

Opposing effects of attention and consciousness on afterimages

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Edited* by Anne Treisman, Princeton University, Princeton, NJ, and approved March 31, 2010 (received for review November 17, 2009)

The brain's ability to handle sensory information is influenced by both selective attention and consciousness. There is no consensus on the exact relationship between these two processes and whether they are distinct. So far, no experiment has simultaneously manipulated both. We carried out a full factorial 2 × 2 study of the simultaneous influences of attention and consciousness (as assayed by visibility) on perception, correcting for possible concurrent changes in attention and consciousness. We investigated the duration of afterimages for all four combinations of high versus low attention and visible versus invisible. We show that selective attention and visual consciousness have opposite effects: paying attention to the grating decreases the duration of its afterimage, whereas consciously seeing the grating increases the afterimage duration. These findings provide clear evidence for distinctive influences of selective attention and consciousness on visual perception.

awareness | continuous flash suppression | Troxler fading | dual-task | visibility

Since the latter part of the past century, interest in the influences of selective attention and consciousness on perception has steadily increased. This discussion has raised the question of the relationship between attention and consciousness. By attention, we refer to selective perceptual attention and not vigilance or arousal; by consciousness, we refer to the content of consciousness (sometimes also referred to as awareness), and not to states of consciousness (e.g., wakefulness, dreamless sleep, or coma). Though some claim that both processes are inextricably connected (1–4), others suggest a certain level of independence (5–14). Psychophysical studies show that observers can pay attention to an invisible stimulus (15, 16), and that a stimulus can be clearly seen in the (near) absence of attention (4, 17). Though these data could be explained by arguing that these two processes covary and therefore any increase (respectively decrease) in one is associated with a similar but smaller increase (respectively decrease) in the other, this argument fails if attention and consciousness were to have opposing perceptual effects on the same stimulus. Finding such opponency would considerably strengthen the hypothesis that these processes are distinct (5).

Afterimage duration is a well-suited measure for the study of attention and consciousness. Changes in afterimage durations reflect the attentional and visibility manipulations during the afterimage induction phase. This permits the temporal separation of the attentional/visibility manipulations on the afterimage inducer and their subjective monitoring, and the measurement of the resultant effects (e.g., on afterimage appearance). This procedure effectively obviates the need for a simultaneous dual-task procedure.

Many afterimage and aftereffect studies are devoted to the influences of attention or consciousness in isolation. For example, removing stimuli from conscious content via various masking techniques that manipulate visibility decreases the motion aftereffect durations (18–20), tilt aftereffect (e.g., ref. 16, but see ref. 21), and face adaptation (22), and they do so as well for afterimages (23, 24; but see refs. 25–27). Similarly, attentional withdrawal decreases the size of the aftereffect for real (16, 28–

30) and illusory lines (31), and for motion (32–36) and face (22) aftereffects. Curiously, though, attentional withdrawal seems to increase the duration of afterimages induced by real (37–40) and illusory adaptors (41). These latter findings beg the question: Could attention and consciousness affect perception in different and experimentally separable ways, even though up to now they have been found to work synergistically (4, 42)? Note that these previous findings cannot answer that question, because they have not been controlled for confounding concurrent changes in attention and consciousness levels. Therefore their interpretation in the present context is merely suggestive.

To our knowledge, no experiment to date has probed the simultaneous effects of both attention and consciousness on perception, while also controlling for possibly confounding stimulus and task changes (recently, one study [40] has gone a long way toward reducing confounding stimulus changes). Therefore, it is not known whether these two processes can induce different perceptual effects within a single controlled stimulus set, when all stimulus parameters and the task structure are identical, and when attention and visibility levels are not confounded.

We carefully investigated this issue, focusing on the formation of afterimages. We used methods that independently vary the amount of selective attention and stimulus consciousness. Therefore, even though until now, attention and consciousness have been shown to act synergistically (e.g., refs. 4 and 42), we are able to show that selective attention and stimulus consciousness can have different, even opposing, effects.

Results

Attention and Visibility Differently Affect Afterimage Duration. In experiment 1, while manipulating attention via a demanding central task, we simultaneously manipulated the visibility of the stimulus via perceptual suppression. The independent manipulation of both allowed us to study high-attention and visible, low-attention and visible, high-attention and invisible, and low-attention and invisible conditions (Fig. 1A) using an identical adaptor stimulus and a single experimental paradigm.

