

LETTERS

Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus

John-Dylan Haynes^{1,2}, Ralf Deichmann¹ & Geraint Rees^{1,2}

When dissimilar images are presented to the two eyes, they compete for perceptual dominance so that each image is visible in turn for a few seconds while the other is suppressed. Such binocular rivalry is associated with relative suppression of local, eye-based representations¹⁻⁴ that can also be modulated by high-level influences such as perceptual grouping^{3,5,6}. However, it is currently unclear how early in visual processing the suppression of eye-based signals can occur. Here we use high-resolution functional magnetic resonance imaging (fMRI) in conjunction with a new binocular rivalry stimulus to show that signals recorded from the human lateral geniculate nucleus (LGN) exhibit eye-specific suppression during rivalry. Regions of the LGN that show strong eye-preference independently show strongly reduced activity during binocular rivalry when the stimulus presented in their preferred eye is perceptually suppressed. The human LGN is thus the earliest stage of visual processing that reflects eye-specific dominance and suppression.

Currently, little is known about the site and mechanisms of eye-specific suppression during binocular rivalry. The earliest stage after the retina at which differential eye-specific modulation could occur is the LGN, which contains monocular neurons segregated into eye-specific layers⁷. Although excited only by monocular stimulation, neurons in primate LGN can nevertheless show robust inhibitory binocular interactions⁸. However, fluctuations in activity associated with changing perception during binocular rivalry have proven inconsistent in cat^{9,10} and are apparently absent in monkey¹¹. There have been no reported investigations of binocular rivalry in the human LGN. Common to all previous studies is the absence of behavioural measures of perceptual dominance, either because the animals were anaesthetized or because they were not required to report their perceptual experience. The lack of behavioural measurements for classifying neuronal responses will have significantly lowered the power of such studies to detect any neural signature of rivalry, as perceptual dominance must instead be inferred indirectly.

We therefore set out to investigate whether the human LGN shows eye-specific changes in signal in association with behaviourally measured changes in perception during binocular rivalry. First, we functionally identified the LGN independently in each of four participants by contrasting contralateral and ipsilateral hemifield binocular stimulation (Fig. 1a, see Supplementary Information). Next, we investigated responses of voxels within the LGN to purely monocular stimulation with a bilateral stimulus (Fig. 1b; see Methods). The human LGN comprises six histologically distinct monocular layers, each approximately 1-mm thick. Although the overall size of the human LGN can vary by a factor of two⁷, individual layers are still below the spatial resolution of conventional human fMRI.

To maximize sensitivity, we used an improved fMRI scanning sequence with twice the spatial resolution of conventional techniques

(1.5 mm isotropic; see Methods). Although this much higher spatial resolution might still be too low to permit direct visualization of each monocular layer, we hypothesized that the ocular preferences of neuronal populations within the LGN would be revealed through each voxel providing a biased sampling of monocular cells. Such biased sampling arises because a randomly placed voxel will sample an anisotropic distribution of ocular preferences, owing to the convoluted nature of the laminar structure of the LGN. Similar biases have been demonstrated for orientation preference in human V1, even at the lower spatial resolution of conventional fMRI, and have been used to directly measure orientation-selective processing^{12,13}.

Confirming our hypothesis of ocular biases in human LGN, voxels within the LGN responded vigorously to stimulation of either eye, but many showed a clear and significant preference or bias towards either right or left eye stimulation (Fig. 1c). For every voxel in the LGN in each participant, we independently computed a measure of this ocular bias. The distribution of these biases across all LGN voxels followed an approximately gaussian distribution (Supplementary Fig. S1). Between 42 and 71% of all LGN voxels in each participant showed a significant ($P < 0.05$) bias towards either ipsilateral or contralateral eye stimulation.

Having established the presence of significant ocular biases within LGN voxels, we could then proceed to test responses within these functionally defined voxels during binocular rivalry. We measured activity in the LGN and V1 using high-resolution fMRI while our participants viewed a novel binocular rivalry stimulus (see Fig. 2 and Methods) consisting of two co-rotating orthogonal gratings (Fig. 2a). This stimulus was specially devised to ensure relatively long perceptual dominance periods with minimal piecemeal rivalry, while strongly driving neuronal activity in the LGN and early visual cortex (Fig. 2a). Participants reported which stimulus was dominant by pressing a button. We confirmed that dominance phases followed a gamma distribution¹⁴, with a relatively long mean perceptual dominance of 10.7 s (Fig. 2b).

