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Feedback Contributions to Visual Awareness in Human Occipital Cortex

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Summary

It has traditionally been assumed that processing within the visual system proceeds in a bottom-up, feedforward manner from retina to higher cortical areas [1]. In addition to feedforward processing, it is now clear that there are also important contributions to sensory encoding that rely upon top-down, feedback (reentrant) projections from higher visual areas to lower ones [2]. By utilizing transcranial magnetic stimulation (TMS) in a metacontrast masking paradigm [3], we addressed whether feedback processes in early visual cortex play a role in visual awareness. We show that TMS of visual cortex, when timed to produce visual suppression of an annulus serving as a metacontrast mask, induces recovery of an otherwise imperceptible disk. In addition to producing disk recovery, TMS suppression of an annulus was greater when a disk preceded it than when an annulus was presented alone. This latter result suggests that there are effects of the disk on the perceptibility of the subsequent mask that are additive and are revealed with TMS of the visual cortex. These results demonstrate spatial and temporal interactions of conscious vision in visual cortex and suggest that a prior visual stimulus can influence subsequent perception at early stages of visual encoding via feedback projections [4].

Results

To determine the influences of early visual cortex on visual awareness, we used TMS to induce visual suppression in a metacontrast masking paradigm (see Figure 1). For all subjects in this experiment, the most robust visual suppression was measured while subjects fixated slightly to the left of the centrally presented stimuli. This is likely due to the further posterior extension of the left occipital lobe in humans [5]; this extension makes the right visual hemifield more susceptible to TMS disruption. The mean TMS intensity across the subjects was 57% (range of 53–60) of the maximum 2.2 T output of the stimulator, and the mean position of the base of the 9 cm coil was 2.9 cm directly above the inion. The results regarding perception of the annuli and disk will be considered separately (see the Supplemental Data available with this article online for detailed Experimental Procedures and for individual subject data).

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Annulus Perception

Figure 2 illustrates the percentage of annulus detections averaged across all subjects for each of the TMS stimulus onset asynchronies (SOA). The mean percentage of trials in which subjects reported seeing the annulus is shown separately for the disk present versus disk absent trials. As can be seen in Figure 2, the participants experienced visual suppression of the annulus when a TMS pulse was administered at and between 100 and 143 ms after the annulus was presented. However, the magnitude of this TMS suppression was dependent upon whether a disk was presented prior to the annulus; subjects consciously perceived the annulus much less often when a disk preceded it than when no disk was presented.

Statistically, the suppression effect can be measured by the magnitude of the quadratic component of the SOA-performance function: much lower performance at the middle SOAs than at either the short or the long SOAs is indicative of a large suppression effect. For these quadratic analyses, the no TMS conditions were excluded because these conditions were unrelated to the SOAs that were used in the other conditions. The quadratic component of the main effect of SOA was statistically significant, indicating that more suppression was measured at the middle SOAs (100–143 ms) than at the longer or shorter ones ($t_3 = 5.65$, $p = 0.006$, one-tailed, H_0: visibility $\mu_{no\ TMS} \leq \mu_{TMS}$, since it has been established that TMS produces visual suppression when delivered over visual cortex at SOAs ranging from ~80 to 130 ms [6]). To confirm the difference between the magnitudes of suppression for disk present versus disk absent trials, we tested the difference between the quadratic components of trend for these types of trials. Specifically, we tested the quadratic component of the disk presence by SOA interaction. This analysis revealed that the quadratic component of the SOA function for the disk present condition was significantly larger than the quadratic component for the disk absent condition ($t_3 = 2.99$, $p = 0.029$, one-tailed, H_0: suppression $\mu_{disk} \leq \mu_{no\ disk}$, since we expected more suppression when a disk was present compared to when it was absent [7, 8]). Thus, when visual suppression occurs, there was more TMS suppression of an annulus when a disk preceded it compared to when the disk was absent.

