

Neuropsychological evidence of high-level processing in binocular rivalry

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One of the most fascinating and challenging questions of cognitive neurosciences is what are the neural correlates of consciousness. We try to answer this question by studying patients having a dissociation between conscious perception and sensory stimulation.

We studied patients with right brain damage (RBD) involving unilateral spatial neglect (USN). USN follows a lesion in the right frontoparietal cortex and involves lack of consciousness of visual stimuli (or parts of them) presented in the contralesional (left) side of space, without any sensory deficit [5]. Even if patients are unable to describe the left side of a stimulus, they show behavioural evidence of preserved visual analysis when tested implicitly [4].

To study visual consciousness in neglect patients, we used binocular rivalry. This involves showing different images to the two eyes. Instead of seeing both images simultaneously, neurologically normal people see one image for a few moments with no trace of the other, then they see the other image for a few moments with no trace of the first, then they see the first again, and so on for as long as they care to look. This phenomenon exhibits a dissociation between sensory input, which is unchanging, and consciousness, which changes continuously.

There are two opposing explanations of binocular rivalry: low-level and high-level theories [8]. Blake [2] proposed that rivalry is resolved at a low level of the visual system, in the primary visual cortex, involving

inhibitory interactions between monocular representations of the two rival stimuli. Logothetis et al. [6], on the other hand, proposed that rivalry is resolved at a high level of the visual system, in the inferotemporal cortex or higher, involving interactions between representations of the two rival images.

In support of high-level theories, neuroimaging studies have consistently shown that binocular rivalry involves activity in the parietal and frontal areas (e.g. [7, 10]), particularly in the right hemisphere. These are the areas that if damaged are associated with USN, so we decided to examine whether binocular rivalry requires these areas to be intact.

There are three possible outcomes:

1. If binocular rivalry is determined by low-level processes, USN patients should show the same rivalry as neurologically healthy subjects.
2. If binocular rivalry is determined by high-level processes, RBD patients should show compromised rivalry.
3. If binocular rivalry depends critically on the areas responsible for USN, such patients should show compromised rivalry that is different from that shown by RBD patients without USN.

After neuropsychological evaluation, we selected two groups of right-handed RBD patients: with unilateral spatial neglect (USN+; 9 patients) and without neglect (USN-; 12 patients). The neuropsychological and demographic data for the two groups are visible in Table 1. We also studied 10 healthy, right-handed, control subjects (CTRL), matched for age ($M = 50.4$;

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Table 1
Demographic and neurological details of the right brain-damaged patients, with and without unilateral spatial neglect (USN). I = infarct; H = hemorrhage; T = temporal; P = parietal, BG = basal ganglia; IC = internal capsule; O = occipital. MMSE adj = MMSE adjusted score; * = MMSE raw data

