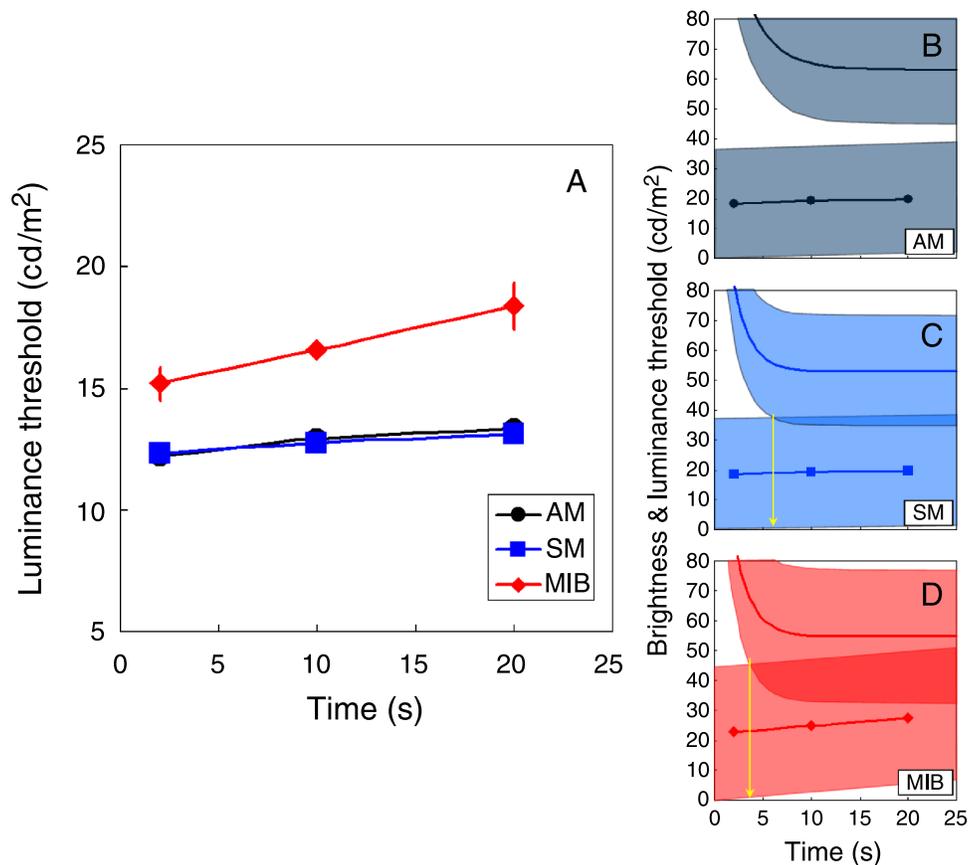


Figure 5. (A) Contrast detection thresholds (straight lines and symbols) averaged over the six observers for the AM, SM, and MIB conditions (black circles, blue squares, and red diamonds, respectively) and for 2-, 10-, and 20-s adaptation periods; vertical bars are ± 1 SE. (B–D) Blow up of the brightness versus adaptation time functions from Figure 3 (smooth curves) together with the detection thresholds from (A) transformed so as to yield a theoretical decision criterion of 1 noise unit in a “virtual” yes/no task; shaded areas show ± 1 internal noise unit derived from the detection thresholds (see text for more details). Vertical yellow arrows in c and d point to the inspection time beyond which brightness and threshold functions start crisscrossing.

the threshold functions of inspection time supports the notion that they reflect different adaptation processes.

Figures 5B–5D show a blow-up of the brightness adaptation functions from Figure 3 (smooth curves) together with the inferred “visible/invisible” luminance levels corresponding to a decision criterion of 1 derived from the detection thresholds of Figure 5A. Shaded areas show ± 1 noise unit (σ) about each brightness and derived criterion function of inspection time. The derivation of these criteria and noise units is detailed in Appendix D. It is clear from these representations that the theoretical variabilities of the threshold and brightness functions of time strongly overlap for MIB, less so for SM and not at all for AM. The larger the overlapping area, the higher the probability of a phenomenal suppression. Also note that the overlap starts at about 7 and 3 s of adaptation for SM and MIB, respectively, and that it may eventually occur for the AM condition but for much longer adaptation periods (>25 s).

The amount of overlap between the brightness and the threshold-related noises in panels b and d does not match

the statistical analyses performed on the rate (R) and duration (D) indices over time (Experiment 1 and Note 3), which showed no significant R and D differences between the SM and the AM conditions. This discrepancy could result from at least two causes. First, the raw R and D data in Figure 2 do show systematic SM–AM differences; their failure to reach statistical significance ($p_R = .12$; $p_D = .11$) may be due to the small number of subjects (4; the random variable) used in that experiment. Second, the amount of overlap illustrated in Figures 5B–5D as well as the time when the crisscrossing begins can be modulated at will by considering more or less than ± 1 noise units (σ). Establishing the quantitative relationship between the threshold-brightness overlap and the R and D functions in Figure 2 would require full-fledged modelling using the whole noise probability density function as well as a number of additional free parameters including those specifying the dynamics of this noise. It is also to be noted that the present account of MIB and the *apparent* (but statistically non-significant) drop of the MIB D-index for inspection durations longer than 20 s (see Figure 2) are

intuitively incongruent. As already mentioned, such D-drop, if confirmed, could be caused by increased fixation instability over time specifically related to the moving background. This conjecture remains to be tested.

Discussion

The present study aimed at establishing the extent to which MIB could be subtended by a time-dependent adaptation and inhibition process. To this end, the MIB target suppression characteristics (distribution of the suppression durations, total suppression percentage of the inspection period, mean duration, and disappearance rate) and target brightness were assessed over a 1-minute inspection period ([Experiment 1](#)) together with MIB target detection thresholds assessed over the first 20 s of adaptation period ([Experiment 2](#)). These indices were contrasted with those assessed under two “non-MIB” conditions, namely, for a target superimposed on a static (rather than moving) mask (SM) and on no mask at all (absent mask, AM). Some readers may argue that the two processes that we presently put forward to account for MIB are definitely no news: adaptation is a process inherent to any prolonged stimulation and inhibition of static by moving stimuli has been repeatedly documented (see [Introduction](#)). It remains that these two processes, including their interplay, have been repeatedly rejected as a cause of MIB. The present study was meant to reverse this tendency.

