



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)



Consciousness and Cognition xxx (2004) xxx–xxx

Consciousness  
and  
Cognition

[www.elsevier.com/locate/concog](http://www.elsevier.com/locate/concog)

## Motion-induced blindness does not affect the formation of negative afterimages

Constanze Hofstoetter <sup>a,\*</sup>, Christof Koch <sup>b</sup>, Daniel C. Kiper <sup>a</sup>

<sup>a</sup> *Institute of Neuroinformatics, Swiss Federal Institute of Technology and University of Zurich, Zurich, Switzerland*

<sup>b</sup> *Division of Biology, 139-74, California Institute of Technology, Pasadena, USA*

Received 22 December 2003

### Abstract

Aftereffects induced by invisible stimuli constitute a powerful tool to investigate what type of neural information processing can occur in the absence of visual awareness. This approach has been successfully used to demonstrate that awareness of oriented gratings or translating stimuli is not necessary to obtain a robust orientation-specific or motion aftereffect. We exploit motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001) to investigate the related question of the influence of visual awareness on the formation of negative afterimages. Our results show MIB does not affect the persistence and intensity of afterimages. Thus, there is no significant contribution to the formation of afterimages beyond the sites mediating MIB. © 2004 Elsevier Inc. All rights reserved.

*Keywords:* Motion-induced blindness; Perceptual suppression; Color; Aftereffect; Visual awareness

### 1. Introduction

In the last two decades, the scientific community's attitude toward consciousness has undergone a profound change. From a topic that was previously considered beyond the boundaries of rigorous, quantitative investigation, it is now often referred to as one of the last frontiers of science (Metzinger, 1995). Thus, neuroscientists set out to study the neural basis for consciousness (for

\* Corresponding author. Fax: +41-1-635-30-53.

E-mail address: [connie@ini.phys.ethz.ch](mailto:connie@ini.phys.ethz.ch) (C. Hofstoetter).

25 review, see e.g., Zeman, 2001). A first step towards this goal is to determine minimal sets of neural  
26 events that are necessary and sufficient to evoke certain conscious experiences (Crick & Koch,  
27 2003; Metzinger, 2000). In our research we focus on the visual system, the most extensively stud-  
28 ied mammalian sensory system, to begin our quest for such neuronal correlates of consciousness  
29 (NCC; Koch, 2004).

30 A common strategy to investigate the neural correlates of visual awareness is to study condi-  
31 tions when a stimulus is present, but observers fail to perceive it (see, e.g., Blake, 1997; Logothetis,  
32 1998; Merikle, Smilek, & Eastwood, 2001; Rajimehr, 2004). In normal human observers, different  
33 spatio-temporal manipulations can induce a dissociation between the physical and the perceived  
34 exposure to a visual stimulus. A stimulus can be rendered completely invisible for a short period  
35 of time by forward or backward masking (Bachmann, 2000; Breitmeyer, 1984; Breitmeyer & Ög-  
36 men, 2000; Lamme, Zipser, & Spekreijse, 2002; Macknik & Livingstone, 1998; Rolls, Tovee, &  
37 Panzeri, 1999), binocular rivalry (Blake & Fox, 1974; Blake & Logothetis, 2002; Engel, Fries, Kö-  
38 nig, Brecht, & Singer, 1999; Lee & Blake, 2002; Leopold & Logothetis, 1996; Logothetis, Leopold,  
39 & Sheinberg, 1996), flash suppression (Wilke, Logothetis, & Leopold, 2003; Wolfe, 1984), or by  
40 motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001). Other manipulations prevent the  
41 perception of a specific stimulus attribute for a prolonged period of time. For example, observers  
42 may fail to perceive the orientation of a grating when its spatial frequency exceeds the resolution  
43 of the eye (He & MacLeod, 2001) or when it is surrounded by similar gratings (He, Cavanagh, &  
44 Intriligator, 1996; Toet & Levi, 1992). By exploiting such stimulus configurations, experimenters  
45 aim to compare the neural events underlying normal visual perception, to those when the physical  
46 stimulus is identical but is not consciously perceived.

47 Visual aftereffects, transient percepts induced by prior exposure to an adapting stimulus, con-  
48 stitute a useful, non-invasive tool to study the neuronal basis of perception in humans. The for-  
49 mation of aftereffects to a particular stimulus attribute is generally thought to reflect adaptation of  
50 neurons processing this attribute. For example, after adapting to a grating whose dominant ori-  
51 entation is slightly tilted toward the left, away from the vertical, a perfectly vertical grating pre-  
52 sented thereafter will appear to be slightly tilted to the right. In addition, the detection threshold  
53 for a grating with the same orientation increases significantly. These aftereffects are generally as-  
54 signed to the adaptation of orientation-selective cells in visual cortex (Blakemore & Campbell,  
55 1969; Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979).

56 By studying aftereffects induced by perceptually invisible stimuli, we can infer the type of neural  
57 information processing occurring in the absence of visual awareness. For example, orientation-  
58 specific adaptation has been studied to gratings that were perceptually invisible because they un-  
59 derwent binocular rivalry (Blake & Fox, 1974), were masked due to crowding (He et al., 1996),  
60 were too fine to resolve (He & MacLeod, 2001; Rajimehr, 2004) or were suppressed by motion-  
61 induced blindness (Kouhsari, Moradi, Zand-Vakili, & Esteky, 2004). These studies consistently  
62 demonstrate that orientation-selective adaptation occurs despite the lack of conscious visual  
63 awareness of the adapting stimulus. Thus, activation of cells mediating this type of adaptation  
64 is not sufficient to generate a conscious percept. Collectively, these findings imply that orienta-  
65 tion-selective cells in V1 are not part of the NCC (Crick & Koch, 1995; Koch, 2004).

66 The purpose of this study was to examine how visual awareness affects the formation of  
67 negative afterimages (AIs). Negative AIs are visual traces whose color and contrast polarity are  
68 reversed relative to that of the adaptor. For example, prolonged exposure to a dark green adaptor

69 results in the subsequent perception of a light, reddish negative AI. We measured negative AIs  
70 induced by stimuli that were temporarily invisible due to motion-induced blindness (MIB). In  
71 MIB, salient stimuli are intermittently suppressed when surrounded by a moving stimulus (Bon-  
72 neh et al., 2001). There is evidence that perceptual suppression caused by MIB occurs in the cortex  
73 (Bonneh et al., 2001; Hsu, Yeh, & Kramer, 2004; Kouhsari et al., 2004; Rajimehr, 2004; see dis-  
74 cussion). While the origin of AIs is often assigned solely to retinal adaptation (Craik, 1940; Lack,  
75 1978; Wilson, 1997), recent studies suggest an additional cortical contribution to the formation of  
76 AIs (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; Shimojo, Kamitani, & Nishida, 2001; Su-  
77 zuki & Grabowecky, 2003). Thus, if MIB modulated AI strength, this would be clear evidence for  
78 an extra-retinal contribution to AI formation.

79 In our experiments, we measured AIs induced by two bright yellow squares, the adaptors. Un-  
80 der MIB conditions, these yellow squares were temporarily suppressed from visual awareness by a  
81 cloud of moving blue random dots evoking the percept of a rotating sphere. In 50% of the trials,  
82 the moving dots were present and induced MIB (MIB trials). In the remaining 50% of the trials  
83 (playback, or PB, trials), the blue dots were absent and the adaptors were physically removed in  
84 a way that precisely mimicked the subject's percept recorded in the preceding MIB trial.

85 For PB trials, we compare AI persistence and intensity induced by an adaptor that has just been  
86 physically removed to one that has been present at all times. It is well established that the longer  
87 an adaptor is presented, the more persistent and the more intense the AI it induces (see, e.g., Kelly  
88 & Martinez-Uriegaz, 1993). The PB data we present clearly reflect this dependence of the strength  
89 of the perceived AI on the *physical* exposure time to the adaptor. Therefore, our method is sen-  
90 sitive enough to detect an effect in our stimulation conditions.