Group	Name	Sex	Age	Edu.	Month onset	Lesion	Lesion site	VFD	MMSE adj	AlbertL	Albert R	DillerL	DillerR	BellL	BellR	LB 16	WJL	WJR	flowers	Reading
USN-	CA	F	55	-	-	I	T, P	0	24*	1	0	15	13	5	7	-4.6	0	0	0	5
USN-	RS	M	53	8	26	-	-	0	27.97	0	0	0	0	1	0	1	0	0	0	6
USN-	GR	M	43	13	3	I	F, T, P	0	27.89	0	0	n.a.	n.a.	4	0	0.4	0	0	0	6
USN-	VM	F	35	13	24	I	F, P	0	27.75	n.a.	n.a.	n.a.	n.a.	1	0	1.2	0	0	0	6
USN-	CF	M	69	13	6	H	T, P	0	30	0	0	0	0	0	0	1.2	0	0	0	6
USN-	FC	F	50	13	9	H	F, P, BG	0	30	0	7	9	3	0	0	-2.8	0	0	0	6
USN-	LS	F	44	8	14	H	F, P	0	29.62	1	0	0	0	5	5	-1	0	0	0	6
USN-	ES	M	71	8	3	I	-	0	30	0	0	9	8	0	2	0.8	2	2	1.2	6
USN-	IM	M	37	14	13	H	-	0	26.1	0	0	1	0	1	3	-2.4	0	0	1	6
USN-	AB	M	67	8	2	H	F, IC	0	27.47	0	0	2	2	2	2	1.6	0	0	0	6
USN-	AT	F	63	17	1	I	F	0	25.46	0	7	7	4	3	3	-2	1	0	0	6
USN-	MG	F	67	13	3	I	T, P, IC	0	26.46	0	0	5	0	0	4	2.8	0	0	0	6
USN+	BT	F	40	13	6	I	-	0	30	0	23	14	12	7	3	1	0	2	4	
USN+	SP	F	52	13	1	I	-	n.a.	19.99	3	0	53	30	n.a.	n.a.	7	0	0	1.2	4
USN+	GB	M	69	5	12	I	T, O, BG	0	23.27	5	0	53	29	16	3	31.8	16	2	1.2	0
USN+	SS	M	40	8	2	H	-	0	28.62	1	0	6	2	5	0	1	0	0	1	6
USN+	EC	M	65	3	1	I	F, T, P	0	23.99	1	0	53	48	17	14	-11.2	0	0	0	3
USN+	AA	M	61	13	8	H	F	0	25.49	0	0	5	1	7	0	4.4	4	0	1	6
USN+	VM2	M	60	5	4	I	F, T, P	0	24.27	11	1	53	12	14	3	8.8	19	0	1	4
USN+	SC	M	66	13	5	I	T, BG, IC	0	26.49	0	0	8	3	2	0	9.6	0	0	1	6
USN+	MG2	F	51	8	10	I	F, T, P	0	24.97	1	0	17	3	6	2	9.8	0	0	1.2	6

SD = 5.6). All subjects had normal acuity in each eye tested separately and normal binocular vision, defined as simultaneous perception and fusion.

We presented pairs of rival images in a stereoscope that was aligned with the midsagittal plane. Rival images varied in complexity:

- Square-wave gratings tilted 45° clockwise and 45° counterclockwise (Orientation) (simple);
- Square-wave gratings with low and high spatial frequencies (Frequency) (simple);
- Two different configurations of illusory motion (Movement) (moderately complex);
- Pictures of two different objects: a face and a house (Object) (complex).

Stimulus size was between 5.37° and 7.15°.

We asked subjects to press one button on a PC's mouse when they saw one rival stimulus with no trace of the other, and another mouse button when they saw the other rival stimulus with no trace of the first.

Responses were recorded using a laptop PC running a script in ePrime software.

Rival stimuli were presented for 60 seconds, twice to allow counterbalancing of image to eye.

We counted the number of alternations from consciousness of one image to the other. We found that RBD patients reported fewer alternations ($M = 3.24$) than control subjects ($M = 14.81$), $F(2, 28) = 25.16$, $p < 0.001$, but with no significant differences between USN+ ($M = 4.29$) and USN- ($M = 2.45$) patients. Control subjects also reported more alternations with the orientation stimuli and fewer with the objects than with any other type, whereas RBD patients had similar number of alternations for all stimulus types, $F(6, 84) = 3.19$, $p < 0.01$.

One possible explanation is that RBD patients had a more conservative criterion for deciding on visibility of an image. If so, patients should show not only a reduced number of alternations, but also a reduced number of key presses. However, the ratio between alternations and key presses is much higher for control subjects (0.76) than for RBD patients (0.38), with no significant differences between USN+ and USN-. That is, control subjects' consciousness tended to alternate between the two rival stimuli, whereas RBD patients' consciousness tended to dwell on one of them. This suggests that rivalry is compromised in RBD patients

independently of USN (outcome 2).

In conclusion we obtained an effect of stimulus complexity in neurologically normal subjects, confirming a slower rivalry alternation rate for more complex stimuli [1]. Patients with right brain damage did not show this effect and showed a reduced alternation rate. Differently from Bonneh et al. [3] we did not find any differences between patients with and without USN, suggesting that the mechanism underlying the suppression of visual input in binocular rivalry is different from that involved in USN.

Because our patients' brain damage is confined to right parietal and frontal lobes, we can conclude that processing within these areas influences the temporal course of visual consciousness. This is consistent with fMRI [7,10] and electrophysiological [9] studies on neurologically normal subjects, which showed an involvement of the right parietal lobe and the frontoparietal system in alternation conditions vs stable conditions.

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