We next investigated whether voxels with left- or right-eye preference showed different responses when the left-eye or right-eye stimulus became dominant. For each LGN voxel, we calculated the fMRI signal associated with perceptual dominance and suppression of each monocular image. We then used the information about the ocular preference of each voxel (obtained from the participant's independent eye-localizer session) to calculate the fMRI signal associated with perceptual dominance and suppression of the stimulus presented to the preferred eye of each voxel. Signals during dominance of either left- or right-eye images were calculated separately for all voxels with biases towards either the left or right eye. This revealed strong and highly significant increases in the LGN signal during rivalry whenever the monocular stimulus corresponding to the independently measured ocular bias of that voxel became

¹Wellcome Department of Imaging Neuroscience, Institute of Neurology, University College London, 12 Queen Square, London WC1N 3BG, UK. ²Institute of Cognitive Neuroscience, University College London, Alexandra House, 17 Queen Square, London WC1N 3AR, UK.

dominant, with corresponding decreases when it was suppressed (Fig. 3a). For example, voxels with left-eye preference under monocular viewing conditions (Supplementary Fig. S1) showed relative enhancement of signals under rivalrous viewing when the left eye stimulus became dominant (Fig. 3a, red symbols in right panel). Conversely, voxels with a preference for right-eye stimulation showed relative enhancement when the right-eye stimulus became perceptually dominant. These monocular signals of eye-specific enhancement and suppression reflecting perceptual dominance during rivalry were replicated independently in every participant (Supplementary Fig. S2). These time courses also closely followed the

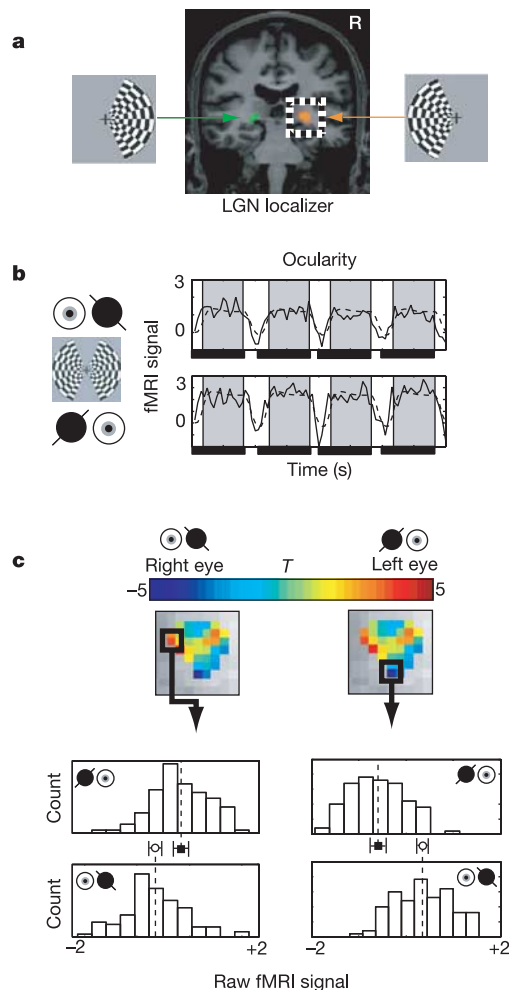


Figure 1 | Ocular biases in the LGN. **a**, The left and right LGN were localized for each participant as the regions in the left and right lateral posterior thalamus responding more strongly to contralateral than to ipsilateral hemifield stimulation³¹. **b**, Eye-specific stimulation. In alternate runs either the right eye alone (top) or the left eye alone (bottom) was stimulated with a double-wedge stimulus that was presented in blocks of 30 s (grey shaded regions). For each voxel in the LGN (see **a**), we extracted the fMRI signal amplitude during stimulation blocks for stimulation of each eye separately (shown here for one voxel in mean corrected scanner units). **c**, For each voxel, we then investigated whether the fMRI responses were stronger to stimulation of the left eye (positive *T*-values) or right eye (negative *T*-values). The coloured graphs show the colour-coded distribution of these ocular preferences for a coronal section through one participant's right LGN (dashed box in **a**), and the black and white histograms show the raw fMRI signal distribution for a left-eye-biased and a right-eye-biased voxel during periods when either the left or the right eye was stimulated (grey shaded periods in **b**). Although the raw signal distributions largely overlap, there was a significant bias for these two voxels as indicated by the means (\pm s.e.m.) for each distribution (shown with dotted lines, open circles and filled squares; see Supplementary Fig. S1 for full results).