One first finding of [Experiment 1](#) was that even though much less frequent and less long lasting than in MIB, both AM and SM conditions did nonetheless entail target phenomenal suppressions: this translated into an MIB gamma function fit yielding a scale parameter (λ) about twice the one obtained for the SM and AM conditions (see [Appendix A](#)). Following Levelt’s (1967) biological interpretation of the Gamma distribution parameters, one may speculate that such λ -doubling reflects a slowing down of the internal “clock” under MIB. Alternatively, the distribution of perceptual alternations may reflect the characteristics of information accumulation over time (Brascamp, van Ee, Pestman, & van den Berg, 2005). If so, the presently assessed distributions would indicate that information accumulation rate under MIB slows down. On either of these two hypotheses, the specifics of the alternation rate under MIB could be prolonged inhibition (see below).

More relevant to the present inquiry, [Experiment 1](#) showed that although very much attenuated, target suppression rates and durations under SM and AM display similar characteristics of inspection time as under MIB: in all three conditions, both rate and duration increase within the first 5–15 s of inspection and level off thereafter ([Figure 2](#)). Inasmuch as adaptation is the most likely

factor entailing target suppression under AM (be it very infrequent and short lived), simple logic requires that adaptation be also a factor subtending SM and MIB suppressions. Additional though indirect evidence for such adaptation process comes from the analysis—during the steady-state adaptation epoch—of target’s brightness during the 1-s post-suppression periods for each of the three experimental conditions ([Appendix C](#)). During these periods, brightness did not differ significantly from its mean steady-state level (although more statistical power may be needed to bear this conclusion). This suggests that the suppressed target persists adapting the “brightness system” as previously suggested (Hofstoetter et al., 2004; Montaser-Kouhsari et al., 2004) though sometimes contested (Blake et al., 2006).⁹ In addition, the equivalent analysis of the pre-suppression 1-s periods also indicates no brightness difference from the mean level. This indicates that phenomenal disappearance does not result from a prior brightness drop as reported under different experimental conditions (Kanai & Kamitani, 2003; May, Tsiappoutas, & Flanagan, 2003).

The comparison of the brightness time courses observed with SM and MIB configurations does not support, however, the proposal that this form of adaptation is by itself a/the main factor in MIB. Indeed, although these two conditions entailed significantly different suppression frequencies and durations, they yielded about identical brightness adaptation functions ([Figure 3](#)). Evidence sustaining the notion that inhibition and adaptation may nonetheless be a/the critical process underlying MIB comes from [Experiment 2](#). In that experiment, target detection thresholds and their elevation with inspection time clearly discriminated between MIB and the remaining two conditions: within the first 2 s of adaptation, MIB thresholds were 1.24 times higher than either the AM or the SM thresholds and increased linearly (slope of 0.18) to reach a factor of 1.4 after 20 s (with AM and SM threshold slopes of 0.06 and 0.04, respectively; [Figure 5](#)). Although small, these differences are statistically significant. The significantly higher MIB thresholds from the very start of the adaptation period most likely reflects a specific transient-to-sustained inhibition process that is absent under AM and SM stimulating conditions (Breitmeyer & Ganz, 1976; Gorea & Fiorentini, 1982; Singer & Bedworth, 1973; Stone & Dreher, 1973). While thresholds increase over time for all three conditions as a consequence of a presumably common adaptation process, their steeper increase under MIB must reflect an additional adaptation process presumably due to *prolonged inhibition* (Dealy & Tolhurst, 1974).

The conjectured existence of two distinct adaptation processes is supported by a number of studies. Unitary recordings in both primary (Albrecht et al., 1984; Albrecht & Hamilton, 1982; Carandini & Ferster, 1997; Ohzawa, Sclar, & Freeman, 1982, 1985; Sclar, Lennie, & DePriest, 1989) and extrastriate (Kohn & Movshon, 2003) visual cortices have already drawn attention to the fact that

adapted neurons show a reduction in both their contrast- and response-gain functions with the former significantly more pronounced than the latter. Contrast-gain (presumably associated with sensitivity) allows the useful regulation of neuron's operating range so that it may encode large stimulus strength variations with a limited dynamic range (Albrecht et al., 1984; Albrecht & Hamilton, 1982; Barlow, MacLeod, & Van Meeteren, 1976; Movshon & Lennie, 1979; Ohzawa et al., 1982, 1985). Instead, response-gain (presumably associated with stimulus appearance) reflects neurons' ability to fire at high rates and may result from deleterious fatigue. Given these neurophysiological findings, the present results suggest that inspection of the MIB configuration entails a response-gain reduction similar to that induced by the presence of a static background but that it causes a more drastic contrast-gain decrease than under either AM or SM conditions (see also Caetta et al., 2007). The two effects combined may well account for the peculiarity of the MIB phenomenon as illustrated in Figures 5B–5D. Random oscillations (shaded areas in Figures 5B–5D) in the adapted response-gain (i.e., brightness) and contrast-gain (i.e., detection threshold) will occasionally bring stimulus appearance below its visibility “threshold.” This is more so for the MIB condition that, although yielding a brightness adaptation function comparable to the AM and SM conditions, yields higher thresholds and a steeper threshold increase with inspection time.

As a matter of course, MIB particularity is due to the moving or more generally to the transient nature of the pattern surrounding the target (see Kawabe & Miura, 2007; New & Scholl, 2008; Wallis & Arnold, 2008). It is then safe to assume that it is this transient-to-sustained inhibition that results into higher MIB than AM or SM thresholds and that it is the build-up of this inhibition that accounts for the more pronounced threshold elevation over time for MIB than for AM and SM. Asymmetric interactions between static and moving/transient stimuli have been evidenced by early psychophysical (e.g., Breitmeyer, 1984; Breitmeyer & Ganz, 1976; Gorea & Fiorentini, 1982) and physiological (Singer & Bedworth, 1973; Stone & Dreher, 1973) studies. At the same time, the fact that stimuli that do not activate a given psychophysical “channel” may nonetheless adapt it has been the major argument in favor of an adaptation process due to prolonged inhibition (Dealy & Tolhurst, 1974). This “adaptation from inhibition” process has been repeatedly evidenced in the neurophysiological literature and specifically pointed out as a putative process subtending the contrast-gain control mechanism (e.g., Kohn & Movshon, 2003; Ohzawa et al., 1985). Such evidence together with the adaptation effects presently described leads to the parsimonious conjecture that MIB is a straightforward adaptation *plus* inhibition phenomenon where, relatively to other stimulus displays, target adaptation is reinforced by prolonged inhibition from mechanisms responding to transient stimulations.

