

herbivores and predators. Densities within field enclosures were measured with an insect suction device. One sample consisted of eight 10-s placements of the sampling head on the marsh surface such that 0.8 m² of *Spartina* was subjected to suction.

Plant productivity

Two measures of plant productivity, aboveground biomass and the number of tillers produced (vegetative reproduction), were measured once at the end of the study. Aboveground biomass was determined for mesocosms by harvesting all live aboveground vegetation and for field enclosures by sampling all live aboveground biomass within a 0.047 m² wire frame. Vegetation was dried in an oven for 3 days at 55 °C and then weighed. The number of tillers produced was determined visually by counting all tillers in mesocosms and counting all tillers within the 0.047 m² sampling quadrat for the field enclosures.

Statistical analyses

The effects of the food web complexity treatments on final planthopper population size, the number of *Spartina* tillers and the aboveground biomass of *Spartina* were each analysed independently with mixed-model analyses of variance in which a block was modelled as a random source of variation. Subsequently, pairwise comparisons of treatment means were performed by using a *t*-test with a Bonferroni correction for multiple comparisons. Data were log-transformed when necessary to meet assumptions of normality and homogeneity of variances.

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Object-based attention determines dominance in binocular rivalry

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A question of long-standing interest to philosophers, psychologists and neuroscientists is how the brain selects which signals enter consciousness^{1,2}. Binocular rivalry and attention both involve selection of visual stimuli, but affect perception quite differently. During binocular rivalry, awareness alternates between two different stimuli presented to the two eyes. In contrast, attending to one of two different stimuli impairs discrimination of the ignored stimulus, but without causing it to disappear from consciousness. Here we show that despite this difference, attention and rivalry rely on shared object-based selection mechanisms. We cued attention to one of two superimposed transparent surfaces and then deleted the image of one surface from each eye, resulting in rivalry. Observers usually reported seeing only the cued surface. They were also less accurate in judging unpredictable changes in the features of the uncued surface. Our design ensured that selection of the cued surface could not have resulted from spatial, ocular or feature-based mechanisms. Rather, attention was drawn to one surface, and this caused the other surface to be perceptually suppressed during rivalry. These results raise the question of how object representations compete during these two forms of perceptual selection, even as the features of those objects change unpredictably over time.

The relationship between attention and rivalry has been debated from the late nineteenth century^{1,2} to the present^{3,4}. The question of what is selected in attention and rivalry has also been disputed. It is well established that spatial locations can be selectively attended^{5,6}, but it is now recognized that objects can be selected as well^{7,8}. For rivalry, the debate has been whether competition is stimulus-based, eye-based or some combination of the two⁹. Using the paradigm illustrated in Fig. 1, we asked whether selection of an object by attention causes that object to be dominant during rivalry. Observers viewed two superimposed patterns of dots presented to both eyes at the start of each trial. The patterns rotated rigidly in opposite directions around a fixation point, yielding a percept of two superimposed transparent surfaces. After a period of dual rotation, one surface was briefly translated in one of eight directions, and the observer reported the perceived direction. Such brief translations are known to cue attention to the translated surface^{10–13}. Hence, we refer to the translated surface as the ‘cued surface’.

After translation, the image of the cued surface was removed from one eye and the image of the uncued surface was removed from the other eye (see Methods). Because the surfaces differed in rotation direction, this dichoptic presentation produced rivalry. To determine whether rivalry favoured the cued surface, we asked observers to report whether one surface was clearly dominant at the end of

dichoptic presentation, and if so, which surface. By varying the duration of dichoptic presentation from trial to trial, we traced the time course of dominance from 0 to 1,850 ms.

As illustrated in Fig. 2a, 150 ms after the switch to dichoptic presentation, the dominance of the cued surface was small but significant. This advantage was, however, quickly amplified. After 300 ms, rivalry was perceived on the majority of trials, and the cued surface was usually dominant. The cued surface remained dominant for at least 900 ms. The translation that cued attention was presented to both eyes. Nonetheless, the cued surface was dominant, regardless of whether it appeared in the right or the left eye during subsequent dichoptic viewing. Therefore, the dominance of the cued surface must have resulted from a selection mechanism that bypassed interocular competition.

