

Striate cortex (V1) activity gates awareness of motion

Juha Silvanto^{1,2}, Alan Cowey³, Nilli Lavie^{1,2} & Vincent Walsh^{1,2}

A key question in understanding visual awareness is whether any single cortical area is indispensable. In a transcranial magnetic stimulation experiment, we show that observers' awareness of activity in extrastriate area V5 depends on the amount of activity in striate cortex (V1). From the timing and pattern of effects, we infer that back-projections from extrastriate cortex influence information content in V1, but it is V1 that determines whether that information reaches awareness.

Of the many visual stimuli that impinge on the retina, few are consciously perceived at any one time. Several lines of evidence have identified V1 as the area most likely to play a central role in awareness: it is the area in which activity correlates most closely with awareness, even if the experience is faulty¹; it receives back-projections from all the extrastriate visual areas²; damage to this area in humans^{3,4} and monkeys⁵ can abolish visual awareness of all stimulus attributes in the corresponding parts of the visual field; and transcranial magnetic stimulation (TMS) to this area interferes with perception of neural activity induced in extrastriate cortex⁶. These studies show that V1 activity correlates with conscious experience but do not establish that it is the recursive connections between extrastriate and striate cortex that determine the content or presence of awareness^{7,8}. It is therefore essential to determine whether activity in V1 arising from back-projections from extrastriate cortex can produce visual awareness. It has never been shown that the attributes of awareness are dictated by these back-projections, yet it is a cornerstone of many current views of visual awareness^{7–10}.

We therefore examined, through direct stimulation of the occipital cortex (see **Supplementary Methods** online), whether the amount of V1 activity dictates awareness and, if so, whether the V5–V1 cortical back-projection determines the content of conscious awareness. All procedures were approved by the ethics committee of University College London and informed written consent was obtained from each subject. We applied single-pulse TMS over V5 and V1 at different onset asynchronies from –80 to +80 ms and asked subjects to report their induced perceptions (see **Supplementary Methods**). Using a modified binary search paradigm¹¹, the intensity of TMS was determined individually for each subject according to their phosphene threshold¹² (the intensity of TMS at which a phosphene is produced on about 75% of occasions).

When TMS was applied to V1 above the phosphene threshold, subjects reported the presence of a small, stationary phosphene located in the contralateral lower visual field within a few degrees of the vertical meridian^{4,6,12}. Suprathreshold TMS over V5 also elicited the experience of a phosphene in the visual field contralateral to stimulation but with different features. As one would expect given the differences between V1 and V5 receptive field properties¹³, it was larger, moving and of a different shape from the V1 phosphene.

When subthreshold TMS (that is, TMS producing no phosphene on its own; intensity 20% below phosphene threshold was used for all subthreshold stimulations) was applied over V5 followed by a subthreshold pulse to V1, subjects did not report any phosphene. Crucially, however, when a subthreshold pulse was applied over V5 followed 10–40 ms later by a suprathreshold pulse over V1, subjects reported a phosphene. Notably, this phosphene was not merely the suprathreshold V1 phosphene. Rather, it acquired features of a suprathreshold V5 phosphene: subjects now reported the perception of movement (**Fig. 1a**) and the shape and size of their percept was a mixture of V1 and V5 phosphenes (**Fig. 1b**). This shows that activity in V5 that, on its own, is insufficient to induce a moving percept can produce such a percept if the level of induced activity in V1 is high enough. Furthermore, this also shows that what reaches awareness via V1 is characterized by back-projections from extrastriate areas.

Although the present study was the first to assess human awareness through direct manipulation of the levels of activity in V1 with TMS, and hence allowed us to determine the critical role of V1 activity in motion awareness, the narrow time window for V5–V1 interaction that we report (10–50 ms) is consistent with previous reports of extrastriate–striate feed-back interactions in motion^{6,13}. Notably, we showed that subthreshold TMS over V5 followed by suprathreshold V1 TMS produces awareness, but when suprathreshold TMS over V5 (which results in the perception of moving phosphene) is followed by subthreshold V1, TMS phosphene perception is suppressed⁶. This contrast emphasizes the importance of activity in V1 in determining the presence of awareness. However, the level of activity in V5 (either supra- or subthreshold) when V5 stimulation is followed by V1 stimulation does not dictate whether phosphenes are perceived in this context.