According to the neurophysiological evidence mentioned above, the site of this inhibitory adaptation could be anywhere from the LGN (Singer & Bedworth, 1973; Stone & Dreher, 1973) to MT (Kohn & Movshon, 2003) including the visual striate cortex (Albrecht et al., 1984; Albrecht & Hamilton, 1982; Carandini & Ferster, 1997; Dealy & Tolhurst, 1974; Ohzawa et al., 1982, 1985; Sclar et al., 1989). The general picture emerging from this literature is however in favor of the fact that the adaptation effects (be they of the contrast- or response-gain type) observed in extrastriate neurons—such as MT—originate at more precocious stages, most likely in V1 (see Kohn & Movshon, 2003). Libedinsky et al. (2009) provided some physiological evidence that V1 responses to a static target are reduced in the presence of a moving mask although they did not observe any correlation between these responses and MIB suppressive states. The absence of correlation between subjects' phenomenal state and V1's spiking activity has been previously noted by Wilke, Logothetis, and Leopold (2006) with a “flash suppression” paradigm (Wilke et al., 2003) and recently confirmed by an fMRI study (Donner, Sagi, Bonneh, & Heeger, 2008). Notably, Wilke et al. (2006) have, however, shown that the amplitude of the local field potentials in V1, V2, or V4 does correlate with the perceptual state. Both Wilke et al. (2006) and Donner et al. (2008) showed a significant V4 spiking activity drop during the suppressive states. In addition, Donner et al. showed that a V4 spiking activity drop was correlated with a spiking activity enhancement in the dorsal visual areas (MT+ complex and V3AB) and around the intra- parietal sulcus. This physiological interaction may well subtend the higher detection thresholds obtained under MIB than under AM or SM stimulating conditions.

It should be pointed out that, despite the neurophysiological literature just cited, the suggested one-to-one correspondence between the presently measured psychophysical indices (i.e., brightness and threshold time courses) and their alleged underlying processes (respectively response- and contrast-gain reduction) should and need not be taken literally. Not only do the cited studies reveal a variety of response- and contrast-gain titrations as a consequence of neural adaptation, but the direct link between such unitary recordings and behavior remains to a large extent tentative. Our account of the MIB phenomenon only requires that brightness- and threshold-related behaviors engage the two physiological processes in different proportions.

As already mentioned in the Introduction, the role of adaptation in MIB has been suggested by studies having shown that the pre-inspection of the MIB target (in the absence of a background) or of its edges facilitates this target's subsequent suppression during MIB (Hsu et al., 2006; Wilke et al., 2003). The possibility that an adaptation process reinforced by a specific motion-to-static inhibition is the *only* substrate of the MIB phenomenon is definitely *not* incongruent with a number

of results in the MIB literature. The most striking observation put forth as an argument for MIB's peculiarity is that, contrary to intuition, the more salient an MIB target, the more it disappears (Bonneh et al., 2001). This result (not replicated in our laboratory) is entirely compatible with an adaptation process whose deleterious (stimulus appearance) and/or beneficial (contrast-gain control/sensitivity) effects overcome the initial excitatory response of the to be adapted mechanism. Ohzawa et al. (1985), for example, have shown that the response of a striate cell adapted to a high contrast stimulus equals or may even underplay its response after adaptation to a lower contrast stimulus. Also, modulation of MIB by the depth ordering of the target and background planes (Graf et al., 2002) may simply reflect a depth asymmetric transient (background) to sustained (target) inhibition that contributes to surface completion in stereo-depth stimuli according to occlusion principles. The fact that MIB can also be induced by a virtual (Kanizsa-like) rotating surface provided it is stereoscopically presented in front of the MIB target does not thwart this logic. Inhibition from sensors of such surfaces (in area 18/V2; Von der Heydt, Peterhans, & Baumgartner, 1984), perhaps via MT, may still be modulated according to occlusion principles. This is not to say that the present findings exclude other non-exclusive interpretations of the MIB phenomenon involving more functional processes such as attentional competition (between target and background; Bonneh et al., 2001), interhemispheric rivalry (Carter & Pettigrew, 2003; Funk & Pettigrew, 2003), or filling-in (of the target area by the moving surround; Hsu et al., 2004, 2006; New & Scholl, 2008). For example, New and Scholl (2008) have shown that when the MIB target is a hole within a static, densely textured background, the hole disappears as expected but, according to observers' reports, its disappearance consists in it being "filled in" by the surrounding grid. Whether such filling in is a cause of MIB or the consequence of the target being first suppressed with the remaining void being subsequently filled in by the background (whether textured or not) remains to be established. In the meantime, our proposal is that the combined effect of adaptation and prolonged inhibition could well be the primary (though not necessarily exclusive) cause of MIB.

Appendix A

Preliminary experiment

This experiment was meant to make sure that the slowly drifting probe (here referred to as "target") used in the [Experiment 1](#) was not prone to luminance adaptation.

Method

Observers

They were three naive volunteers (age range = 15–27 years) and the first author, all with normal or corrected-to-normal vision.

Stimuli

They consisted in two $0.70 \times 0.70^\circ$ white squares, one of which, the target (50 cd/m^2), moved continuously upward on a circular trajectory (radius = 7°) centered on a white fixation cross ($1^\circ \times 1^\circ$, 80 cd/m^2) at an angular speed of $0.09^\circ \cdot \text{s}^{-1}$, with its starting position in the lower left or right quadrant of a virtual circle. The second square (probe) was static and flashed for 100 ms 1, 3, 5, and 7 s after the beginning of the trial at a position symmetrical to the current target position along the horizontal meridian in the opposite hemifield. Probe's intensity was monitored by 8 one-up-one-down staircases with one staircase pair corresponding to one of the four time intervals between the start of the trial and the onset of the probe. Target and probe hemifields were swapped from trial to trial to prevent potential long-term adaptation effects.

Procedure

Observers were asked to maintain fixation on the central cross during the whole session. After each probe presentation, observers pressed one of the two arrow keys to indicate whether probe's brightness was higher/lower than that of the target. The staircases (indexed on the timing of the probe) increased/decreased probe's luminance depending on observer's response. Probe's luminance was set at 15 cd/m^2 at the beginning of each staircase and was increased/decreased in 2, 1.58, and 1.26 dB steps after 0, 2, and 6 reversals, respectively. Staircases were ended once all eight staircases (4 delays \times 2 staircases) yielded a minimum of 15 reversals, and the point of subjective equality (PSE) for each of them was computed as the mean of probes' luminance over the last six reversals. Sessions were repeated twice for each subject.