In addition to circumventing eye-based mechanisms, our paradigm also ruled out spatial and feature-based selection. Spatial selection cannot account for our results, because the dominant and suppressed surfaces always occupied the same region of visual space. Nor can the dominance of the cued surface be explained by selection of an individual feature: it is known that observers can track the features of one of two superimposed stimuli as they change smoothly through feature space¹⁴. However, our study precludes this possibility because rotation followed translation abruptly. After translation, both directions of rotation were present, and only surface identity linked the cueing translation to the particular rotation direction later reported as dominant. Having ruled out ocular, spatial and feature-based selection, and having found that the identity of the cued surface predicted which rotation direction was dominant, we conclude that this selection is object-based.

Investigations of object-based attention have shown that performance in judging multiple visual features is better if the features belong to a single object, as opposed to multiple objects. This has been found to be true both when the two features are defined within different dimensions, such as colour and orientation^{7,14}, and when they are defined within the same dimension, such as visual motion^{10–13}. The latter set of experiments revealed that the second of two successive translations is poorly discriminated if the translations are of two surfaces, as opposed to when they are of the same surface.

In a second experiment, we adapted our paradigm to see whether these object-based effects would also be seen during rivalry. As in experiment 1, both surfaces rotated and then one surface briefly translated in one of eight directions. The observer reported perceived translation direction. One hundred and fifty milliseconds after this cueing translation, we again deleted the image of one surface from each eye, but instead of reporting which surface was then dominant, observers reported the direction of a second translation. We measured accuracy as a function of the time between the end of the cueing translation and the start of the second translation (the interstimulus interval).

To compare attentional selection during rivalrous and non-rivalrous viewing, we interleaved these rivalrous trials with non-rivalrous trials in which the stimuli never became dichoptic and were thus perceived as superimposed transparent surfaces throughout the trial. On half of these ‘transparency’ trials, both surfaces were presented to both eyes throughout the trial, a condition that we refer to as ‘binocular transparency’. On the other half of the transparency trials, both surfaces were deleted from one eye 150 ms after the first translation. This ‘monocular transparency’ condition controlled for any momentary disruption caused by deleting surfaces during the switch from normal binocular viewing to rivalrous viewing. But monocular transparency did not induce rivalry, as there was no competing stimulus in the other eye. Despite this transient event when switching to monocular transparency, there were no significant differences in the observers’ performance on monocular and binocular transparency trials (three-way analysis

of variance with interstimulus interval, viewing condition and surface as factors; see Supplementary Information). We therefore focus on monocular transparency, because it provides a more direct comparison to rivalry.

Observers were impaired in judging the second translation of the uncued surface during both rivalry (Fig. 2b) and monocular transparency (Fig. 2c), but with different time courses. In monocular transparency, the impairment was strongest 150 ms after the first translation. In contrast, the peak impairment during rivalry occurred 450 ms after the first translation. The impairment disappeared within 1,000 ms during transparency, but persisted in rivalry at the longest duration tested. The magnitude and time course of the impairment were significantly different in rivalry and monocular transparency, according to a three-way analysis of variance, with interstimulus interval, viewing condition and surface as factors ($P < 0.05$ for all two-way interactions; see Supplementary Information).

These double translation experiments isolated the contribution of neurons that mediate interocular competition from those that mediate object-based competition. Transparency and dichoptic