Disk Perception

The percentage of trials in which the disk was reportedly perceived, averaged across subjects at each SOA, is plotted in Figure 3. On the half of the trials in which a disk was not presented, subjects reported the presence of a disk in 40% of trials. Some of these erroneous

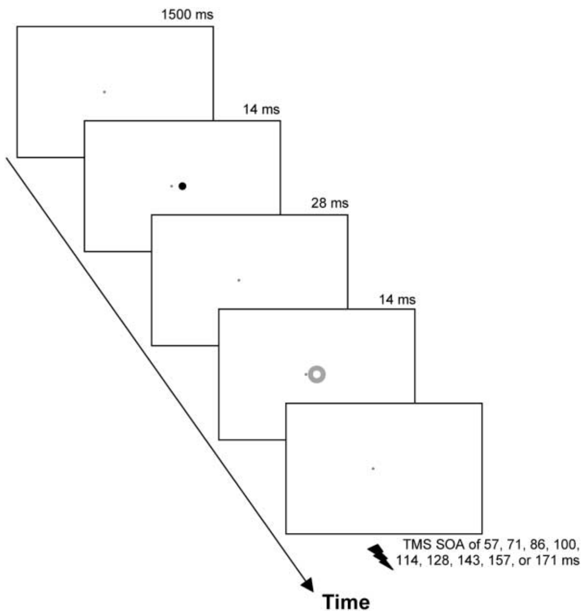

Figure 1. Stimuli, Timings, and Procedures

The stimuli used in this experiment were isoluminant blue and green disks and annuli (15.9 cd/m^2) that were presented at the center of the monitor. The disk was 0.1° of visual angle in diameter, whereas the annulus was 0.2° in diameter, with an inner diameter measuring 0.1°. Since both the disk and the annulus were presented in the center of the screen, there were no overlapping contours between the two stimuli. The disks and annuli were presented on a dim gray background (6.0 cd/m^2). After a pretrial interval of 1500 ms, a blue or a green disk was presented (disk present condition) for 14.2 ms in a random half of the trials. The disk was not present (disk absent condition) in the remaining half of the trials, and a blank interval of 14.2 ms was presented to equalize the time from the start of the trial until annulus presentation. After a stimulus onset asynchrony (SOA) of 42.6 ms, a blue or a green annulus, which served as the mask for the disk present conditions, was presented in every trial. This 42.6 ms interval between the disk and the annulus was selected based on pilot experiments demonstrating that this SOA produced the strongest metacontrast masking. The colors of the disk and annulus were randomly determined in each trial and could therefore be the same or a different color. The TMS pulse was administered in a random 90% of the trials at the indicated varying temporal intervals after the annulus. Participants were told to ignore the TMS pulse as best as possible when it was presented and to simply respond first as to whether or not they saw the disk and then respond as to whether or not they saw the annulus. The subjects input their own responses by pressing the "Y" or "N" keys on the keyboard, which was positioned on their laps.

disk reports may have been due to the induction of phosphenes by TMS [9], which were misattributed to the perception of the disk, or to partial suppression of the mask, which was then presumed to be the disk. However, even when no TMS was administered, the erroneous report of the presence of a disk when it was not presented was 15%. Therefore, in order to get a better picture of true disk recovery in the absence of these false reports, we plotted the difference between the percentage of trials in which a disk was reported to be seen when it was not presented and the percentage of trials in which the disk was reported to be seen when it was presented. This more conservative measure more accurately represents the true perception of the disk (and not phosphenes or erroneous reports, assuming these were equal between the disk present versus disk absent conditions) and is depicted by the solid black line in Figure 3. After this subtraction, recovery of the disk was apparent when the mask to TMS SOA was between 86 and 157 ms; this interval is roughly the same time interval in which TMS suppression of the mask was induced, but recovery is slightly longer on both ends of this scale.

For statistical analyses, as with the mask report, a disk presence by SOA quadratic comparison was performed. Note that this analysis was performed on the raw percentage data, not the difference data, and that this quadratic analysis directly tests whether the difference curve in Figure 3 is greater than zero at specific SOAs. This analysis revealed a significant difference in disk detectability as a function of SOA, with greater detection of a disk when the disk was present and within the range of SOAs at which annulus suppression occurred ($t_3 = 3.83$, $p = .016$, one-tailed, H_0: visibility $\mu_{disk} \leq \mu_{no\ disk}$, since disk recovery was expected). These results illustrate that when there was suppression of the mask, disk recovery occurred.

