Opposing effects of attention and consciousness on afterimages

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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 x 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 gratings decreases the duration of its afterimage, whereas consciously seeing the gratings increases the afterimage duration. These findings provide clear evidence for distinctive influences of selective attention and consciousness on visual perception.

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 invisible, and high-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
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 presented, 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 ± 5% correct when the inducer was visible, and 47 ± 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 ± 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]: ρ = 0.95; P < 0.001), and also between visible and invisible conditions (ρ = 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 ± 8% in the easy task and 61 ± 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 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%.

The effects of CFS (compared with the 0% contrast, no CFS contrast) 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 ($\Delta$AI) 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-

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**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.

**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.
The sole variant was perceptual visibility. The data confirmed the previous experiments: visible trials led to longer afterimages (1.79 ± 0.23 s) than invisible trials (1.52 ± 0.27 s, *P* = 0.02, paired one-tailed *t* test, also significant in 8/10 individual subjects; Fig. 4A). An auxiliary linear regression (Fig. 4B; SI Materials and Methods) showed a slope of 0.13 (*R*² = 0.96, *P* < 0.001), leading to a 0.51-s increase in afterimage duration for 4 s—the trial duration—of visibility. Furthermore, there was a significant correlation between the individual subjects’ effects of visibility in this experiment and in experiment 1 (*ρ* = 0.67, *P* < 0.05), suggesting that the same process was at work.

In experiment 5, we removed the CFS stimulus altogether, and decreased the inducer contrast to 6%, such that intermittent peripheral Troxler fading occurred (54). This fading caused trial-by-trial variations in stimulus visibility. Again we found that the longer the perceptual visibility of the inducer, the longer the afterimage (Fig. 5, linear regression: *R*² = 0.8, *P* < 0.005, slope = 0.25, leading to a 1.0-s increase in afterimage duration for 4 s—the trial duration—of visibility).

Experiments 4 and 5 confirm that perceptual visibility (i.e., whether the subject is conscious of the stimulus) is a significant factor in afterimage formation above and beyond the physical presence of the adaptor. The presence or absence of CFS affects afterimage duration mainly, although perhaps not solely, through the manipulation of perceptual visibility.

**Discussion**

The relationship between selective attention and consciousness has been much debated since the 19th century. We here address this important question via a direct comparison on the basis of a full-factorial 2 × 2 design of afterimage perception, while controlling for the effects of stimulus and task differences, and eye movements. We show that paying more attention to the inducer invariably shortens afterimage duration, while increasing the visibility of the inducer increases afterimage duration compared with invisibility. Clearly, selective attention and stimulus consciousness have separable effects on perception, as reviewed previously (5, 7), and, in the context of afterimages, may even have opposite effects. It will be important to investigate the extent to which such a full-factorial design can show dissociations between attention and consciousness for other perceptual phenomena [a recent study used a full-factorial design in priming (55), but did not observe opposite effects of attention and consciousness].

Why would selective attention and consciousness have opposing effects when so often both act synergistically (4, 42)? What seems paradoxical is that attending to the inducer will reduce the duration of the afterimage. The effects of consciousness (visibility) are straightforward to explain: visible inducers evoke larger neuronal activity during induction of afterimages than invisible ones, resulting in stronger and longer afterimages, compared with invisible inducers. This is consistent with other forms of aftereffects (16, 18–20, 22) and with general findings in neurophysiology (e.g., ref. 56).

The counterintuitive nature of the attentional effects is a bit more difficult to explain. Suzuki and Grabowecky (37) suggested that afterimages are the result of adaptation in two stages. The first stage is sensitive to the contrast polarity of the image. This stage cares about the spatial relationship between dark and light regions of a stimulus (it could, for example, increase its response when presented with a patch that is dark on one side and light on the other side, but not to a patch with the reverse contrast polarity). This stage is the source of the afterimage, because when it is adapted and stimulated with a neutral stimulus, it will produce an afterimage of opposite polarity to the afterimage inducer. In Suzuki and Grabowecky’s framework, this stage is not critically affected by attention. Although a later study (40) did indicate that both attention and consciousness change adaptation states at this level, Suzuki and Grabowecky’s general framework remains plausible.