91 For MIB trials, we compare AI persistence and intensity induced by an adaptor that has just  
92 been temporarily suppressed by MIB to the one induced by an adaptor that had been visible at  
93 all times. The data we present demonstrates that MIB does not disrupt AI persistence and inten-  
94 sity. Thus, there is no significant contribution to the formation of negative afterimages beyond the  
95 site(s) mediating MIB.

## 96 2. Methods

### 97 2.1. Subjects

98 Thirty-two volunteers participated in this study. As described below, the analysis is based on  
99 data of 16 subjects (aged from 25 to 48; mean 29.6 years, 13 male/3 female) with normal or cor-  
100 rected to normal vision.

101 All experiments were undertaken with the understanding and written consent of each subject.  
102 Experiments conform to the institutional and national guidelines for experiments with human  
103 subjects and with the Declaration of Helsinki.

### 104 2.2. Apparatus

105 Stimuli were generated on a Macintosh G4/800 computer (Apple, Cupertino, CA) using MatLab  
106 (Mathworks, Natick, MA) including the Psychophysics Toolbox extensions (Brainard, 1997; Pelli,

107 1997). The stimuli were presented at  $1024 \times 768$  pixel resolution and 120 Hz refresh rate on a 19 in.  
108 computer screen (Hitachi CM 772, Tokyo, Japan). The CIE coordinates of the screen were: red:  
109 0.625, 0.34; green: 0.285, 0.605; blue: 0.150, 0.065. The screen was located at 57 cm viewing distance.  
110 To minimize head movements, subjects placed their forehead and chin against mechanical restraints.

### 111 2.3. Stimulus

112 The two adaptors were static yellow squares with a width of  $0.35^\circ$  visual angle and a luminance  
113 of  $61 \text{ cd/m}^2$  presented on a black background ( $0.132 \text{ cd/m}^2$ ) with a white central fixation cross  
114 (width  $0.4^\circ$ , luminance  $70 \text{ cd/m}^2$ ). The two adaptors were centered at  $1.8^\circ$  on the left and the right  
115 side of the fixation cross.

116 In the MIB stimulus (see Fig. 1), adaptors were superimposed on 250 blue moving dots (diam-  
117 eter:  $0.08^\circ$  visual angle, luminance:  $6.4 \text{ cd/m}^2$ ). The dot's 2D-position resembled a random distri-  
118 bution on the surface of a 3D-sphere ( $10.5^\circ$  in diameter) and their displacement from frame to  
119 frame resulted in the impression of a rotation around a diagonal axis ( $1/3$  rotations/s). No dots

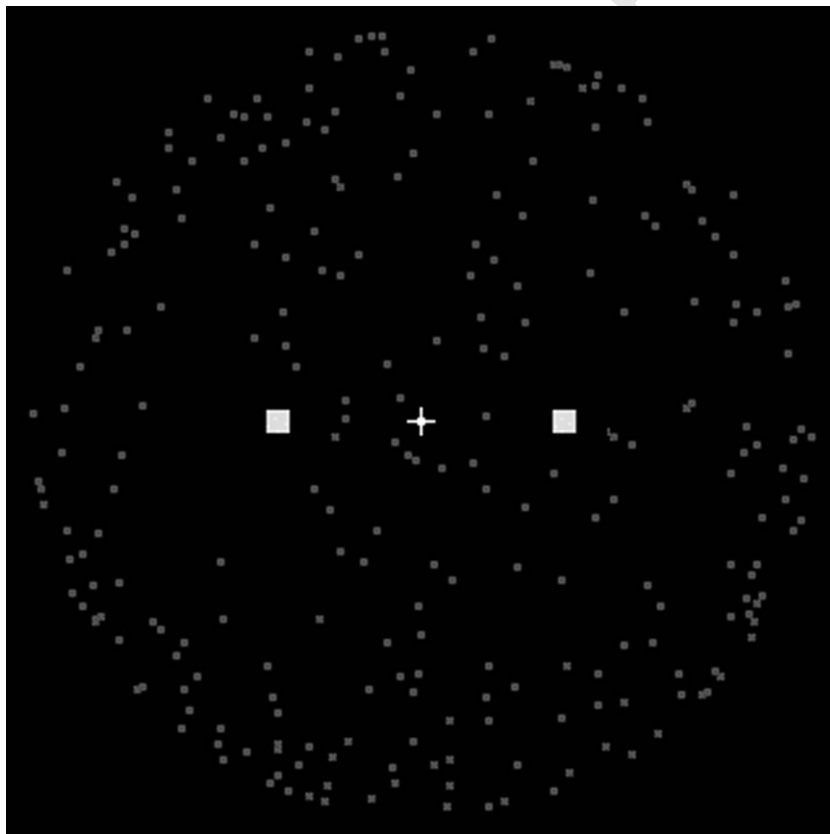


Fig. 1. The MIB inducing stimulus. Two static squares, the adaptors, are presented superimposed on a background of small moving dots that give the impression of a rotating sphere. (The stimulus used in our experiments was comprised of yellow adaptors and blue moving dots, for a demo see [www.ini.unizh.ch/~connie/demos.html](http://www.ini.unizh.ch/~connie/demos.html).)

120 were displayed in the immediate vicinity of the adapting stimuli, giving rise to squared “protection  
121 zones.” These protection zones extended 0.5° around the yellow squares to prevent any local in-  
122 teraction between the adaptors and the small blue dots.

123 Although the adaptors were physically present at all times during the adaptation phase of a MIB  
124 trial, they were occasionally suppressed from conscious awareness (see Fig. 2). The adapting phase  
125 was terminated when one and only one of the adaptors was suppressed for more than 0.4 s. In other  
126 words, after at least 0.4 s of suppression of one adaptor there were two termination criteria: the sup-  
127 pressed adaptor reappeared or the other adaptor disappeared. Therefore, the duration of the MIB  
128 stimulus presentation varied from trial to trial, depending on the subject’s perception.

129 In the PB condition, the yellow adaptors were presented alone. They were physically removed  
130 from the screen, mimicking exactly the suppression periods recorded in the preceding MIB trial.  
131 An adapting phase was thus terminated after one and only one of the adaptors had been presented  
132 alone for more than 0.4 s. The duration of the adaptation phase was thereby equal to that of the  
133 perceptually matched MIB trial, but the physical exposure to the adaptors was reduced.

134 The AIs induced by the two adaptors were observed on a grey square (size 11°, luminance 22 cd/  
135 m<sup>2</sup>). The properties of the background AIs are viewed upon are known to affect AI appearance  
136 (Anstis, Rogers, & Henry, 1978). Pilot studies indicated that subjects felt most comfortable de-  
137 scribing AIs on a background with this luminance. With our stimulation parameters, subjects ex-  
138 perience negative AIs, i.e., bluish AIs appearing as dark squares on the grey background. The