independent predictions of a parameter-free 'forward model', obtained from the perceptual time courses by convolution with a haemodynamic response function (Fig. 3a, solid red and blue lines; see Methods).

To formally characterize the eye-dependence of relative suppression and enhancement, we calculated the difference in activity between periods of perceptual dominance of the left-eye stimulus (red) and the right-eye stimulus (blue) across all voxels dominated by either the left eye (Fig. 4; red bars) or the right eye (Fig. 4; blue bars). Activity in left-eye-dominated voxels was significantly stronger when the left-eye stimulus (red) was dominant than when the right-eye stimulus (blue) was dominant. This is consistent with the notion that binocular rivalry involves differential modulation of eye-specific signals during perceptual dominance and suppression. To estimate the size of this modulation, we compared the signal change associated with eye-specific modulation during rivalry with the signal change evoked by extended monocular viewing of each monocular stimulus in one representative participant (see Supplementary Fig. S3). Although great caution is required in comparing these two very different measures in structures with non-specific monocular inhibitory interactions such as the LGN, eye-specific modulation during rivalry was incomplete compared with purely monocular stimulation (64% modulation; see Methods).

Having shown that LGN voxels with a specific ocular preference showed signals related to perceptual dominance of that eye during rivalry, we next determined whether there was a graded relationship between these two independent measures. For each LGN voxel, we plotted the difference in activation between perceptual dominance of the preferred-eye and the non-preferred-eye stimulus as a function of its ocular preference (Supplementary Fig. S4). There was a monotonic relationship between these two measures, with a modest but statistically significant positive correlation ($P < 0.05$) between the two for every participant. Thus, voxels with relatively strong ocular biases tended to show larger differences in activity during different dominance phases in rivalry. This might arise because signals in voxels with strong ocular biases are dominated by the input mainly from one eye and thus more clearly reflect the difference between rivalry and suppression.

Finally, we used the same methodology to quantify ocular biases and differential activity during perceptual dominance in rivalry in V1 (see Methods). As in the LGN, there was a very similar relationship between the ocular preference of individual voxels in V1 and the presence of differential signals during perceptual dominance during rivalry (Figs 3 and 4). Eye-specific modulation during rivalry was also incomplete compared with purely monocular stimulation (28% modulation; see Supplementary Fig. S3). Small quantitative

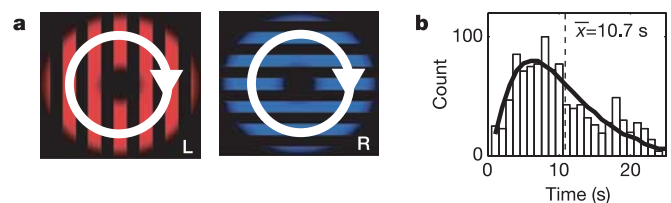


Figure 2 | Binocular rivalry stimulus. **a**, A red grating was presented to the left eye and an orthogonal blue grating was presented to the right eye while both stimuli simultaneously rotated clockwise. They were viewed through red/blue anaglyph glasses, so that the blue grating was visible to the right eye and the red grating was visible to the left eye. During each scanning run, the two stimuli were presented continuously for 5 min, leading to multiple perceptual alternations between the two monocular images while the other image was suppressed. Participants used response buttons to continuously indicate during each run whether they currently perceived either the red or blue grating. **b**, Histogram of dominance phase durations averaged across participants, which reveals that dominance phases were relatively long compared with typical rivalry stimuli, and could be well fitted by a gamma-distribution function (black line).

differences (for example, smaller overall differential activity; compare ordinate axes of Fig. 3a and b) might reflect differences in baseline fMRI signals, in the width of the haemodynamic point-spread function, or in the response gain between LGN and V1 (refs 15, 16).

