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Inducing conscious perception of colour in blindsight

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The phenomenon of blindsight — the manifestation by forced-choice guessing of visual processing despite the total loss of visual awareness caused by damage to striate cortex (V1) [1] — has influenced many current theories of visual awareness [2,3]. We have investigated whether hemianopic subject GY is able consciously to experience colour in his blind field by using a TMS-chromatic adaptation paradigm, in which TMS applied after visual adaptation to a coloured background preferentially facilitates the perception of the adapted attribute [4]. Our results show that GY can perceive colour in his blind field, and that the identity of the colour is determined by the contralesional hemisphere.

After monocular chromatic adaptation (Figure 1), single-pulses of TMS were administered bilaterally over V5/MT (see Supplementary data available on-line with this issue for detailed experimental procedures). TMS was applied over the left and right V5/MT at stimulation onset asynchronies (SOA) of –20 ms (TMS applied first to the normal, right, hemisphere) or +20 ms. These SOAs were used as they are most effective in inducing bilateral phosphenes in GY and in normal subjects [5]. The contralesional (right) V5/MT was stimulated at phosphene threshold (73%) and the ipsilesional (left) V5/MT at 80% of the stimulator's maximum output (as in our previous study [5]). These parameters for left and right V5/MT TMS were used also in the control subjects.

Without adaptation, unilateral stimulation of V5/MT in GY's intact hemisphere induced a moving phosphene similar to those reported by normal subjects. whereas unilateral stimulation of the ipsilesional V5/MT, as expected, never induced a phosphene [5]. After adaptation, consistent with our previous study [4], phosphenes induced with unilateral TMS in the control subjects as well as from GY's intact hemisphere appeared with the colour to which the corresponding area of the visual field had been adapted. As we previously reported [5], bilateral stimulation of V5/MT induced a continuous white arc that intruded 6 to 10 degrees into both hemifields (see Figure 1D). After adaptation to the stimulus depicted in Figure 1A, GY, as well as the three control subjects, reported their phosphenes to uniformly be the same colour as the adapting stimulus. The shape and the extent of the phosphene was the same as before adaptation (Figure 1), and it often appeared to contain motion from the blind to the intact field, the speed of which was consistent across trials. There were no differences regarding which SOA was more efficient in inducing these phosphenes, which could be induced with both adapting colours (red and green).

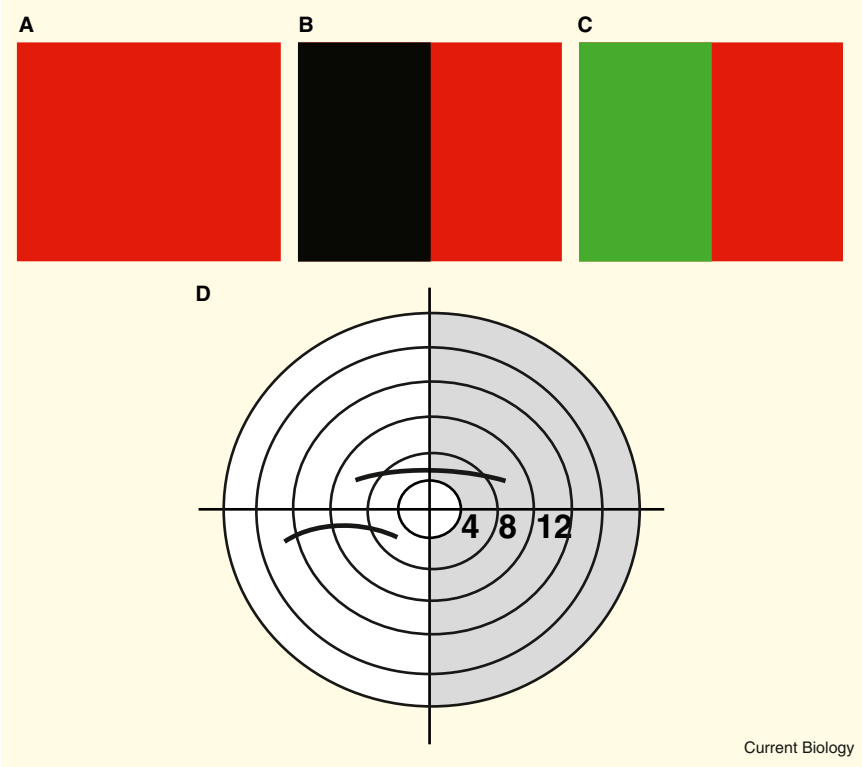

Figure 1. Stimuli and results.

