in E2 binding [17]. The equivalent position typically contains an aromatic or hydrophobic residue in the RING fingers and particularly in the U box, where it is almost invariably aromatic (Figure 1). The structural models show that this aromatic residue in the RING fingers and in the U-box domain is exposed (Figure 2) and could directly contribute to E2–ubiquitin binding via hydrophobic or aromatic stacking interactions. Thus, the RING finger and the U box in E4 proteins are likely to activate ubiquitination and multi-ubiquitination, respectively, in a similar fashion, namely by facilitating the interaction between E2 proteins and their substrates.

In addition to the previously reported combinations of the U box with other interaction domains [4], we detected proteins with fusions of the U box with the WD40 β-propellers in the splicing factor PRP19 and with a cyclophilin-like peptidyl–prolyl isomerase (Figure 1). In these proteins, the U-box domain could recruit E2 proteins for ubiquitination of pre-mRNA splicing complexes and unfolded proteins associated with the proline-isomerase chaperone, respectively. This latter role is consistent with the association of UFD2 with the AAA ATPase CDC48, which possesses chaperone activity [4], and with the presence of a U box in the HSP70-binding protein CHIP [19] (Figure 1).

These observations show that the RING-finger fold can be maintained even as its hallmark pattern of metal-chelating residues is abolished and that the RING fold is the common structural determinant of both E2-dependent ubiquitination and multi-ubiquitination of proteins. Determination of the U-box structure and analysis of its interaction with E2 will put these predictions to test.

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Binocular rivalry and perceptual coherence
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Different images presented simultaneously, one to each eye, result in an alternating perception of each image, rather than their combination [1]. It has been suggested that such binocular rivalry is mediated by reciprocal inhibition of neurones in separate monocular channels [2]. However, recent single-unit [3,4] (see also reviews [5,6]), psychophysical [7,8] and functional magnetic resonance imaging [9,10] studies suggest that binocular rivalry is resolved high in the visual pathway. Despite this evidence, there is ongoing debate over whether it is the eyes or stimulus representations that rival during binocular rivalry [7,11].

With human observers, Logothetis *et al.* [7] rapidly swapped each eye's presented image at a rate of 3 Hz and demonstrated that this does not induce rapidly changing perceptual alternations but rather, smooth and slow alternations indistinguishable from normal rivalry. This finding challenges eye or monocular-channel interpretations, leading the authors to postulate that it is the stimulus

Figure 1

Stimuli used to demonstrate coherence rivalry. **(a)** The stimuli presented to each eye; **(b)** the expected perceptual pattern of eye-competition models of rivalry; **(c)** the pattern expected from an organizing process based on contour coherence. The graphs display the mean percentages of the subjects' total viewing time (excluding mosaic percepts) for which each of the two types of rivalry were perceived. Both half-field and full-field (coherence) rivalry occupy roughly half of each subject's total viewing time (see also Table 1). The periods of coherence rivalry cannot be accounted for by reciprocal inhibition of neurones in separate monocular channels and demonstrate that the brain can organize components of each eye's image (using contour as the organizing cue) to achieve perceptual coherence. In 1928, Diaz-Caneja reported this effect using similar half-field stimuli but with colour cues as well (red horizontal lines and green semi-circles). Try observing the phenomenon of coherence rivalry for yourself using free fusion or a piece of paper to separate each eye's image.
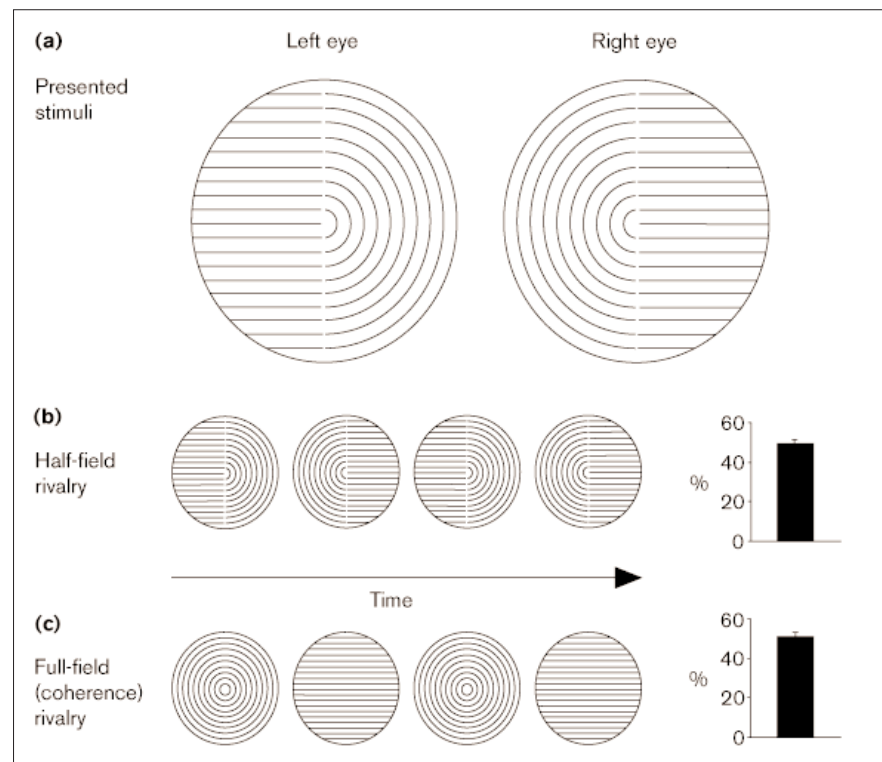
representations at high levels of the visual pathway that rival. Lee and Blake [11] recently replicated and extended this study and found that stimulus rivalry prevails over eye rivalry only under limited conditions such as low contrast.