Discussion

When TMS was delivered to the occipital pole during a specific time window, visual suppression of the annulus was consistently measured in each subject. This visual suppression, presumably due to TMS disruption of the parafoveal representations in V1 and perhaps also V2/V3 [10, 11], was more prominent for right visual field stimuli; this finding is consistent with reports demonstrating a further extending left occipital petalia [5]. Furthermore, TMS suppression of the annulus was also greater when a disk was presented before the annulus. This latter result suggests the presence of feedback contributions of visual processing of the disk that further interfere with the subsequent annulus processing. More specifically, the TMS effects on early visual cortex appear to be additive with feedback disk processing, which produces further suppression of the mask at the appropriate SOA. These results and interpretations are consistent with other reports demonstrating that stimuli presented in between two masks, the disk and TMS in our case, are more effectively blocked from awareness compared to single masks [7, 8].

Also consistent with the feedback interpretation, the disk was perceived more frequently when the TMS eliminated the annulus from visual awareness [12]. Under this account, by eliminating mask processing in early visual cortex, reentrant processing in this region and further upstream areas could be completely dedicated to processing the disk once neural activity recovered from the transient disruptive effects of the TMS. These results suggest that this disk recovery effect and conscious perception in general may arise from reentrant processes to early visual cortex. Interestingly, when the TMS SOA was 86 or 157 ms and full suppression of the annulus was not present, some disk recovery was measured. This suggests that even partial suppression of the annulus, not enough to eliminate it from aware-

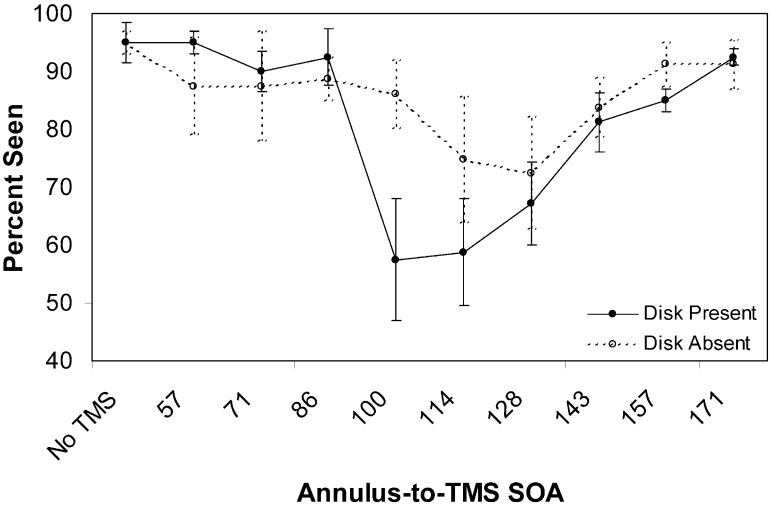

Figure 2. Annulus Perception: Data Demonstrating Greater TMS Visual Suppression of the Annulus with a Preceding Disk

The percentage of annuli that were seen averaged across subjects is plotted as a function of the annulus-to-TMS SOA. The data for the disk present and disk absent conditions are shown separately. Error bars represent ±1 standard error of the mean.

ness, can nonetheless reduce its effectiveness of masking the preceding disk. Extrapolating from this result, it can be inferred that, in backward pattern and metacontrast masking, when masked stimuli are perceived under optimal masking conditions (i.e., when the masks are ineffective even under optimal masking conditions), this might be due to inefficient and incomplete processing of the mask in early visual cortex. We are currently conducting further experiments to determine whether this may be the case.