The three types of adaptation stimulus used: (A) a uniform coloured rectangle that completely filled the CRT display; (B) a uniform coloured rectangle that filled either the intact or blind hemifield (excluding central 4 degrees of macular sparing) of GY while the other hemifield appeared as black; (C) a dual-colour display in which red and green were presented in different hemifields. GY reported a visual afterimage induced by adaptation only in his intact field (see Supplemental data for further details). Another blindsight subject (DB) has reported coloured afterimages in his blind field [11]; however, the completeness of the V1 lesion in this subject, unlike in GY, has never been verified because he cannot be scanned by MRI and CAT scans are distorted by intracranial wound clips. After monocular adaptation subjects were asked to close their eyes and TMS was applied every two seconds, with the SOA condition (–20 ms or +20 ms) changed after five trials. At this point, subjects were asked to report whether their phosphene differed from those they perceived without adaptation. Three contralesional-only TMS trials were also conducted prior to each SOA condition to provide a comparison to phosphenes perceived with bilateral stimulation. This was repeated until the phosphenes returned to their pre-adaptation appearance. (D) Schematic examples of phosphene appearance in GY, depicting his visual field and the eccentricity in degrees of visual angle. The gray area indicates the blind field. The figure is based on GY's drawings, made immediately after each trial. The phosphene restricted to the left hemifield depicts the phosphene induced from V5/MT in GY's intact hemisphere with unilateral application of TMS. When TMS was applied bilaterally, GY perceived a phosphene that intruded into both the blind and the intact fields. After color adaptation, these phosphenes appeared with the color of the adapting stimulus. The size and the shape of these phosphenes were not affected by chromatic adaptation. For the first set of post-adaptation trials for each SOA, GY perceived coloured bilateral phosphenes on more than 70% of trials in all adaptation conditions in which the intact hemifield had been adapted. For the next sets of trials coloured phosphenes were induced on 40% of trials or less, indicating that phosphene perception began to return to its pre-adaptation appearance.

In the control subjects, when adaptation was restricted to one hemifield (Figure 1B), the component of the phosphene overlapping the adapted hemifield appeared coloured, and the component overlapping the unadapted hemifield was colourless. In contrast, in GY the bilateral phosphene appeared uniformly coloured after adaptation restricted to the intact field. When adaptation was restricted to GY's blind field, the phosphene always appeared colourless.

When different adapting colours were presented to the two hemifields, the bilateral phosphenes induced in the control subjects comprised both adapting colours. For instance, if the left and right hemifields were adapted to red and green, respectively, the component of the bilateral phosphene appearing in the left hemifield was red and the component appearing in the right hemifield was green. This occurred with both SOAs. The component of the phosphene overlapping with the region of the visual field where there had been a chromatic border during adaptation contained patches of both colours or appeared colourless. The former percept is similar to those reported by subjects in a study in which the retinal image was stabilized at the boundary between a pair of red and green stripes [6]. In contrast, phosphene colour in GY depended on the colour to which his intact field had been adapted. For instance, if the intact field had been adapted to red and the blind field to green, the bilateral phosphenes appeared uniformly red.

As adaptation of the blind field had no influence on phosphene colour, it must have been adaptation of the wavelength/colour-selective regions (such as V1 and V4) in the normal hemisphere that influenced phosphene colour, with interactions between the intact and damaged hemisphere providing colour perception in the blind field. Recent diffusion tensor imaging (DTI) evidence showing strong callosal connections between V5/MT regions in GY's damaged and intact hemispheres [7] support this view. The intact V1 may have played a role in determining phosphene color, as V1–V5/MT interactions within the intact hemisphere can modulate the interactions between V5/MT regions in the intact and damaged hemisphere. It is also possible that the locus of color adaptation is the LGN, as adaptation effects have been observed in this region [8,9]. V4 in the normal hemisphere could have also been involved, but the possible contribution of V4 in the damaged hemisphere is unclear, as there is no evidence on either the retinotopy of this region in GY or on its connectivity with V5/MT.

In summary, our results show that in the absence of V1, colour perception may be possible via the intact hemisphere. It has been shown previously that unconscious colour detection is possible when V1 is disrupted with TMS [10] and our results show that conscious perception of colour is also possible.

Supplemental Data

Supplemental data are available at http://www.current-biology.com/supplemental/S0960-9822(08)01056-7.

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Visuomotor timing compensates for changes in perceptual latency

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The dimmer a stimulus is, the more time it takes the neural signal from the retina to reach visual cortex [1]. Presumably because of this variation in latency, a dim moving object appears to lag behind where it would appear if it were bright [2,3]. To investigate whether this flaw in perception afflicts our ability to interact with moving objects, we asked subjects to press a button at the moment a rotating bar became aligned with a stationary reference: over a 15-fold range of luminance, they did not respond later when the moving bar was dimmer. This suggests the visuomotor system compensates for changes in visual latency due to luminance variation, despite uncorrected lags in conscious perception.

To successfully interact with the environment, we must move our limbs at specific moments relative to external events. To do so accurately, we must compensate for the neural delays between sensory stimulation and cognitive processing, and between executive commands and muscle contraction [4]. It is not known, however, whether visuomotor timing corrects for the *variation* in neural latencies resulting from the large differences in light levels encountered in the natural environment.

Eight subjects fixated the center of a rotating bar and attempted to synchronize a button-press with the moment it became aligned with two stationary reference bars (Figure 1A). No feedback was provided. The luminance of the reference bars was 4.6 cd/m^2, and the moving bar's luminance varied randomly across trials from 0.3 to 120 cd/m^2, a range spanning photopic (cone-based, daytime) vision to the nighttime levels of mesopic (significantly rod-influenced) vision [5]. See the supplemental section online for detailed methods and results.

Across all luminance values, subjects tended to press the button before alignment, a typical finding with synchronization tasks [6]. As