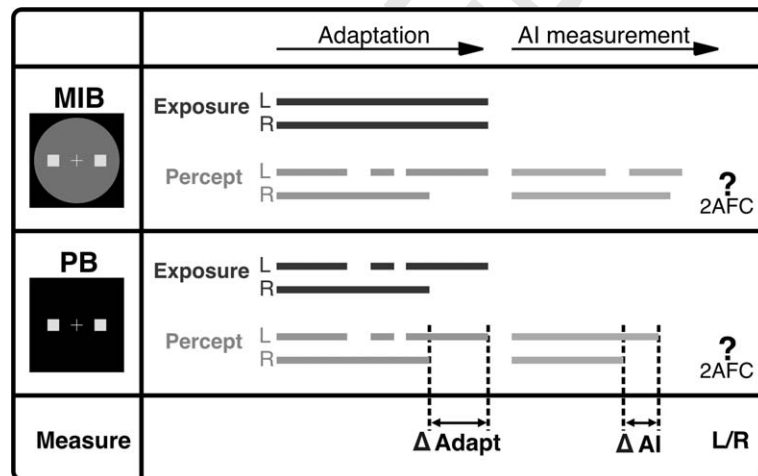


Fig. 2. Trial design. Top row: A trial consists of two phases: The adaptation phase and the phase to measure the AIs, in which the subject is asked to report on his/her perception of the left and right yellow adaptors or AIs, respectively. At the end of the trial, the subject is asked in a 2-AFC manner if the left or the right AI was more intense. Motion-induced-blindness (MIB) trials (second row) and playback (PB) trials (third row) alternated during the experiment. In a MIB trial the physical exposure to the left and right adaptor is equal and continuous. However, due to MIB, the duration for which the two adaptors are perceived will be different. In a PB trial the physical exposure to the left and right adaptor mirrors their perception in the preceding MIB trial. Since there are no moving blue dots in the PB condition, no perceptual suppression occurs. Thus, the perceived exposure to the left and right adaptor will be the same as in the MIB trial, but the physical exposure will be different. Bottom row: The parameters used for the data analysis. The relative difference in perceived adaptation time triggering the AI measuring period ( $\Delta$ Adapt) is compared to the relative difference in the duration of AI perception ( $\Delta$ AI) and the intensity rating (L/R).

139 duration of the AI measurement was dependent on the previous adaptation phase, being twice as  
140 long as the adaptation phase but no shorter than 10s and no longer than 60s. The central fixation  
141 cross turned black for 1s during the AI measurement period. As explained below, this marked the  
142 period during which the subject was asked to make its AI intensity judgment. All stimuli were  
143 viewed binocularly in a darkened room.

#### 144 2.4. Task

145 During the adaptation phase of MIB and PB trials, the subject's task was to report on his/her  
146 percept of the two adaptors by means of button presses. Subjects were told to use the left and/or  
147 right arrow key to independently monitor the disappearance of the left and/or right adaptor. The  
148 key had to be held down while the corresponding adaptor was not visible.

149 Similarly, during the AI measurement, the subject had to indicate when the left and/or right AI  
150 was not perceived. After termination of each AI measurement, the subject was asked to indicate  
151 with a single button press "Which of the two afterimages was more intense?" It has been observed  
152 that the intensity of AIs increases over the first couple of seconds after the removal of an adaptor,  
153 and then begins to wax and wane. Pilot studies had revealed that subjects felt more comfortable  
154 making a relative intensity judgment based on a brief period in time rather than having to judge  
155 the AIs average intensity over a long period. Thus, subjects were asked to base their judgment on  
156 their perception between the third and fourth second in the AI measurement period (indicated by  
157 a short beep and a change in fixation cross brightness). This interval was chosen because AIs had  
158 generally already reached their maximum intensity but had not yet vanished, even for short ad-  
159 aptation times. Thus, AI strength was quantified in terms of duration and relative intensity.

#### 160 2.5. Experimental design

161 An experimental session lasted approximately 40min and consisted of the following stages:

- 162 Instructions and training (approx. 5min).
- 163 MIB-baseline recording (2.5min).
- 164 Alternating MIB and PB trials ( $2 \times 15$ min).

165  
166 After adjusting head and chin rest, subjects were given written instructions on the screen. In the  
167 beginning of the experiment, each subject completed several training trials, during which we made  
168 sure that the instructions were understood correctly. At least two simulated MIB (in which one of  
169 the adaptors was also physically removed after a couple of seconds) and PB trials had to be com-  
170 pleted. After that, the subject could continue training until feeling comfortable with the proce-  
171 dure.

172 Next, the MIB stimulus was presented continuously for 2.5min to measure the range of sup-  
173 pression intervals occurring for each subject. This adaptation to the stimulus was necessary be-  
174 cause naive subjects tend to experience MIB only after some exposure to the stimulus.

175 The rest of the experiment consisted of alternating MIB and perceptually matched PB trials, as  
176 explained above (see Fig. 2). Subjects could rest shortly before initiating a new trial and were giv-  
177 en the chance to take a longer break after 15min.

178 Two assumptions underlie our experimental design: First, we assume that the stronger the dif-  
179 ference in adaptation, the stronger the difference on AI formation. Second, we assume that the  
180 most recent event has the strongest effect on AI strength. Thus, to maximize the chances to detect  
181 a perceptual effect on the formation of AIs, they were measured immediately after a prolonged  
182 perceptual suppression of one and only one adaptor. As discussed in Section 3, there is a tradeoff  
183 between maximizing the perceptual adaptation difference triggering an AI measurement and the  
184 amount of data that can be recorded during an experiment. We chose suppression intervals longer  
185 than 0.4s to trigger an AI measurement. We present our data using  $\Delta\text{Adapt}$ , the length of the lon-  
186 gest and most recent suppression period, as index for the difference in adaptation to the left and  
187 right adaptor (see Fig. 2). However, data analysis was also performed using the total difference in  
188 perceptual suppression of the left and the right adaptor. The results obtained by these two types of  
189 analyses are highly similar.

## 190 2.6. Data analysis

### 191 2.6.1. Recording of data

192 The computation of  $\Delta\text{Adapt}$  and  $\Delta\text{AI}$  was based on the timestamps marking changes in the sta-  
193 tus of the left and right arrow key, which were polled with an average sampling rate of 120 Hz and  
194 a maximal error of 11 ms.

### 195 2.6.2. Exclusion of single trials and data sets

196 Both MIB and AIs are known to show high within- and between-subject variability (see, e.g., Carter &  
197 Pattigrew, 2003; Lack, 1978; Loomis, 1972; Shimojo et al., 2001). To study the effect of MIB on AI  
198 formation, we had to use subjects and trials in which both phenomena were present. To maximize the  
199 chances of detecting an effect of perceptual suppression and physical removal of the adaptor on AI  
200 formation, we applied strict exclusion criteria for single trials and complete data sets. The precise  
201 choice of exclusion criteria, however, does not affect the findings we report.

202 The experiment was terminated after the initial training session if subjects reported to perceive  
203 no or only very faint and brief AIs, or after the 2.5 min baseline recording if subjects did not ex-  
204 perience MIB at all. The data of the remaining subjects was processed offline.

205 Single trials were excluded from analysis if the recorded key presses revealed that:

- 206 • no or only very short AIs were perceived (i.e., AI persistence < 0.5 s);
- 207 • an AI was still perceived at or close to the termination of the AI measurement phase (i.e., AI  
persistence > measuring phase – 0.5 s);
- 209 • it was likely that a motor error occurred when reporting on AIs (i.e., persistence of one  
210 AI > persistence of other AI + 7 s);
- 211 • the induced AI was expected to have saturated (i.e., adaptation phase > 45 s).

212 A subject was completely excluded from the study if he/she:  
213

- 214 • showed little suppression, i.e., less than 10 valid MIB trials;
- 215 • had a strong suppression bias, i.e., if the left or right adaptor triggered the AI measurement in  
216 less than three MIB trials.

217 Based on these criteria, the data of 16 of the 32 subjects were excluded from the analysis: 2 sub-  
218 jects did not perceive strong enough AIs, 4 did not experience MIB, 6 showed too little suppres-  
219 sion, and another 4 had a strong suppression bias.

#### 220 2.6.3. *Analysis across vs. within subjects*

221 The analysis across subjects is based on the data of the 16 subjects that satisfied all criteria. A  
222 within subject analysis was performed with one subject (mk), who completed five experimental  
223 sessions on different days. This subject was very sensitive to MIB (i.e., the adaptors disappeared  
224 soon after presentation of the MIB stimulus and for quite long intervals) and was naïve to the  
225 purpose of the experiment. For the data analysis across all 16 subjects, we used only the data  
226 of the first experimental session of mk.