These findings represent positive evidence for a neural signature of rivalry in the LGN of a conscious individual of any species. Rivalry-related signals are thus not confined to the early visual cortex^{17–20}, but can also be observed in subcortical structures. Using single-unit electrophysiological recording in cats and monkeys, it has proven difficult to establish whether the LGN reflects perceptual dominance in rivalry^{9–11}. These studies used different stimuli (for example, presented at greater eccentricities¹¹) in different species and did not measure perceptual dominance behaviourally, making it unclear at which point during recording any perceptual transitions might have occurred. Such studies thus require a substantially different analytic approach compared to the present study. For example, one study in monkeys¹¹ used power spectral analysis of neural signals, which should in principle allow accumulation of transition-related effects even though their random phase position is unknown. However, this approach is less sensitive than the one taken here, where the times of perceptual transitions are known, allowing for event-related averaging. Our successful demonstration of rivalrous fluctuations in the human LGN might in principle reflect any of these major differences. Alternatively, it might reflect differential sensitivity of the fMRI technique to particular aspects of the neuronal signal (for example, local field potentials rather than spiking activity²¹).

Our findings indicate that dominance and suppression in rivalry are accompanied by a modulation of signals in eye-specific representations in the LGN and V1. This is consistent with previous observations of neural signatures of rivalry in the monocular representation of the blind spot in V1 (ref. 17). However, by demonstrating that individual voxels acquired with high-resolution fMRI show reliable ocular biases, we were able to show that such

monocular rivalrous signatures are not specific to the unusual cortical locale of the blind spot but extend throughout V1 and into the LGN (Figs 3 and 4). The suggestion²² that previous findings of rivalry in the blind-spot representation¹⁷ in V1 might reflect competition between different stimulus preferences in surrounding binocular cells cannot account for our findings in LGN, which has no binocular cells.

Although binocular rivalry can prevent conscious perception of a suppressed image, visual sensitivity during suppression is only moderately decreased^{23,24}. Moreover, suppressed images can still cause simple after-effects^{25,26}. This suggests that the eye-specific modulation we observed in human LGN must necessarily be incomplete, consistent with recent reports that higher visual areas show selective responses to suppressed stimuli²⁷. Similarly, we found that the depth of rivalrous modulation was smaller than the signal evoked by purely monocular stimulation with our stimuli. It is important to note that any differences between monocular stimulation and rivalry are only approximations of modulation depth. Such differences potentially reflect not only rivalry-related signal modulations, but also the absence of non-specific inhibitory interactions under monocular stimulation⁸. Furthermore, differences in the degree of suppression between different structures (here, LGN and V1) may be influenced by differences in response gain^{15,16}. These caveats notwithstanding, our findings are consistent with the notion that suppression during rivalry does not result in a complete inhibition of stimulus-driven signals, and that sensitivity to input from the suppressed eye is moderately (but not fully) reduced^{23,24}. In contrast, selective adaptation by suppressed images can be of equal magnitude as for dominant images²⁶, suggesting that visual responses may reach early visual areas largely unattenuated; but adaptation is moderately reduced when visual saturation of the adapting stimuli is avoided²⁵.

Responses to flashed stimuli in the LGN can show binocular interactions earlier than the first V1 responses⁸, suggesting that such interactions do not require corticofugal feedback. Here, stimuli were presented continuously for several minutes, resulting in a superposition of feed-forward and feedback processing owing to the dense reciprocal connections between V1 and the LGN²⁸. Thus, our data do not distinguish the precise source of the modulatory influence that we observed in LGN. Because our stimuli have rivaling orientations, eye-specific modulations in LGN could potentially reflect a feedback signal from V1, where orientation-selective processing is well established^{12,13}. This is consistent with BOLD signals correlating slightly better with local field potentials than with spikes²¹. If feedback plays such a role then it must necessarily be eye-specific, thus placing specific constraints on the possible underlying neural circuitry²⁸. Alternatively, LGN modulation may instead arise directly from binocular interactions between LGN layers^{8,29} through local inhibitory interneurons³⁰. Such local computations should also be visible in the BOLD response²¹. Note that our findings do not imply that rivalry is exclusively determined by eye-specific