The second stage is not sensitive to the contrast polarity of the image. It will be activated by a patch that is dark on one side and light on the other side, and also a patch of reverse contrast-polarity, as long as the stimulus has the preferred orientation and position. This stage will modulate the strength of the subsequently perceived afterimage (40, 52, 53): when activity in this stage is high, the afterimage is strong, when activity is low, the afterimage is weak or absent. During the adaptation phase, polarity-insensitive cells will adapt more in the presence of selective attention, reducing their activity during the afterimage phase. Subsequently, this will cause the afterimages to be weaker if attention is paid during the induction phase. In this scheme, adaptation works in opposite directions in polarity-sensitive and polarity-insensitive cells. The opposite effects of attention and consciousness in our experiments can be explained if they affect adaptation at these levels differently. A computational model based on such principles reproduces the psychophysical effects of attention (38). Neurophysiological studies also support this idea: though attention modulates the firing rates of neurons in early visual areas (57, 58), perceptual invisibility in binocular rivalry has little effect on their firing activities (59–63). Clearly, attention and consciousness have different ways of influencing early visual activity, which, as we have pointed out, may cause opposing effects on afterimage duration.

There is at least one other explanation for why attention shows these paradoxical effects. We assume a single stage that is more adapted when attention is directed to the stimulus. By itself, this predicts a stronger afterimage in high-attention condition. We furthermore assume that the afterimage decays with a time constant of

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**Fig. 4.** Dependence on visibility with constant stimuli. (A) In experiment 4, with low CFS contrast (10%), about half of the trials were reported to be completely invisible. When we divided the data into completely invisible, and partly/completely visible (*n* = 10 subjects), visible trials produced longer afterimages than invisible trials (1.79 ± 0.23 s vs. 1.52 ± 0.27 s, *P* = 0.02 one-tailed *t* test). (B) When divided into 10 bins (per subject and then averaged over subjects) according to the actual reported visibility duration, there was a clear correlation (*R*² = 0.96, *P* < 0.001, slope = 0.13). Error bars SEM.

**Fig. 5.** Troxler fading. In experiment 5, with a low adaptation contrast, a stimulus would periodically fade (Troxler fading), even without any CFS stimulus present. A clear, positive correlation between visibility duration and afterimage duration was again observed (*R*² = 0.8, *P* < 0.005, slope = 0.25). Error bars SEM.
several seconds (25, 64), and that increased levels of selective attention reduce this time constant. This means that a neuron that has been modulated by increased levels of attention will return quicker from an adapted state to baseline (i.e., reduced time constants) than a neuron not modulated by attention. The shunting effects of synaptic conductance changes (65), in combination with local excitatory feedback, gives rise to effective time constants in the range of seconds (66, 67), which has the correct order of magnitude to underlie afterimages and the seemingly paradoxical effect of attention.

Although detrimental effects of attention are rare, they are not unheard of. Other examples of negative influences of attention include the expression of overlearnt skills in motor learning (68, 69), texture segregation (70), and recognition memory (71). One commonality among all four is the involvement of peripheral neuronal structures that might well be amenable to modulation by selective attention but not by consciousness. In that sense, our findings are fully compatible with the predictions of global workspace theories of consciousness (72, 73).