#### 227 2.6.4. *Type of data analysis—within trial comparison*

228 The analysis of the data is based on an initial within trial comparison of the AIs induced by the  
229 left and the right adaptor. We chose this type of analysis because of the high variability observed  
230 when measuring AIs. This variability can partly be explained by certain factors that change over  
231 the course of the experiment. For example, the degree of fixation, blinking, fatigue or attention  
232 are known to affect AI formation. These factors will affect the two AIs measured within the same  
233 trial equally, but their effect on AIs recorded in different trials may differ greatly. Thus, the first  
234 step in our data analysis was to compare the left and right AIs measured within a trial. Combined  
235 data from different trials were analyzed later.

### 236 3. Results

237 Using single subject data, we first show results to characterize the distribution of MIB suppres-  
238 sion intervals and the dependence of the AI duration on the physical exposure time to an adaptor.  
239 Then, we present data describing the effect of perceptual suppression on relative AI persistence.  
240 Finally, we present data on relative AI intensity.

#### 241 3.1. *MIB suppression periods*

242 The subjective quality of MIB can be evaluated by studying the periods of perceptual suppres-  
243 sion recorded during the MIB baseline measurement. This is illustrated by mk's data recorded in  
244 five experimental sessions (Fig. 3). The left adaptor was suppressed for 18% of the stimulation  
245 time (Fig. 3: top, left), the right for 13% (Fig. 3: top, right). Thus, mk had a small bias for sup-  
246 pression of the left adaptor. The histograms show that this is due to the left adaptor being sup-  
247 pressed often for very short periods. Longer suppression intervals occur equally often for the left  
248 and right adaptor. This is reflected by higher mean and median values for the suppression of the  
249 right than of the left adaptor.

250 As discussed above, the periods where one and only one of the adaptors is perceptually sup-  
251 pressed are relevant. Only these periods could possibly induce a difference in AI formation.  
252 One and only one of the adaptors was suppressed for only 20% of the presentation time (Fig.  
253 3: bottom, right). The difference in the total suppression time and the time that only one of the



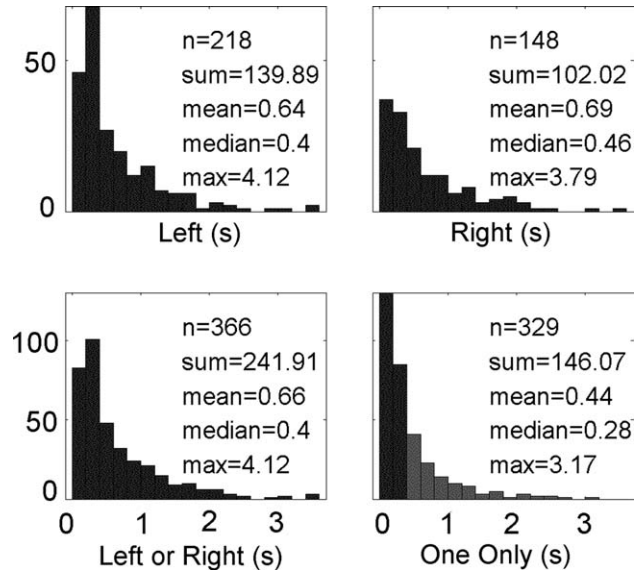


Fig. 3. Histograms of suppression intervals for one subject (mk). Histograms are based on MIB baseline recordings of five experimental sessions (total presentation time = 750s, bin width: 0.2s). Upper left: suppression intervals of left adaptor. Upper right: suppression intervals of right adaptor. Lower left: independently summed suppression intervals of left and right adaptor. Lower right: suppression intervals of one and only one adaptor (*exclusive or*). Light grey bars mark those intervals that would have triggered an AI measurement in MIB trials (>0.4s). The number of suppression instances and the summed, mean, median, and maximal suppression interval (in seconds) are given in each panel.

254 adaptors was suppressed is due to those instances when both adaptors were suppressed. The dis-  
255 tribution of suppression intervals for one and only one adaptor is significantly shifted towards  
256 shorter intervals when compared to that of suppression intervals recorded independently for  
257 the left and the right adaptor (Fig. 3: bottom, left). The shape of the distribution illustrates the  
258 trade-off mentioned above: although it would be best to measure AIs after long differences in sup-  
259 pression of the left vs. right adaptor, such events occur only very rarely. To collect a useful  
260 amount of data per experiment, a relatively low threshold for suppression difference (i.e.,  $\Delta A$ -  
261 dapt > 0.4s, indicated by light grey bars) had to be used, despite the fact that the data are expected  
262 to be more noisy for shorter differences.

### 263 3.2. Effect of physical adaptation on AI persistence

264 The strength of AIs is known to increase with prolonged physical exposure to an adapting  
265 stimulus (see, e.g., Kelly & Martinez-Uriegaz, 1993). We verified this for our stimulation  
266 protocol using AI persistence. Fig. 4 shows this on the data of a single subject (mk) for both  
267 the PB and the MIB condition. Despite high variability in AI duration, data show that the  
268 longer mk was physically exposed to an adaptor, the longer the AI he perceived. Fitting an  
269 exponential constrained to pass through the origin to both sets of data results in very similar  
270 time constants and asymptotic values for these two conditions (time constant of 3.84 and  
271 3.55s and asymptotic values of 7.52 and 7.53s for PB and MIB condition, respectively). Thus,

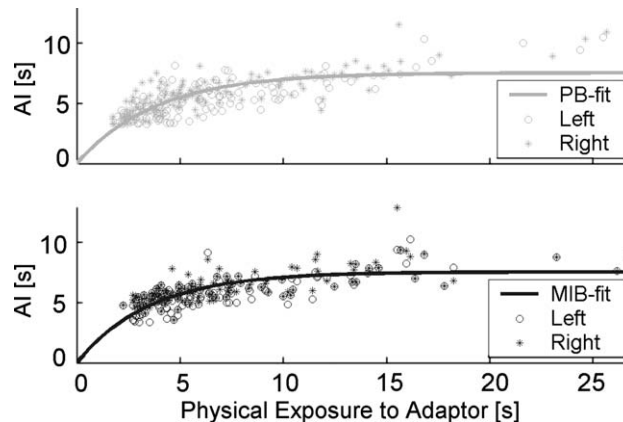


Fig. 4. The longer the physical exposure to the adapting stimulus, the stronger the AI persistence (illustrated on data of subject mk). Top panel: Absolute AI persistence as a function of the physical exposure to the adapting stimulus (less or equal to trial duration) in the PB condition. Bottom panel: Absolute AI persistence as a function of the physical exposure to the adapting stimulus (equal to trial duration) in MIB condition. Circles and stars represent AIs induced by the left and right adaptor ( $n = 276$ ), respectively.

272 despite the absence of blue dots during the PB condition, the AIs measured under the two  
273 conditions behave very similarly.

### 274 3.3. Relative AI persistence

#### 275 3.3.1. Single subject

276 The effect of a physical (PB) and perceptual (MIB) difference in adaptation on the difference in  
277 AI persistence is illustrated in Fig. 5 for subject mk.  $\Delta AI(s)$ , the difference in AI persistence in-  
278 duced by the left and right adaptor, is plotted as a function of  $\Delta Adapt(s)$ , the difference in adap-  
279 tation triggering the AI measurement, for all PB (light grey stars) and MIB (dark grey circles)  
280 trials ( $n = 139$ ). Positive (negative) values denote that the left (right) adaptor or AI was perceived  
281 longer. The mean  $\Delta AI$  plotted over the mean  $\Delta Adapt$  is indicated as medium grey star (circle) for  
282 the PB (MIB) condition. The mean value of  $\Delta Adapt$  indicates that the subject did not have a  
283 strong suppression bias. The sum of the AI measurement triggering suppression is approximately  
284 the same for the left and right adaptor. However, the mean value of  $\Delta AI$  indicates that the subject  
285 did have a bias in respect to AI perception. The mean  $\Delta AI$  for both PB and MIB is about  $-0.4$ ,  
286 which means that right AIs were generally perceived longer.