Results

The brightness of the moving target was indeed constant over the temporal window tested. The brightness PSEs were 32.72 ± 8.44 , 30.11 ± 8.31 , 31.12 ± 9.31 , and $31.20 \pm 8.61 \text{ cd/m}^2$ for probe onset delays of 1, 3, 5, and 7 s, respectively. One-way repeated measures ANOVA (with the temporal delay as factor) shows no significant delay effect, $F(3,9) = 1.16$, $p = .38$. Hence, the chosen

target speed (0.09°s^{-1}) complies with the absence of adaptation requirement. Interestingly, the matched brightness of the flashed probe (mean PSE = 31.29 cd/m^2) was 37% less than the luminance of the moving target (50 cd/m^2). As this effect cannot be attributed to a cumulative adaptation of the moving target (given the systematic hemifield swap), it is most likely due to the transient presentation of the probe (including a “Broca–Sulzer effect”).

Appendix B

Frequency distribution of suppressive states under AM, SM, and MIB conditions

Figure B1 shows histograms of the suppressed target periods (slices of 200 ms) for the three conditions with each duration frequency normalized over the total number of disappearances for each condition. Continuous curves are the corresponding gamma function fits, $\text{Freq}(t) = \lambda^k t^{k-1} / \Gamma(k) \exp(-\lambda t)$, where t is the duration of the suppressive period, Γ is the gamma function [$\Gamma(n)$ the canonical continuous extension of $(n-1)!$], and $\lambda = \sigma^2/\mu$ and $k = (\mu/\sigma)^2$ are scale and shape parameters, respectively, with μ , mean t , and σ the standard deviation of μ . Gamma functions were shown to provide good fits of the suppressive period distributions for MIB (Carter & Pettigrew, 2003) as well as for other unstable phenomena (e.g., Mamassian & Goutcher, 2005). The λ and k parameters of the AM, SM, and MIB gamma fits are, respectively, $\lambda = 0.20, 0.22,$ and 0.40 and $k = 2.68, 2.88,$ and 2.50 . According to Levelt’s (1967) interpretation, λ may represent the mean duration between two ticks generated by a Poisson-clock and k the fixed number of

ticks required for a perceptual alternation. If so, the present gamma fits imply that the rate of the Poisson clock slows down by a factor of two during an MIB suppression period (i.e., $\lambda_{\text{MIB}} \approx 2 \lambda_{\text{SM,AM}}$), while the number of ticks required for coming out of suppression remains more or less constant across the three conditions. This is equivalent to saying that perceived time slows down during an MIB suppressive state, a speculation that could be empirically tested. Surely, such conjecture is strictly based on the putative neural underpinnings of the Gamma model and makes no sense under “accumulation to threshold models” (e.g., Reddi & Carpenter, 2000) presumably more biologically meaningful (Brascamp et al., 2005).

Appendix C

Brightness before and after target suppression

Whether or not phenomenally suppressed targets contribute to the build-up of a number of visual aftereffects has been a long standing question (e.g., Blake & Fox, 1974; Hofstoetter et al., 2004; Lehmkuhle & Fox, 1975; Montaser-Kouhsari et al., 2004; O’Shea & Crassini, 1981; Wade & Wenderoth, 1978). Here we addressed this issue by asking whether the mean target brightness assessed over the 100 raster frames (1 s) following a release from suppression (Brightness after, B_a) equals the mean plateau level, M_p , computed for each observer while excluding all 1-s periods preceding a suppression onset and following its offset. If $B_a = M_p$ and provided that adaptation has reached its steady state (plateau), one should conclude that the suppressed target persisted in adapting the “brightness system” as if it were not

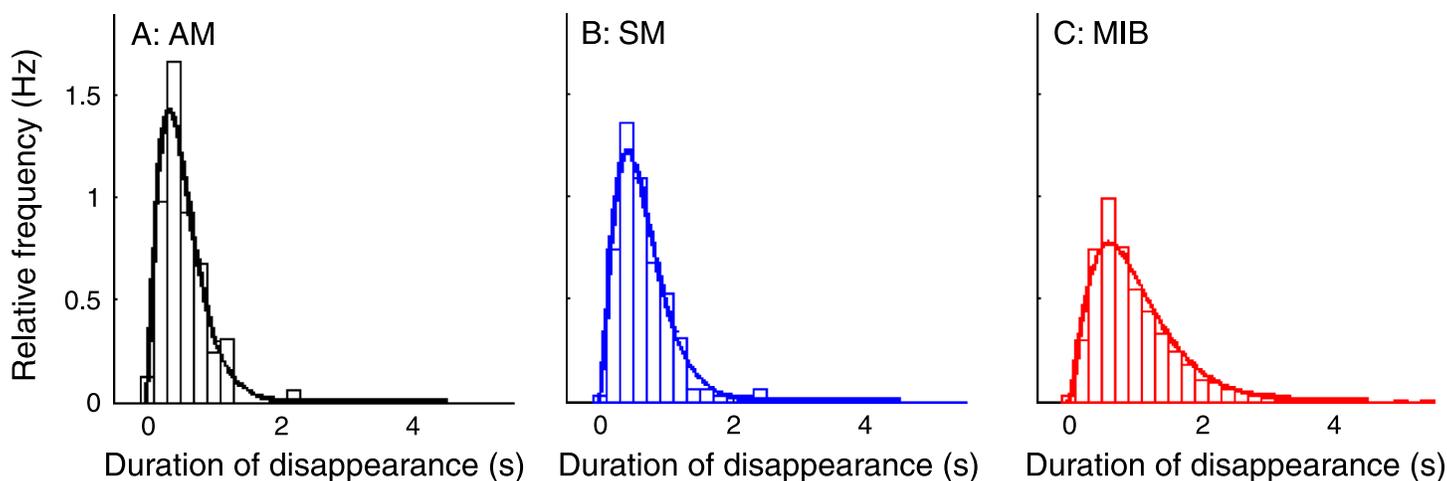


Figure B1. Normalized distributions of the suppression periods (by slices of 200 ms) for the AM (A), SM (B), and MIB (C) conditions. Curves are Gamma fits.