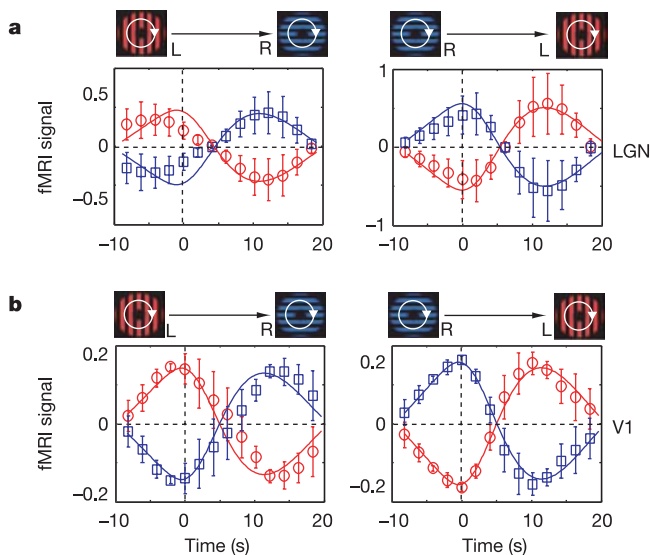


Figure 3 | Rivalry-related responses in LGN and V1. **a**, Event-related BOLD-fMRI signal changes in the LGN averaged across participants, time-locked to perceptual transitions from red to blue (left) and from blue to red (right). Error bars represent standard error across participants. Event-related averages were computed separately for voxels with left-eye preference (red circles) and right-eye preference (blue squares) as determined in the independent localizer sessions. The solid red and blue lines show the prediction of a parameter-free forward model of the haemodynamic response to perceptual transitions reported by the participants (see Methods). A good fit between behaviourally predicted and observed haemodynamic responses is apparent. **b**, As in **a**, but for voxels in the primary visual cortex (V1).

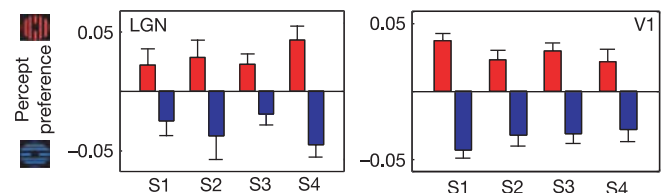


Figure 4 | Percept preference in LGN and V1. A 'percept preference' measure in the LGN (left) and V1 (right) was obtained separately for left-eye-dominated voxels (red bars) and right-eye-dominated voxels (blue bars) by subtracting the average BOLD signal during blue-dominance from the average BOLD signal during red-dominance (see Supplementary Information). Positive values indicate that signal was higher during dominance of the red percept, and negative values that signal was higher during dominance of the blue percept. Data are for subjects S1–S4; error bars represent standard error across voxels.

representations. Coherence between global stimulus-representations can clearly have a role in resolving rivalry^{3,5}. Such global effects might operate through local eye-based modulation in the LGN (or V1), modulated by top-down biases that favour coherent global percepts³. One possible control signal for such modulation could be feedback projections to monocular regions of V1 or even individual eye-specific layers of the LGN²⁸. Thus, rivalry may involve dynamic and competitive multilevel interactions at multiple processing stages¹.

METHODS

Participants and experimental design. Four healthy volunteers with normal vision (29–34 years old) gave written informed consent to participate in the experiment, which was approved by the local ethics committee. One participant was an author, two were experienced psychophysical observers and one was a naive participant.

The experiment consisted of three independent stages. In the first stage ('LGN localizer') we localized the left and right LGN in each participant using standard definitions^{15,31} (see Supplementary Information). The second stage ('eye localizer') sought to identify any ocular preference for individual LGN voxels. Participants fixated centrally while viewing a large contrast-reversing checkerboard stimulus presented bilaterally as two wedges (Fig. 1b), in alternating runs either to the left or right eye alone, while the other eye was covered and thus unstimulated. In the third stage we studied responses in the LGN and V1 to rotating binocular rivalry stimuli presented continuously for 296 s (see Fig. 2a and Supplementary Information). The stimuli yielded very effective rivalry with long phase durations (mean 10.7 s; see Fig. 2b) and very brief transition periods. Piecemeal or patchy rivalry was rare and very brief, and corresponding phases were discarded from the analysis.