287 Further analysis of AI persistence is based on computing a linear regression for  $\Delta AI$  expressed  
288 as function of  $\Delta Adapt$ . The Null hypothesis to be evaluated is that  $\Delta AI$  is independent of  $\Delta Adapt$ ,  
289 i.e., that the slope of a linear regression through the data is not different from zero. The PB data  
290 should reveal a positive slope, reflecting the effect of physical adaptation time onto AI formation.  
291 Thus, for this control, the Null hypothesis should have to be rejected. If perceptual visibility had a  
292 significant effect on AI persistence, the same trends expected for the PB data should be observed  
293 for the MIB data.

294 The best linear fit (least mean squares) through the PB data has a slope of 0.79 with 95% con-  
295 fidence intervals lying between 0.67 and 0.90. Thus, the Null hypothesis can be rejected for the PB

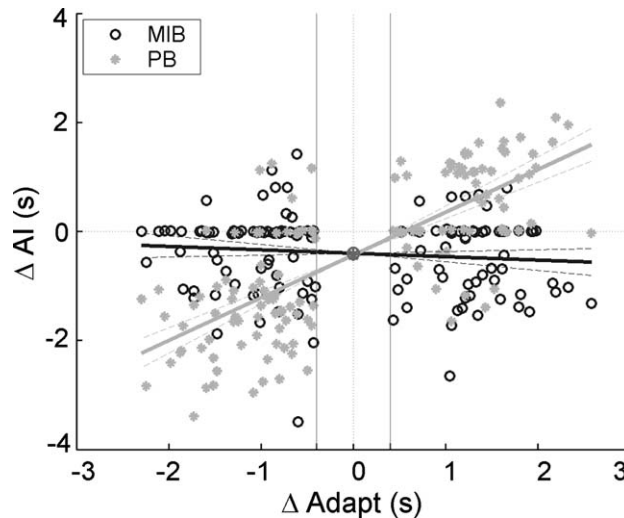


Fig. 5. Effect of physical (PB, light grey stars) and perceptual difference (MIB, dark grey circles) in adaptation on AI persistence for one subject (mk).  $\Delta AI(s)$ , the difference in duration of the AI between left and right adaptors is plotted as a function of  $\Delta Adapt(s)$ , the difference in visibility of the left and right adaptors. The solid lines represent the best linear fits through the data sets ( $n = 139$  per condition). The dashed lines mark the 95% confidence intervals. Vertical lines through the  $x$  values of  $-0.4$  and  $0.4$  s indicate that an AI measurement was only triggered if the left or the right adaptor was suppressed (MIB) or removed (PB) for more than  $0.4$  s. The medium grey circle and star indicate the mean  $\Delta AI$  over the mean  $\Delta Adapt$  for the MIB and PB condition, respectively. As expected, the slope of the PB regression has a positive value, reflecting the effect of physical exposure time on AI formation. The slope of the MIB regression is not significantly different from 0.

296 condition ( $r^2 = 0.56$ ,  $F = 172.97$ ,  $p < 0.5 \times 10^{-3}$ ). The best linear fit through the MIB data has a  
297 slope of  $-0.06$  with 95% confidence intervals lying between  $-0.16$  and  $0.03$ . The Null hypothesis  
298 can thus not be rejected for the MIB condition ( $r^2 = 0.012$ ,  $F = 1.66$ ,  $p = 0.2$ ). Thus, our method is  
299 sensitive enough to detect the expected effect of the physical adaptation time difference on AI per-  
300 sistence in the PB condition. However, no such effect is detected for the MIB condition.

### 301 3.3.2. Across subjects

302 The data obtained for an additional 15 subjects are presented in Fig. 6. Each panel contains a  
303 single subject's data recorded in one experimental session. As explained for Fig. 5,  $\Delta AI$  is plotted  
304 as a function of  $\Delta Adapt$  for PB and MIB trials, where the linear regressions through PB and MIB  
305 data sets are represented by solid lines. The individual slopes for the PB data are positive for all  
306 subjects. This reflects the known dependency of the physical adaptation time on AI persistence.  
307 However, the slopes for the MIB data are only positive for about half (7/15) of the subjects. This  
308 is expected if MIB does not influence AI persistence: by chance, individual slopes are expected to  
309 vary around the value of 0, yielding approximately 50% positive and 50% negative regression  
310 slopes. When computing the average of the 16 regression slopes for the PB data, the value ob-  
311 tained is—as expected—positive ( $0.691$ , std. of mean  $\pm 0.106$ ) and significantly different from 0  
312 ( $p < 1 \times 10^{-5}$ ). However, the average slope for the MIB data ( $0.038$ , std. of mean:  $\pm 0.083$ ) is  
313 not significantly different from 0 ( $p = 0.65$ ). In addition, we found no correlation between the  
314 slopes obtained for MIB and PB data.

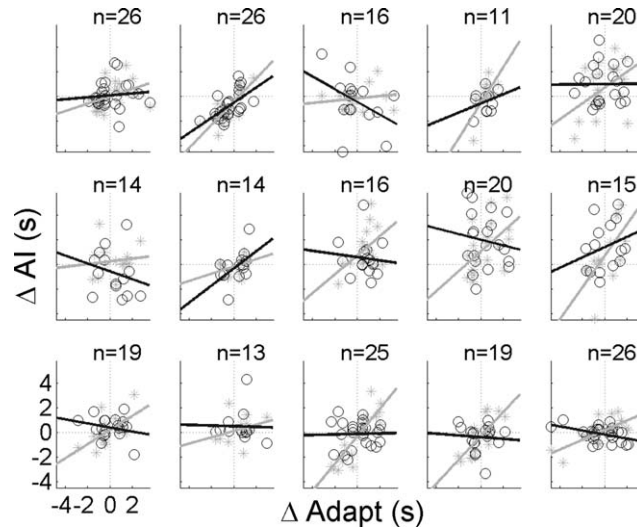


Fig. 6. Effect of physical difference (PB, light grey stars) and perceptual difference (MIB, dark grey circles) in adaptation on AI persistence for 15 additional subjects. Each panel displays  $\Delta AI$  as a function of  $\Delta Adapt$  for the valid trials obtained from a single subject in a single experimental session (see also Fig. 5). The number of valid trials per condition is given in the title of each panel. All axes have the same scale (numerical values are indicated in the panel in the lower left corner). The best linear fit through the data of the MIB and PB condition is indicated by the dark and light solid grey lines, respectively. As expected, the regression slope of all subjects has a positive value for the PB condition. For the MIB condition, only about half (7/15) of the regression slopes have a positive, while the rest have a negative value. This is to be expected if MIB does not affect AI persistence (see text).

315 When computing the average slopes for the PB and MIB data across subjects, each subject's  
316 data and thus each experimental session, is weighted equally, although the amount of data ob-  
317 tained per subject differs (as indicated in Fig. 6). Because the computation of the slopes for a single  
318 subject is based on little data, the 16 underlying values themselves are not very reliable. An alter-  
319 native approach is to first combine all data recorded for all subjects and then compute a linear  
320 regression. To do so, the data of each subject must first be transformed, to account for biases  
321 a subject may have. To eliminate these biases we subtracted the mean of  $\Delta Adapt$  and  $\Delta AI$  of each  
322 subject from each value of  $\Delta Adapt$  and  $\Delta AI$ , respectively. Fig. 7 displays the transformed data  
323 ( $n = 305$ ) of all 16 subjects. The linear regression for the PB data (left, light grey stars) and the  
324 MIB data (right, dark grey circles) is indicated by solid lines, 95% confidence intervals by dashed  
325 lines. The best linear fit (least mean squares) through the PB data has a slope of 0.64 with 95%  
326 confidence intervals lying between 0.52 and 0.76. The best linear fit (least mean squares) through  
327 the MIB data has a slope of  $-0.03$  with 95% confidence intervals lying between  $-0.15$  and  $0.09$ .  
328 The Null hypothesis can be rejected for the PB condition ( $r^2 = 0.27$ ,  $F = 109.57$ ,  $p < 0.5 \times 10^{-3}$ ),  
329 but not the MIB condition ( $r^2 = 0.001$ ,  $F = 0.29$ ,  $p = 0.59$ ).