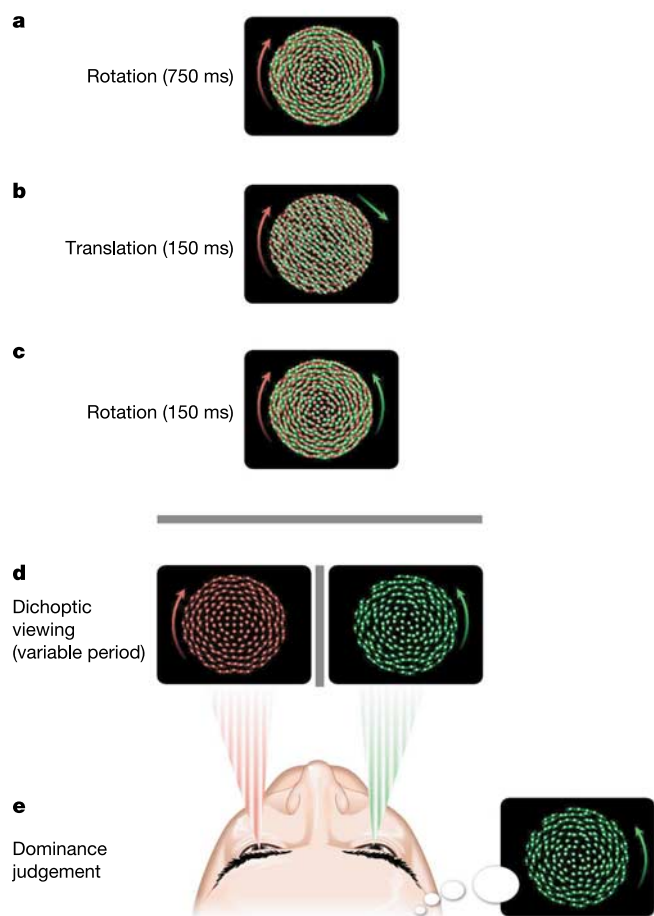


Figure 1 Dominance-judgement task. Panels are arranged from top to bottom according to the sequence of events that occurred on each trial in experiment 1. **a**, Two sets of dots rotated in opposite directions around a common point, yielding a percept of superimposed transparent surfaces viewed through an aperture. For illustration purposes, we show the surfaces with different colours (red and green), but they were actually the same colour. **b**, One of the surfaces, the green surface in this illustration, translated for 150 ms in one of eight directions, while the other surface continued to rotate. Subjects reported the direction of translation. **c**, Both surfaces resumed rotation for 150 ms. **d**, The image of one surface was removed from each eye, resulting in rivalry. Subjects judged which surface was dominant at the end of this variable-length period of rivalrous viewing. **e**, Observers usually perceived the previously translated surface as dominant.

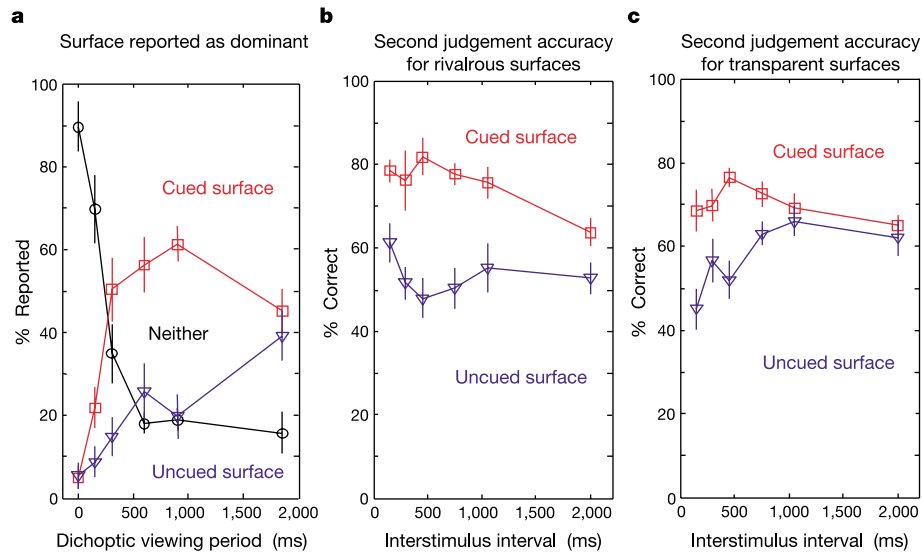


Figure 2 Data from dominance-judgement and double-translation tasks. **a**, Seven observers reported whether either surface was dominant at the end of dichoptic presentation and, if so, which surface was dominant. The mean percentage of trials on which the cued or uncued surface was reported to be dominant is shown in red and blue, respectively. The percentage of trials on which neither surface was clearly dominant appears in black. **b**, Mean accuracy in reporting the direction of the second translation averaged across trials in which the surfaces were presented dichoptically. **c**, Mean

accuracy in reporting the direction of the second translation when both surfaces were presented to one eye, and thus appeared transparent. Line colour in **b** and **c** indicates whether the cued (red line) or uncued (blue line) surface translated second. The interstimulus interval is the delay between the end of the cueing translation and start of the second translation (interstimulus interval = dichoptic viewing period + 150 ms). Error bars indicate standard errors of the mean across subjects.