Conditions	AM		SM		MIB	
	Δb	Δa	Δb	Δa	Δb	Δa
Observers						
FC	-1.76	-5.01	-4.52	-5.60	1.21	-0.71
PC	-16.39	-17.13	10.79	-0.22	3.08	-1.29
CT	-2.25	-3.37	-6.37	-6.23	-1.62	-1.68
EC	-5.80	-5.06	-7.41	-9.44	0.71	-0.73
SG	-28.53	-32.70	-20.47	-20.90	-26.67	-27.89
Means	-10.95	-12.65	-5.60	-8.48	-4.66	-6.46
SE	5.13	5.59	4.97	3.44	5.55	5.36

Table C1. Mean brightness differences (in cd/m^2) with respect to the steady-state adaptation for 1-s periods before the beginning, Δb and after the end, Δa , of a suppression period for the three background conditions (AM, SM, MIB) and for each observer. Negative Δb and Δa values indicate that brightness was *below* the steady-state adaptation level of a given observer.

suppressed. Instead, a B_a significantly above or below M_p would indicate, respectively, a recovery from or an enhanced adaptation during the suppressed state.

MIB suppressive states are reputedly sudden events but this phenomenal observation has never been objectified. It is possible that the onset of a suppressive period be preceded (possibly *caused*) by a transient decrease in target's brightness. In line with this idea, Libedinsky et al. (2009) found more frequent MIB suppressions during the decreasing phases of a target whose luminance was modulated sinusoidally over time (see also Kanai & Kamitani, 2003; May et al., 2003). As for B_a , mean Brightness *before* (B_b) was computed over the 100 raster frames (1 s) *preceding* each suppression onset. The computation of B_a and B_b excluded the last suppression in a session if its ending was less than 1 s before the termination of the 1-minute inspection period as well as all suppressions starting less than 16 s (15 + 1 s) after the beginning of the adaptation period. This latter condition insured that only suppressions occurring during the steady adaptation state were considered (see Figure 3 and related text).

Table C1 displays $\Delta b = B_b - M_p$ and $\Delta a = B_a - M_p$ values for AM, SM, and MIB conditions and for each observer. Most Δb and Δa values (26 out of 30) are negative indicating a brightness drop just before and after a phenomenal suppression. Notice the outlying behavior of SG. When including this observer, Student t -tests fail to yield significant Δb or Δa differences from 0 whatever the experimental condition. When excluding her, the Δa effect for the MIB condition turns significant [$t(3) = -4.71$, $p = 0.02$]. Whether including or excluding this observer, repeated measures ANOVAs with condition (AM, SM, MIB) and temporal interval (before, after) as factors fail to show any significant global or partial effects. Provisional conclusions are that the system does not recover from adaptation during the suppressive states (in agreement with Blake & Fox, 1974; Hofstoetter et al., 2004; Montaser-Kouhsari et al., 2004; but see Blake et al., 2006) and that such states are not preceded/caused by less

drastic brightness drops (e.g., Kanai & Kamitani, 2003; May et al., 2003). Given the large inter-observer variability, the valuation of these conclusions needs, however, more statistical power (more observers).

Appendix D

Derivation of “visibility/invisibility” luminance levels and of internal noise

Detection thresholds in Experiment 2 were measured with a 2AFC, one-up-two-down staircase procedure that converges at 71% correct, equivalent to a d' of 0.77 (Macmillan & Creelman, 1991). In signal detection theory (SDT), d' values obtained with a 2AFC technique are $\sqrt{2}$ higher than those obtained with a yes/no method (Green & Swets, 1966; Macmillan & Creelman, 1991). In practice, this ratio may go up to 2 or even more (Macmillan & Creelman, 1991; Yeshurun, Carrasco & Maloney, 2008). As the standard MIB task is intrinsically of the yes/no (i.e., seen/not seen) type, one should assume that the presently 2AFC thresholds overestimate observer's sensitivity during the brightness tracking task by at least a factor of 1.41. It follows that the equivalent yes/no d' value (noted d'_{actual}) in the brightness tracking task should be at most $0.77/1.41 = 0.55$. It is also standard knowledge that when free to set their “invisibility threshold” (in any detection task; e.g., via an adjustment procedure), subjects operate at significantly higher d' levels than in a 2AFC task. Moreover, SDT excludes the notion of threshold and posits that “invisibility” states should occur any time the internal activity drops below some critical decision criterion, c' , somewhere in-between the means of the noise and signal-evoked internal activities. If signal and noise are equiprobable (see below), the optimal c' equals $d'/2$. On the assumption that this critical “invisibility” c'

(or “threshold,” noted c'_P with P standing for “presumed”) equals 1, one may derive the corresponding intensity, I , from the standard c' (or d') versus I relationship, i.e., $c' = kI^\beta$, with k a scale factor and β the slope of the psychometric function (Pelli, 1985). Simple algebra yields that the predicted/presumed luminance “invisibility threshold,” I_P , should be a factor of $\left(\frac{c'_P}{d'_{\text{actual}}}\right)^{1/\beta} = 1.82^{1/\beta}$ larger than the presently measured 2AFC thresholds once adjusted for a yes/no task, I_M . Using the MIB configuration in a target luminance discrimination task, Caetta et al. (2007) estimated the β value to about 1.5. Inserting this value in the formula above yields $I_P = 1.5 I_M$. These inferred I_P “thresholds” for the AM, SM, and MIB conditions together with the corresponding segments of the brightness adaptation functions (from Figure 3) are shown in Figures 5B–5D. Note that the “signal” (a suppression event) in an MIB (seen/not seen) task is highly less probable (about 17% in the present experiments) than a “noise” (no suppression) event. Under such low “signal” probability, SDT and actual measurements indicate that observers use a highly conservatory decision behavior, i.e., set their criterion to internal response values significantly higher than $d'/2$. Hence, the presently inferred “invisibility” level, c'_P , is underestimated.

According to SDT, the internal noise of the system, σ , equals the signal strength yielding a yes/no d' of 1. Using the intercept at the origin (I_0) of the linear regressions fit to each of the AM, SM, and MIB threshold functions of Figure 5A and applying the same conversion logic as above, the internal noise is also given by $\sigma = 1.5 I_0$. These $\pm\sigma$ values are shown in Figures 5B–5D as the shaded areas about each brightness and derived threshold function of inspection time. Note that the derivation of σ is valid on the assumption that the internal noise is signal independent (Gorea & Sagi, 2001). This assumption is necessary for two reasons: (i) the adapted thresholds may and probably do reflect a change in the transducer and therefore in signal strength; and (ii) the brightness adaptation functions are obtained for much higher luminance values than the threshold functions.

