Attention But Not Awareness Modulates the BOLD Signal in the Human V1 During Binocular Suppression

Masataka Watanabe,1,2,3† Kang Cheng,3 Yusuke Murayama,2 Kenichi Ueno,3 Takeshi Asamizu,3 Keiji Tanaka,3 Nikos Logothetis2,4

Although recent psychophysical studies indicate that visual awareness and top-down attention are two distinct processes, it is not clear how they are neurally dissociated in the visual system. Using a two-by-two factorial functional magnetic resonance imaging design with binocular suppression, we found that the visibility or invisibility of a visual target led to only nonsignificant blood oxygenation level–dependent (BOLD) effects in the human primary visual cortex (V1). Directing attention toward and away from the target had much larger and robust effects across all study participants. The difference in the lower-level limit of BOLD activation between attention and awareness illustrates dissociated neural correlates of the two processes. Our results agree with previously reported V1 BOLD effects on attention, while they invite a reconsideration of the functional role of V1 in visual awareness.

Attention and awareness in everyday life are closely interwoven; when we attend to an object, we become visually aware of its attributes, and being aware of an object may lead to attention directed toward it. However, recent progress in psychophysics indicates that visual attention and visual awareness are two dissociated functions in the visual system (J). Top-down attention directed toward perceptually invisible stimuli leads to negative aftereffects (2) or priming (3), whereas the gist of scenes can be perceived despite the near absence of attention (4–7). Until now, there has been no clear evidence of differential neural correlates for attention and awareness.

We separately examined the effects of top-down attention and visual awareness on the blood oxygenation level–dependent (BOLD) signal in the human primary visual cortex (V1). We focused on V1 because measurements from neuromaging and electrophysiology are incongruent for both attention (8–15) and awareness (16–21), and hence the lower limit of neural modulation has become a key question for both subjects.

The experiment had a two-by-two factorial design, the factors being visibility of the target stimulus (target visible or invisible) and directed attention (attention to target or nontarget location). In conditions where attention is directed away from the target stimulus, it is of critical importance to guarantee the visibility and/or invisibility of the target without relying on a subjective report. We thus implemented a modified version of continuous flash suppression [see supporting online material (SOM)] that can constantly render a motion target stimulus invisible (22, 23). To ensure continuous visual stimulation, we presented a motion grating in one eye as the perceptual target, while multiple patches of smaller motion gratings (dynamic Mondrians) were presented either to the opposite or the same eye to manipulate the visibility. When they were shown to the opposite eye, the target was rendered invisible because of binocular suppression (Fig. 1A); when they were shown to the same eye, the target remained visible (Fig. 1B) (SOM). The overall content of visual components within a 1-s duration was counterbalanced between visible and invisible stimuli by interleaving video frames at 30 Hz. In order to obtain V1 voxels that retinotopically correspond to the target stimulus alone, a monocular region was positioned at the center of the target by placing the dynamic Mondrians in a ring-shaped region (inner diameter, 6°; outer diameter, 10°) around the periphery of the disk-shaped target (Fig. 1, A and B, and SOM).

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Supporting Online Material

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Materials and Methods

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Table S1

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*These authors contributed equally to this work.
†To whom correspondence should be addressed. E-mail: watanabe@tuebingen.mpg.de
contained 16 presentations of visible stimuli or invisible stimuli as described above (Fig. 1C). In the “visible stimulus block,” two invisible stimuli were intermingled with remaining 14 visible stimuli as catch trials in a pseudo-randomized order. Likewise in the “invisible stimulus block,” two visible stimuli were mixed with remaining 14 invisible stimuli. We set the ratio of the two types of stimuli within a block to 14:2 so that we could reliably direct the participant’s attention to the target when necessary and in the meantime maintain the high contrast in target visibility to measure the potential difference in BOLD response between the two blocks.

Attention was manipulated by asking the participant to switch between two behavioral tasks. In the “attention to target block,” the person was instructed to report the visibility of the target (a two-alternative forced choice between visible and invisible) for 16 consecutive stimulus presentations within a block. Conversely, in the “attention to nontarget block,” the person was required to detect a given character in a rapidly presented series of characters at the center of fixation (SOM). Supplementary psychophysical results indicate that inattentional blindness was less likely to occur in our stimulus condition; the participants were capable of reporting the existence of the target when interviewed after they performed the character detection task (SOM). Performance of all participants was above 90% correct for the target visibility task and above 75% correct for the letter detection task, thus ensuring that the visibility and/or invisibility of the target were indeed as intended, and that the person’s attention was faithfully directed toward the central fixation in attention to nontarget blocks.