Attention was manipulated by having subjects perform an attention-demanding central rapid serial visual presentation (RSVP) task (37, 43, 44; *Materials and Methods*) that drew attention away from the inducing stimulus, a gray Gabor patch (a Gaussian-windowed grating; i.e., inducer not/slightly attended), or having subjects report on the possible perceptual disappearances of the physically present Gabor (i.e., inducer highly attended). Note that throughout the text, we will refer to conditions where subjects attend to a central task as low-attention condition, in the sense that the amount of attention available for the adaptor is low (43). To

Author contributions: J.J.A.v.B., N.T., and C.K. designed research; J.J.A.v.B. performed research; J.J.A.v.B. analyzed data; and J.J.A.v.B., N.T., and C.K. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.0913292107/-DCSupplemental.

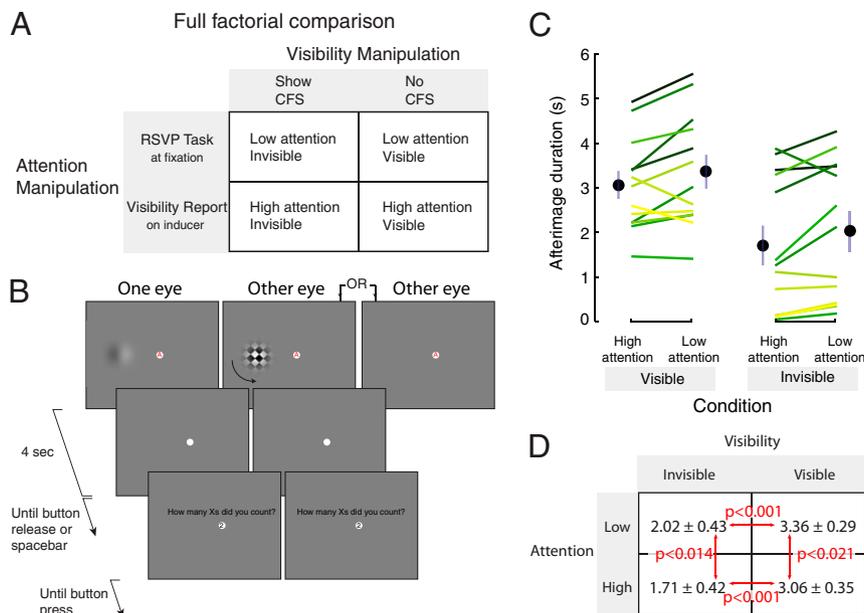


Fig. 1. Experiment 1. (A) Our study used a 2×2 full-factorial design, independently manipulating the levels of attention and visibility. (B) Each trial started with 4-s peripheral adaptation of a Gabor patch. Attention was modulated by having observers report on the perceptual (dis)appearance of the inducer (high-attention condition) or count the number of Xs that appeared in a central RSVP task (low-attention condition). Perceptual visibility was modulated by showing, or not showing, a rapidly flickering and rotating high-contrast stimulus in the eye contralateral to the afterimage inducer, while the adaptor was physically present throughout the trial (23). After the induction phase, observers indicated how long their afterimage lasted, by pressing and releasing a button. Finally, they entered how many Xs were counted (or they ignored the question in the high-attention conditions). (C) Afterimage durations depend on visibility and attention levels ($n = 13$ subjects; each subject has a different color). When the inducer stimulus is highly attended, afterimages are shorter than when the stimulus is not/ slightly attended (in both visible and invisible conditions). Visible trials have longer afterimage durations than invisible trials, for both high-attention and low-attention conditions. (D) A table with mean \pm SEM afterimage durations, and P values of statistical comparisons based on paired one-tailed t tests.

maximize the difference between high-attention and low-attention conditions, subjects did not report the visibility of the Gabor when they were performing the RSVP task (i.e., no dual task) (31, 45). We independently manipulated the visibility of the afterimage inducer, which was always present, by showing (or not) a strongly competing stimulus in the contralateral eye (23, 24). This continuous flash suppression (CFS) technique renders the Gabor perceptually invisible, even though the stimulus is physically present at the retina (Fig. 1B).

We first verified that our attentional manipulation worked. Average performance on the RSVP task was $54 \pm 5\%$ correct when the inducer was visible, and $47 \pm 4\%$ when the inducer was invisible (not significant, $P > 0.15$, two-tailed paired t test). Both measures were significantly higher than chance, 25% (both $P < 0.0005$, two-tailed t test), but also below 100%, indicating that the task was demanding. Only correct trials were included in the following analyses.