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Corresponding author: Andrei Gorea.

Email: andrei.gorea@parisdescartes.fr.

Address: Laboratoire Psychologie de la Perception, Université Paris Descartes and CNRS, Biomédicale des Saints Pères, 45 rue des Saints Pères, 75006 Paris, France.

Footnotes

¹As these distributions are skewed (see Appendix B), the total durations cannot be directly obtained by multiplying the number of suppression events and their mean duration.

²For the SM and the AM conditions only, one of the four observers reported target disappearance within the first time bin.

³Two-way repeated measures ANOVAs (factors: condition and time bin) were run on each of the two (R and D) indices. For the R index, both the condition, $F(2,8) = 98.96$, $p < .001$, and time bin, $F(5,20) = 28.38$, $p < .001$, factors yielded significant effects and a significant interaction, $F(10,40) = 11.58$, $p = .001$. Planned comparisons between condition pairs (collapsed across time bins) showed that the MIB differs from both the SM, $F(1,4) = 84.23$, $p < .001$, and AM, $F(1,4) = 141.63$, $p < .001$, conditions with no significant difference between the latter two, $F(1,4) = 3.95$, $p = .12$. Planned comparisons within conditions (across time bins) yield significant R differences between bin 1 and 2 for both AM, $F(1,4) = 14.44$, $p < .05$, and MIB conditions, $F(1,4) = 39.82$, $p < .01$ (AM: MIB) and no significant differences between bin 2 and bins 3–6. For the SM condition, a significant R difference is not found between bins 1 and 2 but is present between bins 1 and 3, $F(1,4) = 9.11$, $p < .05$, with no significant difference between bin 3 and bins 4–6. With one exception, the ANOVA on the D index yielded similar effects, namely, significant condition, $F(2,8) = 9.94$, $p < .01$, and time bin, $F(5,20) = 6.23$, $p < .001$, effects with, this time, no significant interaction, $F(10,20) = 1.59$, $p = .14$, between the two. Planned comparisons on D also showed significant differences between MIB and SM, $F(1,4) = 84.23$, $p < .001$, and between MIB and AM, $F(1,4) = 141.63$, $p < .001$, with no significant difference between SM and AM, $F(1,4) = 3.95$, $p = .11$. Both AM and SM conditions showed a significant D difference between bin 1 and 2 [AM: $F(1,4) = 9.38$, $p < .05$; SM: $F(1,4) = 11.76$, $p < .01$, and no significant difference between bin 2 and bins 3–6. However, (and contrary to visual observation), no D difference between successive bins was significant for the MIB condition. It should be pointed out that failure to reach statistical significance for at least some of the partial R and D comparisons may be simply due to the small number of subjects used in this experiment.

⁴Alternatively, Mamassian and Goutcher (2005) propose that any bistable process starts with an arbitrary bias for one percept and that this bias is progressively released so that the process reaches a stable regime. This remains a purely speculative interpretation, while adaptation is an established empirical fact.

⁵For each condition and observer, 32 brightness tracks were drawn with replacement out of the total 32 repeats (12

for one observer). This procedure was repeated 1,000 times and the mean brightness values were computed frame by frame (to the exclusion of the suppression periods).

⁶Most of these casual observations are confirmed by two ANOVAs performed on the y_0 and $t_{0.5}$ values of Table 1. None of them yields a global condition (AM, SM and MIB) effect [y_0 : $F(2,8) = 4.268$, $p = .06$; $t_{0.5}$: $F(2,8) = 0.887$, $p = .45$]. Partial AM versus (SM, MIB) comparisons show a significant plateau effect, $F(1,4) = 7.752$, $p = .05$, but no half-life time effect, $F(1,4) = 1.513$, $p = .29$. The analysis confirms the absence of significant y_0 , $F(1,4) = 0.232$, $p = .66$, and $t_{0.5}$, $F(1,4) = 0.033$, $p = .86$, differences between the SM and MIB conditions.

⁷Initially, thresholds were measured for targets presented for 10 ms with sharp onsets and offsets. This procedure not only rendered the *direct* threshold–brightness comparison impossible, but it presented the disadvantage of allowing observers to base their detection on target’s sharp onsets and offsets. As pointed out by one reviewer, such transients could have been selectively masked (or adapted) by the *moving* mask in the MIB configuration but not in SM or AM. Be it as it may, those thresholds showed a relative pattern similar to the one presented here.

⁸This qualitative analysis is supported by a two-way repeated measures ANOVA (with adaptation time and conditions as factors) performed on the luminance thresholds. It shows significant condition, $F(2,10) = 49.38$, $p < .0001$, and adaptation, $F(2,10) = 24.51$, $p < .0001$, global effects, as well as a significant Condition \times Duration interaction, $F(4,20) = 4.84$, $p = .007$. Planned comparisons show a significant difference between SM and AM taken together and MIB, $F(1,5) = 58.48$, $p = .0006$, but no significant difference between the SM and AM conditions, $F(1,5) = 0.107$, $p = .75$. A separate ANOVA run to assess the adaptation effect on the AM and SM conditions alone yields a significant result, $F(2,10) = 8.12$, $p = .008$, but no Condition \times Duration interaction, $F(2,10) = 0.306$, $p = .74$.

⁹These authors’ argument against adaptation during suppression is based on the notion that the internal activity evoked by highly suprathreshold stimuli (as those used in most previous studies as well as in the present one) is on its saturated branch so that a short stimulus suppression (or removal) will entail a negligible activity drop, difficult to measure.