fMRI acquisition. A 3T Allegra head scanner (Siemens Medical Systems) with a standard transmit-receive head coil was used to acquire functional data with a single-shot gradient echo isotropic high-resolution echo planar imaging sequence (matrix size 128 × 128; field of view 192 mm; in-plane resolution 1.5 mm; 20 slices with interleaved acquisition; slice thickness 1.5 mm; echo time 30 ms; acquisition time per slice 102 ms; repetition time 2,040 ms; echo spacing 560 μs; receiver bandwidth 250 kHz; 30% ramp sampling; twofold read oversampling to allow for *k*-space re-gridding; read gradient amplitude 34.47 mTm⁻¹; read gradient slew rate 344.7 mTm⁻¹ ms⁻¹). In order to maximize statistical power, we used only 20 slices that were optimized to cover the entire LGN, slightly angled to also achieve coverage of the calcarine sulcus.

In the main rivalry experiment, between 7 and 8 runs of 145 functional MRI volumes were acquired per participant. For the LGN localizer we acquired one run with 203 volumes, and for the eye localizer we acquired two runs of 163 volumes. For each participant a T1-weighted structural image was also acquired as well as 2–3 retinotopic mapping runs of 165 volumes, during which participants viewed standard flickering checkerboard stimuli that stimulated either the horizontal or vertical meridians.

fMRI analysis. Each participant's left and right LGN and V1 were identified using standard methods. An index of eye-dominance was then computed for each voxel in LGN and V1 (see Supplementary Information). To study the effects of rivalry on responses, we then investigated whether any significant response differences could be found between left-eye- and right-eye-dominated voxels during left-eye (red) and right-eye (blue) dominance phases. First we computed event-related responses (Fig. 3a, b and Supplementary Fig. S2) by selectively averaging the BOLD fMRI signal separately for left-eye-dominated and right-eye-dominated voxels, time-locked to changes in perceptual dominance either from red to blue or from blue to red. Error bars reflect standard errors across participants (Fig. 3a, b) or standard errors across all repetitions of one event-type for one participant (Supplementary Fig. S2). A parameter-free forward model of event-related responses was computed by selectively averaging a predicted fMRI time course obtained by convolving the perceptual time series with a canonical haemodynamic response function provided by the statistics package SPM2 (solid lines in Fig. 3). For a more formal comparison (Fig. 4) we also modelled responses separately for each voxel, using a general linear model with a regressor that modelled the difference in response amplitude between left-eye and right-eye perceptual dominance (see Supplementary Information).

Received 10 May; accepted 22 August 2005.

Published online 23 October 2005.

- Blake, R. & Logothetis, N. K. Visual competition. *Nature Rev. Neurosci.* **3**, 13–21 (2002).
- Blake, R., Westendorf, D. & Overton, R. What is suppressed during binocular rivalry? *Perception* **9**, 223–231 (1980).