Our findings that moving phosphenes are perceived only when suprathreshold V1 stimulation follows, but not precedes, subthreshold V5 stimulation, together with the gradual increase in motion perception from the 10–50 ms period, precludes a simple feed-forward summation account and points instead to a critical time of back-projection arrival in V1. A feed-forward summation account, in which V5 activity is primed with subthreshold TMS before being summed with a feed-forward input from a suprathreshold V1 stimulation, remains logically possible if the present finding is taken in isolation. However, recent findings that V1 stimulation has an effect on motion perception both before and after the critical V5 stimulation period,

¹Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK. ²Department of Psychology, University College London, 26 Bedford Way, London WC1H 0AP, UK. ³Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford, OX1 3UD, UK. Correspondence should be addressed to J.S. (juha.silvanto@ucl.ac.uk).

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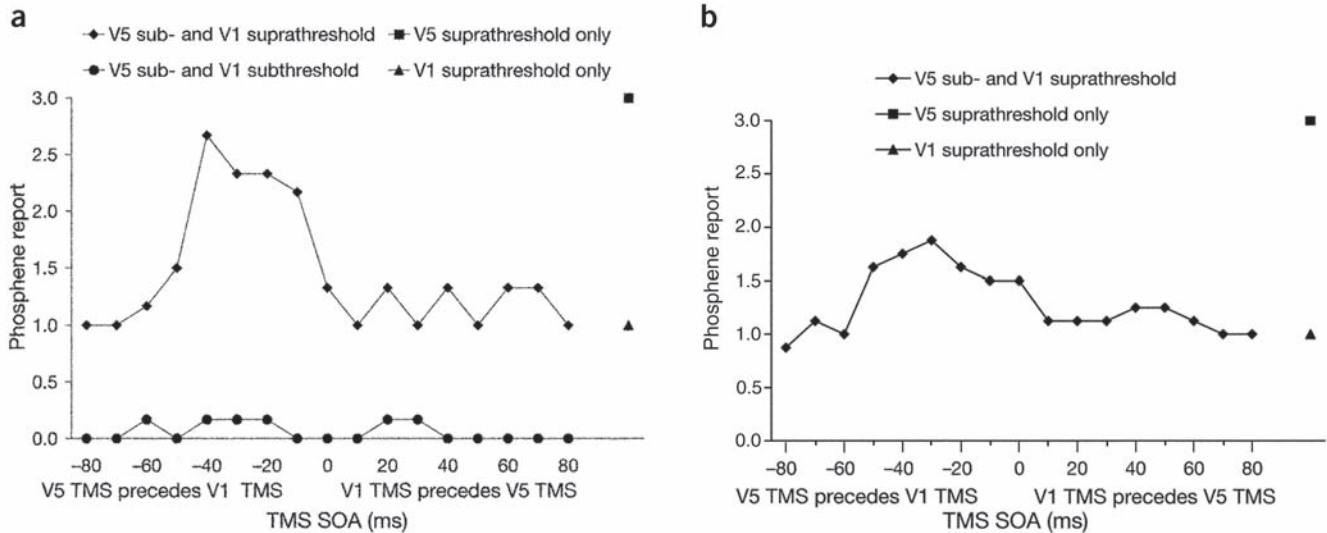


Figure 1 Motion and size of reported phosphenes. **(a)** Motion judgments of the six subjects who perceived moving phosphenes when V5 was stimulated above threshold. Scale was adapted from a previous study⁹: 0 = phosphene was absent; 1 = phosphene was stationary; 2 = subject was uncertain whether phosphene was moving or stationary; 3 = the phosphene was moving. When subthreshold TMS was applied over V5 40 ms before V1 was stimulated above threshold, five of the six subjects reported the perception of moving phosphenes. In contrast, V1 suprathreshold stimulation by itself always induced stationary phosphenes in all subjects. This difference in subjects' motion judgments is statistically significant ($Z = 2.236$; $P < 0.025$, Wilcoxon test). When both V1 and V5 were stimulated below threshold, only one subject reported the perception of a (stationary) phosphene. **(b)** Shape/size judgments ($n = 8$). 1 = percept was like a V1 phosphene; 2 = percept was like a mixture of V1 and V5 phosphenes; 3 = percept was like a V5 phosphene; 0 = phosphene was absent. Five of the eight subjects perceived a mixture of V1 and V5 phosphenes when TMS was applied over V5 30 ms before V1. Subjects' percepts in this condition differed significantly from those induced by suprathreshold TMS over V1 by itself ($Z = 2.236$; $P = 0.025$; Wilcoxon).

whereas V5 stimulation affects motion perception only during one critical time period before a later V1 stimulation, make this account unlikely¹⁴ because it predicts that V5 stimulation effects should post-date the latest of V1 effects.

Finally, we confirmed the specificity of the timing and direction of the V5–V1 interaction by stimulating the frontal eye fields 0–60 ms after V5 and also by stimulating both V5s 40 ms apart. Neither manipulation had the effects we describe here (**Supplementary Note 1**).

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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