In an additional scan session, we localized the portion of V1 corresponding to the monocular target (Fig. 1, C and D, and SOM). To assess the effects of top-down attention and visual awareness on BOLD responses within the targeted monocular region in V1, we compared measured BOLD amplitudes in the four types of stimulus blocks (represented by four color traces for each person in Fig. 2). There was no consistent effect of visibility on BOLD responses across the four participants. In two out of four participants, the visible stimulus in the attention to nontarget condition evoked a slightly higher BOLD response than the invisible stimulus ($P < 0.05$; compare red and blue traces in Fig. 2, A and C), and in one participant, the invisible stimulus in the attention to target condition led to an increased BOLD signal as compared to the visible stimulus ($P < 0.05$; compare cyan and magenta traces in Fig. 2C). In contrast, we found a highly significant effect of attention regardless of visibility conditions ($P < 0.001$) for all four participants studied. Additional experiments with simultaneously measured eye positions have ruled out the possibility that the

**Fig. 1.** Stimulus design and the location and BOLD response in the targeted monocular region. (A) The visible stimulus: The dynamic Mondrian pattern and target motion grating were both presented to the nondominant eye and were interleaved in successive video frames (at 60 Hz). This arrangement induced a transparent percept where the two stimuli spatially overlapped but the central portion (6° in diameter) of the target motion grating was constantly visible. (B) The invisible stimulus: The dynamic Mondrian pattern was presented to the dominant eye, whereas the target motion grating was presented to the nondominant eye. Video frames of the two stimuli were similarly interleaved to match the contents of the visible stimulus. During the experiment, the task instruction was signaled by the color of fixation: Red characters instructed the participant to report the visibility of the target motion grating [as exemplified in (A)], and blue characters required the participant to perform a letter detection task [as exemplified in (B)]. (C) Visible and invisible stimulus blocks: Catch stimuli were introduced so that the participant could reliably maintain attention to the target when instructed. (D) Portions of V1, shown on two oblique slices for one participant from a separate localization scan. Red pixels indicate the targeted monocular region activated by a disk-shaped counter-phasing checkerboard, and green pixels indicate the region activated by the Mondrian pattern. Slice positions on a sagittal slice and anatomical landmarks on the two oblique slices are shown on the left. CS, calcarine sulcus; V1d, dorsal V1; V1v, ventral V1; L, left. (E) Time courses of average BOLD responses in the targeted monocular region [red pixels in (D)] to the counter-phasing checkerboard (red trace) and to the ring-shaped dynamic Mondrian pattern presented either to the dominant eye (blue) or nondominant eye (cyan).
reported effects might be caused by the differences in involuntary eye movements among stimulus-task conditions (SOM).

The current results, as revealed by univariate BOLD effects, indicate that neural processes of top-down attention may extend to lower levels in the visual hierarchy as compared to the neural correlates of visual awareness. We have also conducted a multivariate pattern analysis; the results from all participants showed a near-chance classification between visible and invisible stimuli for both attentional conditions (SOM). This is in line with recent psychophysical findings that top-down attention may affect neural representations of invisible stimuli, resulting in aftereffect (2) and priming (3). The increase of the BOLD signal with attention in V1 agrees with the previous literature (8–13). However, the results regarding awareness in our study challenge the currently established view that the BOLD signal in V1 correlates robustly with the contents of percept.

The extent of the modulation of visual awareness on neuronal activity in V1 is crucial because V1 lies at the bottom of the cortical visual hierarchy. Previous studies have shown a large and significant awareness modulation on the BOLD signal in both human and monkey V1 (17, 18, 21), whereas single-unit studies have failed to detect robust perception-lock changes (16, 19–21). A similar twist exists for attention; single-unit studies claim only modest attentional effects in monkey V1 (14, 15), whereas numerous functional magnetic resonance imaging studies report a strong attentional modulation on the BOLD signal in human V1 (8–13). The previously observed discrepancy between single-unit activity and BOLD signal in V1 in visual awareness experiments could be simply explained by attentional modulation, because attention was not thoroughly controlled in these previous studies. This is indeed a major experimental complication because, without adequate control, attention and awareness are intimately interrelated. Our results suggest that this is actually the case, and the previously reported awareness modulation on the BOLD signal in V1 is likely to be an artifact caused by the concurrent attentional modulation.

Previous findings claim a functional role of V1 in awareness, which seems to be immune to the problem of attentional confounds. The phenomenon of blindsight (namely, the manifestation of residual visual processing despite the total loss of visual awareness) caused by lesions in V1 suggests a role for V1 in awareness (25, 26). However, if we assume the existence of a hypothetical area downstream of V1 as a neural correlate of awareness, a lesion in V1 would also heavily affect this area by removing a large portion of its afferent input. Transcranial magnetic stimulation (TMS) studies suggest that the feedback activity from the middle temporal area to V1 is crucial for visual awareness of TMS-induced motion phosphens (27) and motion stimuli (28). These, too, seem to contradict our results, but the claim that feedback activity to V1 is a necessary condition for awareness does not necessarily point to V1 as an area for neural modulation by the contents of conscious percept. As in the case of blindsight, downstream areas can be equally affected by the consequences of TMS application to V1. However, it should be emphasized that our current conclusions, based solely on BOLD measurements, do not completely rule out the involvement of V1 in visual awareness (see SOM for a hybrid conceptual model providing a possible interpretation of our results under the assumption that V1 activity is not modulated by awareness). Future efforts, using nonbiased and fine-scale neuronal measurement techniques that can capture the modulation in local circuits in V1 (such as specific neuronal subtypes), or using neural dynamics instead of firing rates (such as synchronization) that differ from hemodynamic measurements and conventional neural recordings, are needed to further clarify the involvement of V1 in visual awareness.

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Fig. 2. (A to D) Time courses of averaged BOLD responses and 95% confidence intervals in the targeted monocular region. The four time courses in each panel (for each of four participants) were obtained from the target visible with attention to target block (magenta), target invisible with attention to target block (cyan), target visible with attention to nontarget location block (red), and target invisible with attention to nontarget block (blue), respectively.

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