References

- Albrecht, D. G., Farrar, S. B., & Hamilton, D. B. (1984). Spatial contrast adaptation characteristics of neurones recorded in the cat’s visual cortex. *The Journal of Physiology*, 347, 713–739. [PubMed] [Article]
- Albrecht, D. G., & Hamilton, D. B. (1982). Striate cortex of monkey and cat: Contrast response function. *Journal of Neurophysiology*, 48, 217–237. [PubMed]
- Allman, J., Miezin, F., & McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Annual Review of Neuroscience*, 8, 407–430. [PubMed]
- Arnold, D. H., Grove, P. M., & Wallis, T. S. (2007). Staying focused: A functional account of perceptual suppression during binocular rivalry. *Journal of Vision*, 7(7):7, 1–8, <http://journalofvision.org/7/7/7/>, doi:10.1167/7.7.7. [PubMed] [Article]
- Barlow, H. B., & Hill, R. M. (1963). Evidence for a physiological explanation of the waterfall illusion. *Nature*, 200, 1345–1347. [PubMed]
- Barlow, H. B., MacLeod, D. I., & Van Meeteren, A. (1976). Adaptation to gratings: No compensatory advantages found. *Vision Research*, 16, 1043–1045. [PubMed]
- Blake, R., & Fox, R. (1974). Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature*, 249, 488–490. [PubMed]
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews: Neuroscience*, 3, 1–11. [PubMed]
- Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 4783–4788. [PubMed] [Article]
- Blakemore, C., & Campbell, F. W. (1969). Adaptation to spatial stimuli. *The Journal of Physiology*, 200, 11–13. [PubMed]
- Blakemore, C., & Sutton, P. (1969). Size adaptation: A new aftereffect. *Science*, 166, 245–247. [PubMed]
- Bonneh, Y., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normals observers. *Nature*, 411, 798–801. [PubMed]
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433–436. [PubMed]
- Brascamp, J. W., van Ee, R., Pestman, W. R., & van den Berg, A. V. (2005). Distributions of alternation rates in various forms of bistable perception. *Journal of Vision*, 5(4):1, 287–298, <http://journalofvision.org/5/4/1/>, doi:10.1167/5.4.1. [PubMed] [Article]
- Breitmeyer, B. G. (1984). *Visual masking: An integrative approach*. Oxford: Clarendon Press.
- Breitmeyer, B. G., & Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *Psychological Review*, 82, 1–36. [PubMed]

- Caetta, F., Gorea, A., & Bonneh, Y. (2007). Sensory and decisional factors in motion-induced blindness. *Journal of Vision*, 7(7):4, 1–12, <http://journalofvision.org/7/7/4/>, doi:10.1167/7.7.4. [PubMed] [Article]
- Carandini, M., & Ferster, D. (1997). A tonic hyperpolarization underlying contrast adaptation in cat visual cortex. *Science*, 276, 949–952. [PubMed]
- Carter, O., Luedeman, R., Mitroff, S., & Nakayama, K. (2008). Motion induced blindness: The more you attend the less you see [Abstract]. *Journal of Vision*, 8(6):237, 237a, <http://journalofvision.org/8/6/237/>, doi:10.1167/8.6.237.
- Carter, O. L., & Pettigrew, J. D. (2003). A common oscillator for perceptual rivalries? *Perception*, 32, 295–305. [PubMed]
- Clarke, F. J. J., & Belcher, S. J. (1962). On the localization of Troxler's effect in the visual pathway. *Vision Research*, 2, 53–68.
- Cui, J., Wilke, M., Logothetis, N. K., Leopold, D. A., & Liang, H. (2009). Visibility states modulate microsaccade rate and direction. *Vision Research*, 49, 228–236. [PubMed]
- Dealy, R. S., & Tolhurst, D. J. (1974). Is spatial adaptation an after-effect of prolonged inhibition? *The Journal of Physiology*, 241, 261–270. [PubMed] [Article]
- Donner, T. H., Sagi, D., Bonneh, Y. S., & Heeger, D. (2008). Opposite neural signatures of motion-induced blindness in human dorsal and ventral visual cortex. *Journal of Neuroscience*, 28, 10298–10310. [PubMed] [Article]
- Funk, A. P., & Pettigrew, J. D. (2003). Does interhemispheric competition mediate motion-induced blindness? A transcranial magnetic stimulation study. *Perception*, 32, 1328–1338. [PubMed]
- Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, 20, 453–467.
- Gorea, A., & Fiorentini, A. (1982). Interactions orientazionali entre des réseaux stationnaires et en mouvement. *L'Année Psychologique*, 82, 45–65.
- Gorea, A., & Sagi, D. (2001). Disentangling signal from noise in visual contrast discrimination. *Nature Neuroscience*, 4, 1146–1150. [PubMed]
- Gorea, A., & Tyler, C. W. (1986). New look at Bloch's law for contrast. *Journal of the Optical Society of America A, Optics and Image Science*, 3, 52–61. [PubMed]
- Graf, E. W., Adams, W. J., & Lages, M. (2002). Modulating motion-induced blindness with depth ordering and surface completion. *Vision Research*, 42, 2731–2735. [PubMed]
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory*. New York: Wiley.
- He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, 383, 334–338. [PubMed]
- Hermens, F., Luksys, G., Gerstner, W., Herzog, M. H., & Ernst, U. (2008). Modeling spatial and temporal aspects of visual backward masking. *Psychological Review*, 115, 83–100. [PubMed]
- Hsieh, P. J., & Tse, P. U. (2009). Microsaccade rate varies with subjective visibility during motion-induced blindness. *PLoS ONE*, 4, e5163. [PubMed] [Article]
- Hofstoetter, C., Koch, C., & Kiper, D. C. (2004). Motion-induced blindness does not affect the formation of negative afterimages. *Consciousness and Cognition*, 13, 691–708. [PubMed]
- Hsu, L. C., Yeh, S. L., & Kramer, P. (2004). Linking motion-induced blindness to perceptual filling-in. *Vision Research*, 44, 2857–2866. [PubMed]
- Hsu, L. C., Yeh, S. L., & Kramer, P. (2006). A common mechanism for perceptual filling-in and motion-induced blindness. *Vision Research*, 46, 1973–1981. [PubMed]
- Kanai, R., & Kamitani, Y. (2003). Time-locked perceptual fading induced by visual transients. *Journal of Cognitive Neuroscience*, 15, 664–672. [PubMed]
- Kawabe, T., & Miura, K. (2007). Subjective disappearance of a target by flickering flankers. *Vision Research*, 47, 913–918. [PubMed]
- Klein, S. A., Stromeyer, C. F., & Ganz, L. (1974). The simultaneous spatial frequency shift: A dissociation between the detection and perception of gratings. *Vision Research*, 14, 1421–1432. [PubMed]
- Knau, H., & Spillman, L. (1997). Brightness fading during Ganzfeld adaptation. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, 14, 1213–1222. [PubMed]
- Kohn, A., & Movshon, J. A. (2003). Neuronal adaptation to visual motion in area MT of the macaque. *Neuron*, 39, 681–691. [PubMed] [Article]
- Krauskopf, J. (1963). Effect of retinal image stabilization on the appearance of heterochromatic targets. *Journal of the Optical Society of America*, 53, 741–744. [PubMed]
- Lehmkühle, S. W., & Fox, R. (1975). Effect of binocular rivalry suppression on the motion aftereffect. *Vision Research*, 15, 855–859. [PubMed]
- Levelt, W. J. (1967). Note on the distribution of dominance times in binocular rivalry. *British Journal of Psychology*, 58, 143–145. [PubMed]