### 330 3.4. AI intensity

331 So far our data analysis focused on AI persistence as a measure for AI strength. The same type  
332 of results was obtained when analyzing the AI intensity data. AI intensity was measured using a

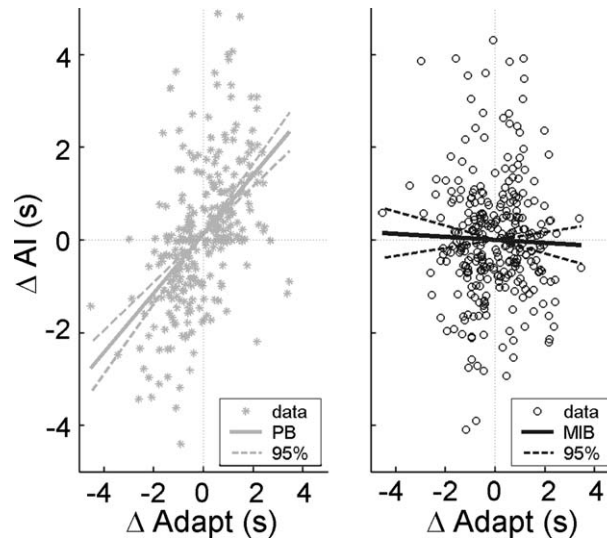


Fig. 7. Transformed data of all 16 subjects. For each subject,  $\Delta AI$  minus mean  $\Delta AI$  is plotted over  $\Delta Adapt$  minus mean  $\Delta Adapt$ . Left: PB data (light grey stars). Right: MIB data (dark grey circles). The solid lines show the linear regression, the dashed lines mark the 95% confidence intervals. The slope of the PB regression has a positive value, reflecting the effect of physical exposure time on AI formation. The slope of the MIB regression is not significantly different from 0.

333 two alternative forced-choice (2AFC) paradigm, leading to a binary measure for AI intensity (left  
334 AI more intense vs. right AI more intense). The analysis of AI intensity is based on studying the  
335 distribution of  $\Delta Adapt$  intervals for which the AI evoked by the left or right adaptor was rated as  
336 most intense.

337 In the top row of Fig. 8 the left (right) panel displays the distribution of  $\Delta Adapt$  in PB (MIB)  
338 trials for which subjects reported to have perceived a more intense right AI (dark grey, inverted  
339 bars) or left AI (light grey, upright bars). The bins closest to  $\pm 0.4$ s are represented strongest, be-  
340 cause trials with short  $\Delta Adapt$  occurred more often than those with long  $\Delta Adapt$ . Subjects did not  
341 show a significant suppression bias. They did show a bias for perceiving a more intense right AI in  
342 the MIB condition, but not the PB condition. The bottom panels show normalized data from the  
343 panel above: for each bin the number of trials when the right AI was perceived to be more intense  
344 was subtracted from that when the left AI was perceived to be more intense and then divided by  
345 their sum. Thus, a  $y$  value of +1 (–1) means that for all trials in this  $\Delta Adapt$  interval the left  
346 (right) AI was perceived as more intense, while a value of 0 indicates that the left and right AI  
347 were rated most intense equally often. The PB data show clearly the expected trend: the longer  
348 one adaptor was presented compared to the other, the more likely it is that it induced the more  
349 intense AI. Such a trend does not occur for the MIB condition. When the left adaptor was sup-  
350 pressed, subjects were about equally likely to perceive the right or left AI to be more intense. Sur-  
351 prisingly, when the right adaptor was suppressed, subjects were more likely to perceive the right  
352 AI to be more intense.

353 The analysis of AI intensity data recorded for subject mk revealed similar results: a clear effect  
354 of the physical difference in adaptation on AI intensity, and no effect of a perceptual difference in  
355 adaptation (data not shown). In summary, the results obtained by averaging across 16 individual  
356 subjects are in perfect accord with those described in detail for one subject.

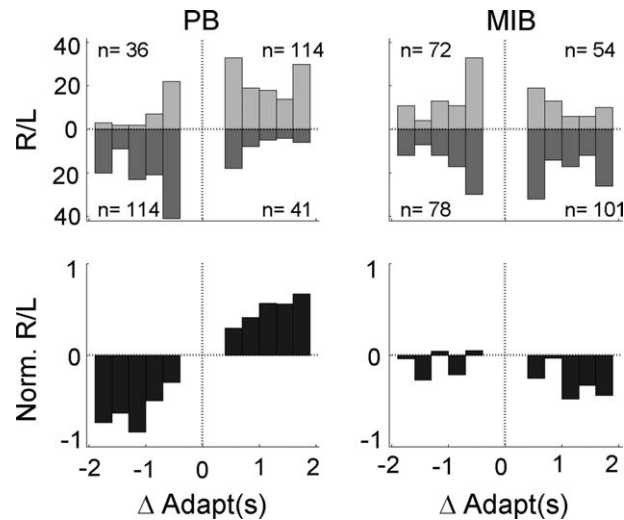


Fig. 8. Histograms analyzing the 2AFC intensity rating over  $\Delta$ Adapt intervals. The left and the right plots display the results for the PB and MIB condition, respectively. Bins of 0.3 s width range from  $-1.9$  s (left triggering suppression) to  $+1.9$  s (right triggering suppression). Top panels: distributions when the left (light grey, upright bars) and right (dark grey, inverted bars) AI was rated as most intense. The values in the corner of the four quadrants are the sum of their histograms, i.e., indicate how often the left/right AI was rated as more intense when the left/right adaptor was perceived longer. Bottom panels: Normalized histograms  $[L - R/(L + R)]$ . As expected, the adaptor presented for the longest time tended to yield the more intense afterimage. There is no such trend when the adaptor was suppressed by MIB.

#### 357 4. Discussion

358 Aftereffects have been referred to as the “psychologist’s microelectrode” (Frisby, 1979) because  
359 they permit the noninvasive study of the relationship between perception and its underlying neural  
360 processes. Crick and Koch suggested that aftereffects induced by invisible stimuli constitute a use-  
361 ful tool in the search of the neuronal correlates of consciousness, NCC (Crick & Koch, 1995; see  
362 also Blake, 1997). Here, we present experiments that study the effect of MIB of the inducing stim-  
363 uli on the persistence and intensity of negative AIs.

364 We measured AIs immediately after one of two moderate-intensity, colored adaptors had been  
365 temporarily perceptually suppressed due to MIB. Playback (PB) trials, in which the adaptors were  
366 physically removed in a way mimicking the perception in MIB trials served as controls. As expect-  
367 ed, the intensity and duration of AIs were reduced by the physical removal of the adaptor in the  
368 PB condition. However, equivalent perceptual suppression of the adaptor in the MIB condition  
369 did not reduce intensity or persistence of AIs.

370 As discussed in Section 2, we assumed that the more recent the physical or perceptual removal  
371 of the adaptor, the stronger its impact on the strength of the AI. Accordingly, we analyzed  $\Delta$ AI as  
372 a function of  $\Delta$ Adapt, the duration of the suppression interval that triggered the AI measurement  
373 (see Fig. 2). It could be argued, however, that the total difference in suppression between the left  
374 and the right adaptor during the adaptation phase would constitute a more appropriate measure  
375 for the difference in adaptation. We performed this analysis and obtained highly similar results for  
376 both AI persistence and AI intensity.