viewing trials began identically, with one of the two surfaces cued by a sudden translation. Stimulus conditions were identical during cueing, so the same neurons logically must have been engaged, regardless of whether transparent or rivalrous viewing ensued. From this, we surmise that the same object-based mechanisms initiated selection for both transparency and rivalry trials. However, after the cueing phase, the sole difference between the rivalry and monocular transparency conditions was that the two deleted stimuli were removed from different eyes in one condition and from a single eye in the other. Thus, whereas dominance during rivalry and transparency must have been triggered by the same object-based mechanisms, the differences in the time courses of selection can only be due to neurons with eye-of-origin information. One intriguing difference is that the cueing effect was strongest at the shortest latency for transparency, but was initially disrupted during rivalry. This delay agrees with the relatively weak perceptual dominance found in experiment 1 at the shortest period of dichoptic viewing (Fig. 2a) and may reflect the time required for object-based mechanisms to influence interocular competition.

Our findings illuminate the long-standing debate about the relationship between rivalry and attention^{1,2}. Although some have concluded that attention has no influence on rivalry, recent studies suggest otherwise. Cueing spatial⁴ and feature-based¹⁵ attention during rivalry have been found to influence perceptual dominance. The present results show that when an object is cued during normal binocular viewing, it then dominates during subsequent rivalry. Besides revealing an unambiguous influence of attention, these results establish a connection between object-based attention and rivalry.

The present experiments also add to the literature showing that rivalry is not exclusively eye-based. Before our study, it was known that under certain conditions a stimulus can maintain its dominance, even when swapped between eyes^{16,17}. It was also known that complementary parts of two stimuli can be distributed across the eyes and fused into a coherent whole^{18–25}. Feature-based mechanisms can explain some of these earlier results, but other findings implicate more sophisticated, potentially object-based, mecha-

nisms^{22,25}. The present findings extend these earlier studies by showing that competition during rivalry can occur between representations of objects that change their attributes (here, directions of motion) unpredictably. This requires that the different motions be ‘bound’ into a coherent representation. Although the underlying mechanism is unknown and controversial^{26,27}, the binding of attributes is a hallmark of object-based representation^{26,27}.

Finally, these studies are consistent with the view that binocular rivalry, like other multi-stable phenomena, such as the Necker cube and the face–vase illusion, involves competition between high-level stimulus representations^{28–30}. Our results raise the possibility that selection of one of multiple possible interpretations of the visual scene (as with multi-stable percepts) and selection of one of several objects in the visual scene (during selective attention) engage common competitive mechanisms. □

Methods

Subjects viewed stimuli through a mirror stereoscope in a dark, quiet room. Sessions began with adjustment of the mirrors to allow binocular fusion of two nonius lines, displayed dichoptically on a Trinitron Multiscan TC running at 60 Hz. A bite bar stabilized the head while eye position was monitored using infrared tracking operating at 60 Hz (ISCAN). Trials terminated if fixation strayed from a one-degree square window. Reliable eye positions were obtained in five of seven subjects. The other subjects had eye shapes that precluded eye position monitoring, but showed similar cueing effects. The luminances of the left and right images were adjusted to compensate for ocular biases. Subjects discriminated a brief translation during rivalrous presentation of two, photometrically isoluminant (68 candelas per m²) dot patterns. If mean accuracy was better for translations presented to one eye, then luminance in that eye was reduced to equate performance. Both surfaces were the same colour, either red or green, chosen with equal probability. All experimental sessions consisted of 5 blocks of 100 trials, lasting 1.5–2 h with 5–10 min breaks between blocks. All judgements were indicated by key press.