When attention is withdrawn, even salient stimuli can become perceptually invisible. From that perspective it may seem puzzling that we observed opposite effects when comparing low attentional processing with invisibility due to perceptual rivalry. A failure to report on a stimulus that is physically present can be induced by different psychophysical techniques (75). In particular, invisibility can be induced by perceptual suppression, such as CFS (e.g., ref. 23) or backward masking (e.g., ref. 74), or by inattention, such as inattentive blindness (4) or change blindness (42). Though the neurophysiological operations underlying perceptual invisibility remain unclear, some evidence suggests that perceptual suppression and inattentive blindness are supported by similar mechanisms (75, 76). Our findings are inconsistent with such a framework, arguing instead for distinct mechanisms. Furthermore, a recent report (77) demonstrated that subjects’ confidently report stimulus absence (i.e., miss) during perceptual suppression but not during attentional distraction. The results were quantified using type-2 signal detection theory (78). These studies imply different neuronal mechanisms for perceptual suppression (possibly due to suppressed sensory activity in the ventral visual pathway) (76) and for inattentional invisibility (possibly due to a failure of top-down attentional amplification of sensory signals from frontal-parietal cortex) (77, 78).

We suggest that selective attention and stimulus consciousness affect the perception of afterimages differently, and even oppositely. As pointed out previously (74), this makes it all the more critical to distinguish the neuronal correlates of selective attention from those of the current content of consciousness.

**Materials and Methods**

**Stimuli.** Adaptation was induced by presenting a 0.23 cycles°, 34% Michelson contrast, Gaussian-windowed (σ = 1.43°), randomly oriented grating, located 4.9° peripherally. Presentation was monocular, and balanced over the eyes over trials. This Gabor was always presented throughout the induction period (4 s). The suppressor stimulus was a Gaussian-windowed (σ = 1.43°) checkerboard (0.78 cycles°) which rotated at 150°/s, and reversed contrast every 67 ms. The contrast of this suppressor stimulus was 100% in experiments 1, 2a, and 2b, systematically varied in experiment 3, tailored for each subject in experiment 4 (for 8/10 of the subjects it was set to 9%, for 2/10 subjects it was set to 20%), and 0% for experiment 5. At subsequent trials, the Gabor was shifted around the fixation dot in counterclockwise fashion by 45°, preventing repeated adaptation at a single location. Depending on afterimage durations, and delays between subsequent trials, this leads to at least 30° (generally >50°) of deadaptation between adaptation periods at identical locations. Background luminance was 49 cd/m². All experiments were performed on a gamma-corrected monitor.

**Procedure.** In experiment 1, in the low-attention trials, attention was distracted from the afterimage-inducing stimulus by having subjects perform a rapid serial visual presentation (RSVP) task. We used RSVP of letters (red Helvetica 12-point), which were shown (133 ms, no interletter interval) within the boundaries of the fixation dot. Subjects had to count the number of Xs (n = 2–5), which was reported after the afterimage had disappeared. In the high-attention trials, the RSVP task was not performed (but the letters were shown). Instead, subjects tracked the subjective visibility of the inducer by pressing and releasing a button. Subjects did not report visibility in the low-attention trials, avoiding the need to employ attention to the inducer (in standard dual-task paradigms, subjects are forced to attend to the stimulus).

After the adaptation period, subjects indicated the duration of the afterimage with a button press and release. In experiments 1, 2a, 3, 4, and 5, when subjects perceived no afterimage, they pressed a separate button, in which case the duration of the afterimage was recorded as being 0 s in duration. Experiment 2b had no such button, and subjects merely had to quickly release the button with which the afterimage duration was indicated.

In experiment 2a and 2b, we manipulated attentional load. The attention-demanding central RSVP task was to count the number of times (n = 1, 2, 3, or 4) a cross (height: 1.9°, width: 1.4°) of a particular orientation and color appeared. Crosses were presented at fixation for 133 ms and blanked for 133 ms. Two target crosses were at least separated by one other cross. The easy task was to count the upright and inverted red crosses. The hard task was to count the number of upright yellow and inverted green crosses (but not the opposite conjunction).

According to the load theory of attention (43), in trials with the easy task the observer had more “free” attention to direct to the inducer than in trials with the hard task. Therefore, without changing the task or the stimuli, we could change the amount of attention paid to the afterimage inducer. An additional advantage of this experiment is that eye movements are highly unlikely to differ between the different conditions (47), which we empirically confirmed in experiment 2b.

Information on the number of trials, the trial inclusion criteria, and the eye movements can be found in SI Materials and Methods.

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