We found that afterimage duration (as indicated by the subjects' button presses) depended on both attention and visibility: paying attention to the stimulus reduces afterimage duration (from mean \pm SEM: 3.36 ± 0.29 s to 3.06 ± 0.35 s in visible conditions, and from 2.02 ± 0.43 s to 1.71 ± 0.42 s in invisible conditions), whereas visibility of the stimulus increases afterimage duration (from 1.71 ± 0.42 s to 3.06 ± 0.35 s in high-attention conditions, and from 2.02 ± 0.43 s to 3.36 ± 0.29 s in low-attention conditions; Fig. 1C). This observation is confirmed with a two-way repeated-measures ANOVA, which showed significant main effects of attention ($P < 0.001$) and visibility ($P = 0.006$), with no interaction ($P > 0.9$). Both of these effects were also significant in two-way ANOVAs in four individual subjects; an additional seven subjects showed a significant effect of visibility. Further support for separable influence of attention and consciousness comes from comparing the different conditions separately (Fig. 1D). We found that the attentional effects are significant in both visible and invisible conditions (both

show a decrease of 300 ms, $P < 0.021$ and $P < 0.014$, respectively, paired one-tailed t test). Our observation that attention affects the processing of invisible stimuli is consistent with a recent fMRI study (46). Likewise, visibility effects are significant in both high- and low-attention conditions (increases of 1.4 s and 1.3 s, respectively, both $P < 0.001$, paired one-tailed t test). Furthermore, there is a strong correlation between afterimage duration in high- and low-attention conditions (Spearman rank correlation [over subjects]: $\rho = 0.95$; $P < 0.001$), and also between visible and invisible conditions ($\rho = 0.75$; $P < 0.005$), suggesting that the same underlying processes are responsible for the afterimage production in high- versus low-attention conditions, and visible versus invisible conditions.

Based on our task design, we believe eye movements were unlikely to influence these effects in experiment 1 (SI Materials and Methods; Fig. S1). We also confirmed that the results did not change when we excluded trials in which subjects reported not seeing any afterimage (SI Materials and Methods; Fig. S2). These data clearly show that attention and visibility can have opposite effects on visual perception, and that these effects do not interact significantly.

Control for Task Differences. Although our comparison of high- and low-attention conditions was based on similar conditions, the attention task during the adaptation, as well as during the afterimage monitoring, differed (the subject had to remember a number in the low-attention condition, which was not required in the high-attention condition).

In experiment 2a, attention to the inducer was manipulated by making a single central RSVP task more or less difficult (47) (Materials and Methods). We confirmed that the attentional manipulation worked: performance on the RSVP task was $80 \pm 8\%$ in the easy task and $61 \pm 5\%$ in the hard task ($P < 0.01$, paired t test). Again, we found a significant effect of attention and visibility (Fig. 2). A two-way repeated-measures ANOVA showed significant

effects of attention ($P < 0.01$) and visibility ($P < 0.03$), and no interaction ($P > 0.15$). The effect of attention was significant in both visible and invisible cases ($P < 0.030$ and $P < 0.021$, respectively, paired one-tailed t tests), and the effect of visibility was significant under both high and low attention (both $P < 0.001$). Therefore, when the task structure was kept identical, and only perceptual load on the central task differed, increased attention to the inducer reduced afterimage duration.

In experiment 2b, we reran experiment 2a on 10 subjects (of which four participated in the previous version as well) while monitoring their eye movements. Eye movements can potentially influence our data in three ways: (i) small eye-movements will jitter the stimulus on the retina, thereby decreasing adaptation (48) and consequently reducing afterimage duration; (ii) subjects might keep fixation at the central task when it is difficult, while fixating the peripheral stimulus when the central task is easy, potentially introducing a confound; and (iii) eye movements during the induction phase might cause the interocular suppression to fail (49), thereby making the stimulus visible when it should be invisible. When analyzing subjects' eye movements, we found no correlation between SDs in eye position parallel or orthogonal to the stimulus orientation and the afterimage duration, (control for point *i* above; *SI Materials and Methods*). We excluded trials in which subjects did not fixate the fixation mark, and trials in which a saccade was detected (control for points *ii* and *iii*). With these controls in place, the results (Fig. S3) confirm that attention decreased afterimage duration, whereas visibility increased afterimage duration [repeated-measures ANOVA: main effects of attention ($P = 0.03$) and visibility ($P = 0.005$), with no interaction ($P > 0.25$)].