- Libedinsky, C., Savage, T., & Livingstone, M. (2009). Perceptual and physiological evidence for a role for early visual areas in motion-induced blindness. *Journal of Vision*, 9(1):14, 1–10, <http://journalofvision.org/9/1/14/>, doi:10.1167/9.1.14. [PubMed] [Article]
- Ling, S., & Carrasco, M. (2006). When sustained attention impairs perception. *Nature Neuroscience*, 9, 1243–1245. [PubMed] [Article]
- Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. New York: Cambridge University Press.
- Mamassian, P., & Goutcher, R. (2005). Temporal dynamics in bistable perception. *Journal of Vision*, 5(4):7, 361–375, <http://journalofvision.org/5/4/7/>, doi:10.1167/5.4.7. [PubMed] [Article]
- Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron*, 49, 297–305. [PubMed] [Article]
- Maruya, K., Watanabe, H., & Watanabe, M. (2008). Adaptation to invisible motion results in low-level but not high-level aftereffects. *Journal of Vision*, 8(11):7, 1–11, <http://journalofvision.org/8/11/7/>, doi:10.1167/8.11.7. [PubMed] [Article]
- May, J. G., Tsiappoutas, K. M., & Flanagan, M. B. (2003). Disappearance elicited by contrast decrements. *Perception & Psychophysics*, 65, 763–769. [PubMed] [Article]
- Mitroff, S. R., & Scholl, B. J. (2005). Forming and updating object representations without awareness: Evidence from motion-induced blindness. *Vision Research*, 45, 961–967. [PubMed]
- Montaser-Kouhsari, L., Moradi, F., Zandvakili, A., & Esteki, H. (2004). Orientation-selective adaptation during motion-induced blindness. *Perception*, 33, 249–254. [PubMed]
- Movshon, J. A., & Lennie, P. (1979). Pattern selective adaptation in visual cortical neurones. *Nature*, 278, 850–852. [PubMed]
- New, J. J., & Scholl, B. J. (2008). “Perceptual scotomas”: A functional account of motion-induced blindness. *Psychological Science*, 19, 653–659. [PubMed]
- Ohzawa, I., Sclar, G., & Freeman, R. D. (1982). Contrast gain control in the cat visual cortex. *Nature*, 298, 266–268. [PubMed]
- Ohzawa, I., Sclar, G., & Freeman, R. D. (1985). Contrast gain control in the cat's visual system. *Journal of Neurophysiology*, 54, 651–667. [PubMed]
- O'Shea, R. P., & Crassini, B. (1981). Interocular transfer of the motion after-effect is not reduced by binocular rivalry. *Vision Research*, 21, 801–804. [PubMed]
- Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America A, Optics and Image Science*, 2, 1508–1532. [PubMed]
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442. [PubMed]
- Reddi, B. A., & Carpenter, R. H. (2000). The influence of urgency on decision time. *Nature Neuroscience*, 3, 827–830. [PubMed]
- Robson, J. (1966). Spatial and temporal contrast-sensitivity functions of the visual system. *Journal of the Optical Society of America*, 56, 1141–1142.
- Ross, J., & Speed, H. D. (1996). Perceived contrast following adaptation to gratings of different orientations. *Vision Research*, 36, 1811–1818. [PubMed]
- Schölvinck, M. L., & Rees, G. (2009). Attentional influences on the dynamics of motion-induced blindness. *Journal of Vision*, 9(1):38, 1–9, <http://journalofvision.org/9/1/38/>, doi:10.1167/9.1.38. [PubMed] [Article]
- Sclar, G., Lennie, P., & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research*, 29, 747–755. [PubMed]
- Sekuler, R. W., & Ganz, L. (1963). Aftereffect of seen motion with a stabilized retinal image. *Science*, 139, 419–420. [PubMed]
- Singer, W., & Bedworth, N. (1973). Inhibitory interaction between X and Y units in the cat lateral geniculate nucleus. *Brain Research*, 49, 291–307. [PubMed]
- Snowden, R. J., & Hammett, S. T. (1998). The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. *Vision Research*, 38, 1935–1945. [PubMed]
- Stone, J., & Dreher, B. (1973). Projection of X- and Y-cells of the cat's lateral geniculate nucleus to areas 17 and 18 of visual cortex. *Journal of Neurophysiology*, 36, 551–567. [PubMed]
- Tolhurst, D. J., & Thompson, P. G. (1975). Orientation illusions and after-effects: Inhibition between channels. *Vision Research*, 15, 969–72. [PubMed]
- Troxler, D. (1804). Über das Verschwindern gegebener Gegenstände innerhalb unsers Gesichtskrcises. In K. Himley & J. A. Schmidt (Eds.), *Ophthalmologisches bibliothek* (vol. II, pp. 51–53). Jena: Fromann.
- Von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, 224, 1260–1262. [PubMed]
- Wade, N. J., & Wenderoth, P. (1978). The influence of colour and contour rivalry on the magnitude of the tilt after-effect. *Vision Research*, 18, 827–835. [PubMed]
- Wallis, T. S., & Arnold, D. H. (2008). Motion-induced blindness is not tuned to retinal speed. *Journal of*

- Vision*, 8(2):11, 1–7, <http://journalofvision.org/8/2/11/>, doi:10.1167/8.2.11. [[PubMed](#)] [[Article](#)]
- Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Generalized flash suppression of salient visual targets. *Neuron*, 39, 1043–1052. [[PubMed](#)] [[Article](#)]
- Wilke, M., Logothetis, N. K., & Leopold, D. A. (2006). Local field potential reflects perceptual suppression in monkey visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 17507–17512. [[PubMed](#)] [[Article](#)]
- Wilson, H. R., & Humanski, R. (1993). Spatial frequency adaptation and contrast gain control. *Vision Research*, 33, 1133–1149. [[PubMed](#)]
- Yeshurun, Y., Carrasco, M., & Maloney, L. T. (2008). Bias and sensitivity in two-interval forced choice procedures: Tests of the difference model. *Vision Research*, 48, 1837–1851. [[PubMed](#)]