377 In summary, MIB does not disrupt the formation of afterimages. To discuss the implications of  
378 this finding, we will briefly review what is known about the formation of AIs and the sites involved  
379 in MIB.

#### 380 4.1. *The formation of AIs*

381 Although AIs have been investigated for centuries (see, e.g., Goethe, 1810/1970; Helmholtz,  
382 1867/1962; Hering, 1874), the processes underlying their formation is still not completely under-  
383 stood. The term “afterimage” is used to describe a family of phenomena which are likely to have  
384 different origins (Gerrits, van Erning, & Eijkman, 1988; Sakitt, 1976). At least two types of AIs  
385 must be differentiated: positive and negative AIs. A positive AI has a color and contrast polarity  
386 similar to that of the adapting stimulus. Positive AIs are induced by brief exposure to high inten-  
387 sity stimuli and are mostly attributed to photochemical bleaching in rods and cones (Brindley,  
388 1962; Sakitt, 1976). We study negative AIs induced by prolonged exposure to non- or only weakly  
389 bleaching adaptors. The origin of negative AIs is generally assigned to neural adaptation (see, e.g.,  
390 Wilson, 1997). Electrophysiological and psychophysical studies clearly demonstrate a contribu-  
391 tion of retinal and LGN cells to the formation of negative AIs (Virsu & Laurinen, 1977; Virsu,  
392 Lee, & Creutzfeld, 1977). Assigning the formation of AIs purely to such low-level processes is con-  
393 sistent with the general finding that AIs do not transfer from the adapted eye to the other. How-  
394 ever, it has been suggested that cortical neurons also participate in and modulate the formation of  
395 negative AIs (Chan, Crutch, & Warrington, 2001; Davis, 1973; Hayhoe & Williams, 1984;  
396 Loomis, 1972, 1978; Schiller & Dolan, 1994; Weiskrantz, 2002; Weiskrantz, Cowey, & Hodi-  
397 nott-Hill, 2002). For example, Hadjikhani et al. (1998) presented fMRI data indicating that per-  
398 ception of negative AIs correlates with an increase in the BOLD signal in an extrastriate area  
399 (which they call V8), much more than it does in earlier cortical areas. Suzuki and Grabowecy  
400 (2003) demonstrated that attention during adaptation modulates consecutive AI perception and  
401 argue that this effect is most likely caused by attentional modulation of polarity sensitive cells  
402 in IT and V4. Shimojo et al. (2001) showed that negative AIs can be induced in the absence of  
403 a local adaptor, i.e., without the direct stimulation of retinal cells. The authors studied AIs in-  
404 duced by perceptually filled-in surfaces. The strength of these AIs correlated with the subjects’  
405 ability to perceptually fill-in the illusory contour generated by several inducers in the adaptation  
406 phase. It did not correlate—but instead rived—with the AIs produced by the inducers them-  
407 selves. The authors concluded that this type of negative AIs must be caused by the adaptation  
408 of a cortical representation of surface. Such findings imply that low-level processes alone are in-  
409 sufficient to explain the generation of AIs and that these phenomena are more complex than often  
410 assumed.

#### 411 4.2. *What do we know about MIB?*

412 Even in the absence of a moving background, perceptual fading of stimuli eventually occurs  
413 under stabilized viewing conditions (Troxler, 1804). MIB, however, occurs suddenly, may be ex-  
414 perience after very brief observation times, and is stronger when the contrast of the target is high  
415 (Bonneh et al., 2001). Because slowly moving or flickering target stimuli can also be perceptually  
416 suppressed by MIB, this phenomenon is unlikely to be caused by retinal, local adaptation

417 (Bonneh et al., 2001). Furthermore, MIB is not a form of local masking, as suppression still oc-  
418 curs if a protection zone around the stationary, yellow stimuli prevents spatial interactions be-  
419 tween the moving elements and the target. Recent studies revealed that MIB has no detectable  
420 effect on orientation-specific adaptation (Kouhsari et al., 2004) and that MIB is sensitive to cues  
421 that affect grouping (Bonneh et al., 2001; Hsu et al., 2004) or surface completion (Graf, Adams, &  
422 Lages, 2002), processes usually assigned to striate and even extrastriate visual areas. Thus, there is  
423 evidence that MIB is a cortical phenomenon, and indications that it originates in extrastriate cor-  
424 tex.

425 This study demonstrates that MIB does not significantly affect the strength of negative AIs in-  
426 duced by moderate intensity, colored adaptors. Therefore, in the presence of a physical adaptor,  
427 there is no significant contribution to the formation of negative AIs beyond the sites mediating  
428 MIB. These findings are consistent with an earlier study suggesting that binocular rivalry does  
429 not reduce afterimage formation (Lack, 1978) and the common hypothesis that the generation  
430 of negative AIs is generated mostly by low-level processes. Our study is restricted in that it only  
431 allows us to infer the relative location of sites governing AI formation and MIB. A better under-  
432 standing of the precise mechanisms underlying MIB will enhance the power of this study. Our re-  
433 sults show that AI perception is not modulated by the perceived exposure time. It has been  
434 suggested, that afterimages constitute a tool for defining the visual NCC (Kirschfeld, 1999).  
435 Our findings imply that the neurons mediating the formation of AIs are not part of the visual  
436 NCC.

#### 437 **Acknowledgment**

438 This research was supported by grants from NSF, NIMH, and the Keck Foundation to C.K.,  
439 and Swiss National Science Foundation Grant 31-67980.02 to D.C.K. We thank Peter König for  
440 providing laboratory equipment and Wolfgang Einhäuser, Jörg Hipp, and Farshad Moradi for  
441 valuable feedback on the manuscript.

#### 442 **References**

- 443 Anstis, S., Rogers, B., & Henry, J. (1978). Interactions between simultaneous contrast and coloured afterimages. *Vision*  
444 *Research*, 18, 899–911.
- 445 Bachmann, T. (2000). *Microgenetic approach to the conscious mind*. Amsterdam: Johns Benjamins.
- 446 Blake, R. (1997). What can be perceived in the absence of visual awareness? *Current Directions in Psychological*  
447 *Science*, 6, 157–162.
- 448 Blake, R., & Fox, R. (1974). Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature*, 249,  
449 488–490.
- 450 Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, 3, 13–21.
- 451 Blakemore, C. B., & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively  
452 sensitive to the orientation and size of retinal images. *Journal of Physiology*, 203, 237–260.
- 453 Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature*, 411,  
454 798–801.
- 455 Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433–436.
- 456 Breitmeyer, B. G. (1984). *Visual masking: An integrative approach*. Oxford: Oxford University Press.