Although it could be argued that the effects we observed may be due to the disruption of unidirectional, intrinsic activity occurring completely within early visual cortex, rather than feedback processes to this area from higher cortical regions, we feel that this explanation is unlikely for two reasons. First, when TMS was administered at specific SOAs in this study, the TMS had selective and independent effects on the disk and the mask. If our effects were due to the disruption of intrinsic mechanisms entirely in early visual cortex, we should have suppressed both the disk and the mask rather than inducing recovery of the disk from suppression of the mask, as we observed. More importantly, if disruption of unidirectional, intrinsic activity was responsible for our effects, there should not have been influences in early visual cortex of the previously presented disk on the visibility of the mask. Therefore, unless a complex explanation involving differential effects of TMS on visual cortex activity is advanced, which seems less plausible, a feedback mechanism is the most straightforward and likely explanation of these results.

In addition, consistent with our interpretations, there is also some electrophysiological evidence suggesting that feedback mechanisms in early visual cortex may induce suppression in metacontrast masking [13–18]. These electrophysiological studies show changes in single-unit activity for up to 400 ms in striate cortex and changes in components of the visual evoked potential for up to 200 ms following a metacontrast masking procedure; these findings suggest that masking influences later feedback activity rather than early stimulus-induced responses in visual cortex. Furthermore, this lengthened modulation in visual cortex corresponded with the brightness discriminations of the masked stimulus and likely signaled feedback processes used to perform this discrimination task [14, 16]. Taken together,

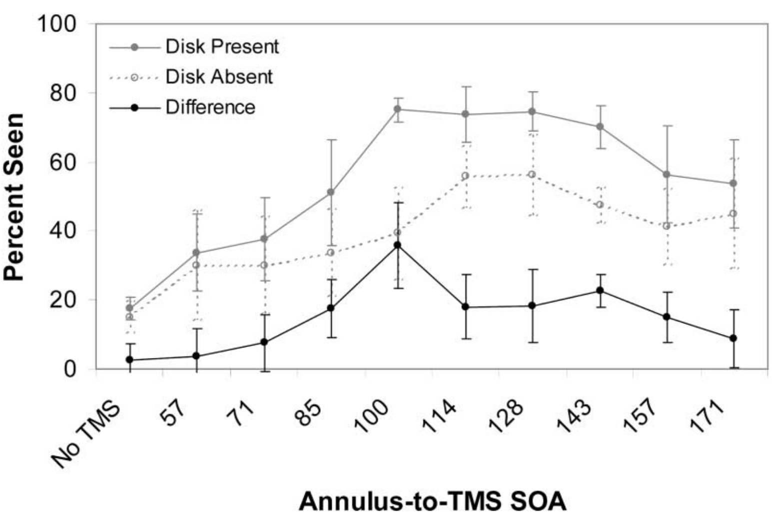

Figure 3. Disk Perception: Recovery or Unmasking of the Disks from TMS Suppression of the Metacontrast Masks

The percentage of disks that were seen averaged across subjects is plotted as a function of the annulus-to-TMS SOA. The data for the disk present and disk absent conditions, as well as the difference between these two conditions, are shown separately. Error bars represent ±1 standard error of the mean.

these other studies provide further support for our results suggesting that a feedback contribution to visual awareness is likely to be operating in early visual cortex (for similar accounts, see [19]).

Conclusions

Our results demonstrating a larger TMS suppression effect of a stimulus when preceded by an adjacent, but nonoverlapping, visual stimulus suggest a role of feedback processes in visual cortex that leads to conscious awareness. This type of reentrant process in visual cortex has been suggested to be critical for visual consciousness [20, 21], and the inability to induce moving phosphenes with TMS over V5 in a patient with left occipital damage is also consistent with this account [22]. We extend these findings by showing that feedback to early visual cortex is critical for the detection of even basic primitive visual stimuli such as colored disks and annuli. They further suggest that, although we may not be aware of the activity within early visual cortex [23], processing within and feedback to this cortical region is necessary for our visual awareness.

Supplemental Data

Supplemental Data including the details of the Experimental Procedures and the data from the individual subjects of this experiment are available at http://www.current-biology.com/content/supplemental.

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