Experiment 1: dominance-judgement task

Each trial began with fixation of a central grey point (0.25 × 0.25 degrees of visual arc) presented to both eyes. After the subject had pressed a key, two circular patterns of dots appeared, rotating in opposite directions around a central fixation point (see Fig. 1). These binocularly presented patterns appeared as two overlapping, rigidly moving, transparent surfaces. On each trial, one surface was selected at random to rotate clockwise and the other rotated anticlockwise. Each surface subtended 5.5 degrees of visual arc, was composed of 120 dots (averaging 5 dots per square degree of arc), and rotated at 50 degrees per second.

Trials began with 750 ms of dual rotation, after which one surface, chosen at random,

briefly (150 ms) translated in one of eight directions while the other surface continued rotating. Sixty per cent of the dots translated coherently while each of the remaining dots was randomly assigned to one of the other 7 directions, thus discouraging tracking of individual dots. The translation velocity was 1.5 degrees of visual arc per second. Observers reported translation direction at any time during the trial. Translation judgements were accurate (mean, 86.7% correct). Breaks of fixation, incorrect responses and correct responses were signalled by different sounds.

After translation, both surfaces rotated for 150 ms. The image of one surface, selected at random, was then deleted from one eye and the image of the other surface was deleted from the other eye. The surfaces then continued rotating for one of six dichoptic viewing periods (0, 150, 300, 600, 900 or 1,850 ms), after which both disappeared. Observers reported whether the clockwise, anticlockwise or neither surface had been dominant at the end of the trial. To confirm accuracy of these reports, we interleaved catch trials (20% of the total), in which either one surface appeared in both eyes or both surfaces appeared in both eyes. On most trials subjects correctly reported that neither surface was dominant when both were present (82.8% correct), and correctly identified the direction of rotation when a single surface was present (85.1% correct).

Experiment 2: double-translation task

The double-translation task was identical to the dominance-judgement task except that subjects judged a second translation (in one of eight directions) rather than dominance. The surface that underwent this second translation was selected at random on each trial. Translation was subsequently masked by 500 ms of dual rotation.

Three conditions were interleaved. In the rivalry condition, as in the dominance-judgement task, surfaces were presented dichoptically 150 ms after the cueing translation ended. In the monocular transparency condition, the images of both surfaces were deleted from one eye at this same time point. In the binocular transparency condition, both surfaces were presented throughout the trial.

We traced the time course of selection by varying the interstimulus interval (the period between the end of the cueing translation and the onset of the second translation). We used six interstimulus intervals (150, 300, 450, 750, 1,050 or 2,000 ms). The interstimulus interval was selected at random on each trial.

Subjects practised until they achieved 70% accuracy in judging the second translation of the cued surface under non-rivalrous conditions. Data from practice sessions were discarded. We then ran four experimental sessions (20 blocks in total). From session to session we adjusted the duration of the second translation so that the mean performance in judging the second translation of the cued surface remained approximately 70% for all conditions. The duration was varied from 33 to 100 ms in each condition.

Observers

Seven observers (five women and two men) participated in both of the main experiments. All had normal, or corrected to normal, vision. Five were naive. Ages ranged from 19 to 31 years.

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VEGF delivery with retrogradely transported lentivector prolongs survival in a mouse ALS model

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Amyotrophic lateral sclerosis (ALS) causes adult-onset, progressive motor neuron degeneration in the brain and spinal cord, resulting in paralysis and death three to five years after onset in most patients¹. ALS is still incurable, in part because its complex aetiology remains insufficiently understood. Recent reports have indicated that reduced levels of vascular endothelial growth factor (VEGF), which is essential in angiogenesis and has also been implicated in neuroprotection^{2–4}, predispose mice and humans to ALS^{5,6}. However, the therapeutic potential of VEGF for the treatment of ALS has not previously been assessed. Here we report that a single injection of a VEGF-expressing lentiviral vector into various muscles delayed onset and slowed progression of ALS in mice engineered to overexpress the gene coding for the mutated G93A form of the superoxide dismutase-1 (SOD1^{G93A}) (refs 7–10), even when treatment was only initiated at the onset of paralysis. VEGF treatment increased the life expectancy of ALS mice by 30 per cent without causing toxic side effects, thereby achieving one of the most effective therapies reported in the field so far.

Because delivery of therapeutically attractive neuroprotective factors to motor neurons is a formidable challenge in ALS therapy, we recently developed a lentiviral gene transfer system to deliver