- 457 Breitmeyer, B. G., & Ögmen, H. (2000). Recent models and findings in visual backward masking: A comparison,  
458 review, and update. *Perception & Psychophysics*, *62*, 1572–1595.
- 459 Brindley, G. S. (1962). Two new properties of foveal after-images and a photochemical hypothesis to explain them.  
460 *Journal of Physiology*, *164*, 168–179.
- 461 Carter, O. L., & Pattigrew, J. D. (2003). A common oscillator for perceptual rivalries. *Perception*, *32*, 295–305.
- 462 Chan, D., Crutch, S. J., & Warrington, E. K. (2001). A disorder of colour perception associated with abnormal colour  
463 after-images: A defect of the primary visual cortex. *Journal of Neurology, Neurosurgery and Psychiatry*, *71*, 515–517.
- 464 Craik, W. J. K. (1940). Origin of afterimages. *Nature*, *148*, 512.
- 465 Crick, F., & Koch, C. (1995). Are we aware of neural activity in the visual cortex? *Nature*, *375*, 121–123.
- 466 Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, *6*, 119–126.
- 467 Davis, P. (1973). The role of central processes in the perception of visual after-images. *British Journal of Psychology*, *64*,  
468 325–338.
- 469 Engel, A. K., Fries, P., König, P., Brecht, M., & Singer, W. (1999). Temporal binding, binocular rivalry, and  
470 consciousness. *Consciousness and Cognition*, *8*, 128–151.
- 471 Frisby, J. P. (1979). *Seeing: Illusion, brain, and mind*. Oxford: Oxford University Press.
- 472 Gerrits, H. J., van Erning, L. J., & Eijkman, E. G. (1988). Afterimages: A collective term for percepts of different origin.  
473 *Experimental Brain Research*, *72*, 279–286.
- 474 von Goethe, J. W. (1810/1970). *Theory of colours* (English translation by Eastlake, C. L.). Cambridge, MA: The MIT  
475 Press.
- 476 Graf, E. W., Adams, W. J., & Lages, M. (2002). Modulating motion-induced blindness with depth ordering and surface  
477 completion. *Vision Research*, *42*, 2731–2735.
- 478 Hadjikhani, N., Liu, A. K., Dale, A. M., Cavanagh, P., & Tootell, R. B. (1998). Retinotopy and color sensitivity in  
479 human visual cortical area V8. *Nature Neuroscience*, *1*, 235–241.
- 480 Hayhoe, M. M., & Williams, D. R. (1984). Disappearance of afterimages at ‘impossible’ locations. *Perception*, *13*,  
481 455–459.
- 482 He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, *383*,  
483 334–337.
- 484 He, S., & MacLeod, D. I. (2001). Orientation-selective adaptation and tilt after-effect from invisible patterns. *Nature*,  
485 *411*, 473–476.
- 486 von Helmholtz, H. (1867/1962). *Treatise on physiological optics* (Vol. 3, English translation by Southall, J. P. C.). New  
487 York: Dover Press.
- 488 Hering, E. (1874/1964). *Outlines of a theory of the light sense* (English translation by Hurvich, L. M.). Cambridge, MA:  
489 Harvard University Press.
- 490 Hsu, L. C., Yeh, S. L., & Kramer, P. (2004). Linking motion-induced blindness to perceptual filling-in. *Vision Research*  
491 (in press).
- 492 Kelly, D. H., & Martinez-Uriegaz, E. (1993). Measurement of chromatic and achromatic afterimages. *Journal of the*  
493 *Optical Society of America*, *10*, 29–37.
- 494 Kirschfeld, K. (1999). Afterimages: A tool for defining the neural correlate of visual consciousness. *Consciousness and*  
495 *Cognition*, *8*, 462–483.
- 496 Koch, C. (2004). *The quest for consciousness: A neurobiological approach*. Denver, Colorado: Roberts Publishers.
- 497 Kouhsari, L. M., Moradi, F., Zand-Vakili, A., & Esteky, H. (2004). Orientation-selective adaptation in motion-induced  
498 blindness. *Perception*, *33*, 249–254.
- 499 Lack, L. C. (1978). Selective attention and the control of binocular rivalry. In Barendregt, et al. (Eds.). *Psychological*  
500 *studies* (Vol. 11). The Hague, The Netherlands: Mouton Publishers.
- 501 Lamme, V. A., Zipser, K., & Spekreijse, H. (2002). Masking interrupts figure-ground signals in V1. *Journal of Cognitive*  
502 *Neuroscience*, *14*, 1044–1053.
- 503 Lee, S. H., & Blake, R. (2002). V1 activity is reduced during binocular rivalry. *Journal of Vision*, *2*, 618–626.
- 504 Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkey’s percepts during  
505 binocular rivalry. *Nature*, *379*, 549–553.
- 506 Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivaling during binocular rivalry?. *Nature*, *380*,  
507 621–624.

- 508 Logothetis, N. K. (1998). Single units and conscious vision. *Philosophical Transactions of the Royal Society of London.*  
509 *Series B, Biological Sciences, 353*, 1801–1818.
- 510 Loomis, J. (1972). The photopigment bleaching hypothesis of complementary afterimages: A psychophysical test.  
511 *Vision Research, 12*, 1587–1594.
- 512 Loomis, J. (1978). Complementary afterimages and the unequal adapting effects of steady and flickering light. *Journal*  
513 *of the Optical Society of America, 68*, 411–416.
- 514 Macknik, S. L., & Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual  
515 system. *Nature Neuroscience, 1*, 144–149.
- 516 Maffei, L., Fiorentini, A., & Bisti, S. (1973). Neural correlate of perceptual adaptation to gratings. *Science, 182*,  
517 1036–1038.
- 518 Merikle, P. M., Smilek, D., & Eastwood, J. D. (2001). Perception without awareness: Perspectives from cognitive  
519 psychology. *Cognition, 79*, 115–134.
- 520 Metzinger, T. (1995). The problem of consciousness. In T. Metzinger (Ed.), *Conscious experience*. Imprint Academic,  
521 Schöningh.
- 522 Metzinger, T. (2000). In T. Metzinger (Ed.), *Neural correlates of consciousness*. The MIT Press, Cambridge,  
523 Massachusetts.
- 524 Movshon, J. A., & Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature, 278*, 850–852.
- 525 Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial*  
526 *Vision, 10*, 437–442.
- 527 Rajimehr, R. (2004). Unconscious orientation processing. *Neuron, 41*, 663–673.
- 528 Rolls, E. T., Tovee, M. J., & Panzeri, S. (1999). The neurophysiology of backward visual masking: Information  
529 analysis. *Journal of Cognitive Neuroscience, 11*, 300–311.
- 530 Sakitt, B. (1976). Psychophysical correlates of photoreceptor activity. *Vision Research, 16*, 129–140.
- 531 Schiller, P. H., & Dolan, R. P. (1994). Visual aftereffects and the consequences of visual system lesions on their  
532 perception in the rhesus monkey. *Visual Neuroscience, 11*, 643–665.
- 533 Shimojo, S., Kamitani, Y., & Nishida, S. (2001). Afterimage of perceptually filled-in surface. *Science, 293*, 1677–1680.
- 534 Suzuki, S., & Grabowecy, M. (2003). Attention during adaptation weakens negative afterimages. *Journal of*  
535 *Experimental Psychology: Human Perception and Performance, 29*, 793–807.
- 536 Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision*  
537 *Research, 32*, 1349–1357.
- 538 Troxler, D. (1804). Über das Verschwinden gegebener Gegenstände innerhalb unsers Gesichtskreises. In K. Himley, &  
539 J. A. Schmidt (Eds.). *Ophthalmologische Bibliothek* (Vol. 2). Jena: Fromann.
- 540 Virsu, V., & Laurinen, P. (1977). Long-lasting afterimages caused by neural adaptation. *Vision Research, 17*, 853–860.
- 541 Virsu, V., Lee, B. B., & Creutzfeld, O. D. (1977). Dark adaptation and receptive field organization of cells in the cat  
542 lateral geniculate nucleus. *Experimental Brain Research, 27*, 35–50.
- 543 Weiskrantz, L. (2002). Prime-sight and blindsight. *Consciousness and Cognition, 11*, 568–581.
- 544 Weiskrantz, L., Cowey, A., & Hodinott-Hill (2002). Prime-sight in a blindsight subject. *Nature Neuroscience, 5*, 101–  
545 102.
- 546 Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Generalized flash suppression of salient visual targets. *Neuron*,  
547 39, 1043–1052.
- 548 Wilson, H. R. (1997). A neural model of foveal light adaptation and afterimage formation. *Visual Neuroscience, 14*,  
549 403–423.
- 550 Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research, 24*, 471–478.
- 551 Zeman, A. (2001). Consciousness. *Brain, 124*, 1263–1289.
- 552