Attention and Visibility Effects over a Range of Contrasts. Are our visibility findings simply due to the strong interocular suppressor? In experiment 3, we measured the effects of attention and visibility on afterimage duration while varying the contrast of the suppressing CFS. The CFS contrast ranged from 0% (i.e., no CFS) to perithreshold (1.6–6.3%) to suprathreshold (12.5–100%) contrast values; the inducing Gabor patch contrast was fixed at 34%.

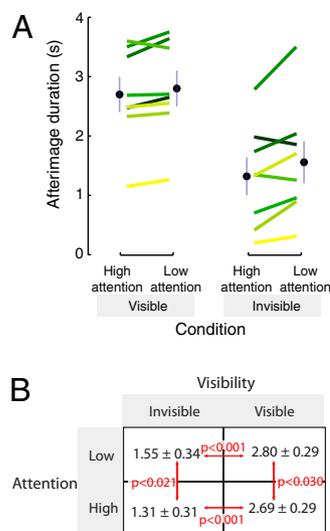


Fig. 2. Experiment 2: Changing perceptual load. The amount of attention paid to the afterimage-inducing stimulus was manipulated by using a difficult or easy RSVP task at fixation, leading to low- and high-attention conditions respectively. (A) Increased attention to the inducer stimulus led to decreased afterimage durations, whereas increased visibility led to increased afterimage durations (both $P < 0.03$, two-way repeated-measures ANOVA). (B) A table with mean \pm SEM afterimage durations, and P values of statistical comparisons based on paired one-tailed t tests.

The effects of CFS (compared with the 0% contrast, no CFS condition) are significant ($P < 0.05$, one-tailed t test) for contrasts $>6\%$ and $>12\%$ for high- and low-attention conditions, respectively (Fig. 3A), which is also the contrast when it was strong enough to cause visibility changes in the inducer stimulus. The effect of increased attention (ΔAI) was significant (i.e., $P < 0.05$, one-tailed t test) for CFS with 0% contrast, and for contrasts $>12\%$ (Fig. 3B). Therefore, our conclusions in experiment 1 are not just the result of the specific settings of the CFS stimulus.

We fail to see significant attentional effects with CFS at perithreshold contrasts of 1.6–6.3% (Fig. 3B). It is now well established that stimuli around the detection threshold attract attention (50, 51). Therefore, the perithreshold CFS stimuli probably attracted the subjects' attention, even when the distracting RSVP task was performed. This explains why at these contrasts the low-attention conditions fall on top of the attended conditions (as if they were "highly attended" conditions; Fig. 3A).

Controls for Stimulus Differences. Could the mere presence or absence of the CFS stimulus have caused our visibility effects? Conceivably, interocular masking could increase contrast adaptation, thereby increasing detection thresholds and, ultimately, reducing afterimage durations (40, 52, 53). However, we already showed that qualitatively identical and significant results are obtained at CFS mask Michelson contrasts as low as $\sim 10\%$ (see previous section). To more stringently control for the possible influences of CFS and contrast threshold increases on visibility, we performed an experiment in which subjects always viewed the same Gabor, and the same CFS mask.

In experiment 4, the contrast of the CFS mask was determined for each subject, such that in about half of all trials the afterimage-inducing Gabor patch was perceptually invisible, whereas in the remaining half the Gabor was visible to a variable extent. Because all conditions were otherwise identical (including the CFS stim-

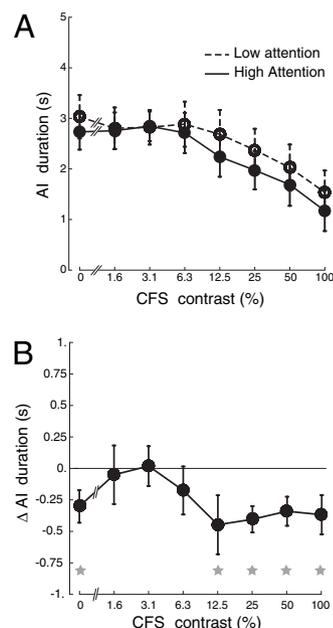


Fig. 3. Effects of CFS contrast. (A) The CFS mask started to have a suppressing effect on afterimage durations at contrasts higher than $\sim 6\%$. This is also when the mask started to have effects on the visibility of the afterimage inducer, which was kept at a fixed contrast of 34%. (B) The difference in afterimage duration between high- and low-attention conditions. The effects of attention were present without suppressor CFS (i.e., zero contrast), and for CFS contrasts larger or equal to 12%. Stars represent significance at the 0.05 level for one-tailed t tests, e.g., $P < 0.025$ for 0% and 100% contrast. Bars are SEM.

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