- Lee, S. & Blake, R. A fresh look at interocular grouping during binocular rivalry. *Vision Res.* **44**, 983–991 (2004).
- Lehky, S. R. An astable multivibrator model of binocular rivalry. *Perception* **17**, 215–228 (1988).
- Kovacs, I., Papatthomas, T. V., Yang, M. & Feher, A. When the brain changes its mind: interocular grouping during binocular rivalry. *Proc. Natl Acad. Sci. USA* **93**, 15508–15511 (1996).
- Logothetis, N. K., Leopold, D. A. & Sheinberg, D. L. What is rivaling during binocular rivalry? *Nature* **380**, 621–624 (1996).
- Andrews, T. J., Halpern, S. D. & Purves, D. Correlated size variations in human visual cortex, lateral geniculate nucleus, and optic tract. *J. Neurosci.* **17**, 2859–2868 (1997).
- Schroeder, C. E., Tenke, C. E., Arezzo, J. C. & Vaughan, H. G. Binocularity in the lateral geniculate nucleus of the alert monkey. *Brain Res.* **521**, 303–310 (1990).
- Varela, F. J. & Singer, W. Neuronal dynamics in the visual corticothalamic pathway revealed through binocular rivalry. *Exp. Brain Res.* **66**, 10–20 (1987).
- Sengpiel, F., Blakemore, C. & Harrad, R. Interocular suppression in the primary visual cortex: A possible neural basis of binocular rivalry. *Vision Res.* **35**, 179–195 (1995).
- Lehky, S. R. & Maunsell, J. H. R. No binocular rivalry in the LGN of alert macaque monkeys. *Vision Res.* **36**, 1225–1234 (1996).
- Haynes, J. D. & Rees, G. Predicting the orientation of invisible stimuli from activity in primary visual cortex. *Nature Neurosci.* **8**, 686–691 (2005).
- Kamitani, Y. & Tong, F. Decoding the visual and subjective contents of the human brain. *Nature Neurosci.* **8**, 679–685 (2005).
- Levelt, W. J. Note on the distribution of dominance times in binocular rivalry. *Br. J. Psychol.* **58**, 143–145 (1967).
- Schneider, K. A., Richter, M. C. & Kastner, S. Retinotopic organization and functional subdivisions of the human lateral geniculate nucleus: a high-resolution functional magnetic resonance imaging study. *J. Neurosci.* **24**, 8975–8985 (2004).
- Scialo, G., Maunsell, J. H. & Lennie, P. Coding of image contrast in central visual pathways of the macaque monkey. *Vision Res.* **31**, 1148–1157 (1990).
- Tong, F. & Engel, S. A. Interocular rivalry revealed in the human cortical blind-spot representation. *Nature* **411**, 195–199 (2001).
- Polonsky, A., Blake, R., Braun, J. & Heeger, D. J. Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neurosci.* **3**, 1153–1159 (2000).
- Lee, S. H., Blake, R. & Heeger, D. J. Traveling waves of activity in primary visual cortex during binocular rivalry. *Nature Neurosci.* **8**, 22–23 (2005).
- Lee, S. H. & Blake, R. V1 activity is reduced during binocular rivalry. *J. Vis.* **2**, 618–626 (2002).
- Logothetis, N. K. & Wandell, B. A. Interpreting the BOLD signal. *Annu. Rev. Physiol.* **66**, 735–769 (2004).
- Andrews, T. J. Binocular rivalry and visual awareness. *Trends Cogn. Sci.* **5**, 407–409 (2001).
- Wales, R. & Fox, R. Increment detection thresholds during binocular rivalry suppression. *Percept. Psychophys.* **8**, 827–835 (1970).
- Watanabe, K., Paik, Y. & Blake, R. Preserved gain control for luminance contrast during binocular rivalry suppression. *Vision Res.* **44**, 3065–3071 (2004).
- Sobel, K. V., Blake, R. & Raissian, T. A. Binocular rivalry suppression does impede buildup of the motion aftereffect. *J. Vis.* **4**, Abstract 243 (2004).
- Blake, R. & Fox, R. Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature* **249**, 488–490 (1974).
- Fang, F. & He, S. Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neurosci.* advance online publication, 4 September 2005 (doi:10.1038/nm1537).
- Ichida, J. M. & Casagrande, V. A. Organization of the feedback pathway from striate cortex (V1) to the lateral geniculate nucleus (LGN) in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.* **454**, 272–283 (2002).
- Singer, W. Control of thalamic transmission by corticofugal and ascending reticular pathways in the visual system. *Physiol. Rev.* **57**, 386–420 (1977).
- Montero, V. & Zempel, J. The proportion and size of GABA-immunoreactive neurons in magnocellular and parvocellular layers of the lateral geniculate nucleus of the monkey. *Exp. Brain Res.* **62**, 215–223 (1986).
- Kastner, S. et al. Functional imaging of the human lateral geniculate nucleus and pulvinar. *J. Neurophysiol.* **91**, 438–448 (2002).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements This work was supported by the Wellcome Trust. We thank J. Driver and P. Sterzer for comments, and E. Freeman for advice regarding the stimuli.

Author Contributions J.-D.H. and G.R. conceived the experiment, R.D. wrote the pulse sequence and J.-D.H. carried out the experiment and data analysis. G.R., J.-D.H. and R.D. co-wrote the paper.

Author Information Reprints and permissions information is available at npg.nature.com/reprintsandpermissions. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to J.-D.H. (haynes@fil.ion.ucl.ac.uk).