In 1928, Diaz-Caneja [12] reported that half-field stimuli similar to those shown in Figure 1a do not rival as alternating half-field images (Figure 1b) but rather as alternating coherent images (Figure 1c). This demonstrated that the brain is able to organize aspects of each eye's image into rivalling coherent percepts. In his original experiment using half-field stimuli with red horizontal lines and green semi-circles, both colour and contour coherence may have been organizing cues [12]. Colour was indeed shown to be an organizing cue in a recent study that similarly demonstrated the brain's synthetic capacity during binocular rivalry ([8] and see earlier studies reviewed in [8]). In these experiments, dichoptically presented patchwork images were shown to rival as coherent images, though some training was required for observers to achieve this effect.

Diaz-Caneja's conclusion that binocular rivalry must be a high level process has tended to be overlooked because of the relative obscurity of the publication [12]. We therefore welcomed the opportunity to briefly replicate and quantify his work. We used the half-field stimuli shown in Figure 1a, which are devoid of colour cues. We demonstrate that subjects reported half-field perceptions (Figure 1b) for approximately half of their total viewing time (excluding mosaic percepts), with the remaining half spent perceiving full-field (coherent) percepts. The graphs beside Figure 1b,c provide the relative percentages of half-field versus full-field rivalry for sixteen right-handed male subjects (aged 18–25 years), and Table 1 shows each subject's data. All subjects reported periods of full-field rivalry without training or prompting.

Data were collected over half an hour, divided into three blocks, each with four 100 second trials. Subjects sat three metres from a monochrome display monitor and recorded their perceptual alternations by pressing one of three response keys: one for either of the two half-field percepts; one for either of the two coherent percepts (these designations were counterbalanced across subjects); and the third for mixed or mosaic percepts. The latter were excluded from the percentage calculations shown in Figure 1 but are reported in Table 1. The stimuli were presented in an elliptical patch, and had a visual angle of 2.8 degrees (height) by 2.1 degrees (width), spatial frequency of 8.7 cycles/degree, and contrast of 0.9. The presentation of a different image to each eye was achieved using a VisionWorks package with NuVision stereoscopic goggles that allow the superimposition of each eye's image so no special training in fixation was required. The results

Table 1

Rivalry data for individual subjects.

Subject	Coherence		Half-field		Mosaic
	Percentage	Number	Percentage	Number	Number
1	37.2	265	62.8	265	1
2	39.5	191	60.5	192	2
3	43.3	93	56.7	86	64
4	46.0	124	54.0	125	2
5	47.1	171	52.9	172	42
6	48.9	51	51.1	49	1
7	50.9	152	49.4	148	24
8	51.1	76	48.9	76	14
9	52.8	120	47.2	124	11
10	53.0	107	47.0	104	33
11	53.1	68	46.9	167	6
12	54.0	61	46.0	62	24
13	55.3	67	44.7	64	0
14	57.0	100	43.0	96	11
15	60.7	247	39.3	246	1
16	64.3	120	35.7	116	37

Relative percentages of half-field versus full-field (coherence) rivalry for sixteen male right-handed subjects. The percentages for each subject are calculated over approximately 20 min of viewing the stimuli shown in Figure 1a and exclude mosaic percepts, which do not fall into either category shown in Figure 1b,c. Also shown is the number of times mosaic, coherent and half-field percepts were reported during the viewing period.

indicate clearly that the brain can unite aspects of each eye's image to create coherent rivalling images on the basis of contour coherence. We refer to this as 'coherence rivalry' rather than 'stimulus representation rivalry' since the coherent percepts are different from either of the presented stimuli, and 'stimulus representation rivalry' does not necessarily suggest that reorganization of image components is taking place.

The fact that a substantial portion of all subjects' viewing time involves coherent percepts supports Diaz-Caneja's early suggestions and proves that eye rivalry does not account for these periods. Our use of high-contrast stimuli shows that non-eye rivalry is not limited to low contrast conditions (compare this to [11]). The presence of substantial periods in which half-field images are perceived suggests that perceptual coherence is not always achieved.

Although Lee and Blake [2,11] do not deny the existence of stimulus representation rivalry, they would presumably support an eye interpretation of the alternating half-field periods. They suggest that the search for the neurophysiological mechanisms of binocular rivalry "should not overlook neurons whose signals retain some signature of their monocular origins" ([11], page 1454). However, this suggestion must contend with the compelling demonstration by Logothetis and colleagues that monocular neuron activity bears no relationship to the perceptual reports of monkeys during binocular rivalry [3].

The data presented here quantify Diaz-Caneja's 1928 finding and serve as a timely reminder that coherence rivalry is not due to rivalling eyes. Our data also show that contour alone can serve as an organizing cue in coherence rivalry. Moreover, we have shown that subjects report periods of coherence rivalry without training or prompting. The search for the neural mechanism of binocular rivalry continues and will require new empirically verifiable models.

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