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Research report

ERP time course of perceptual and post-perceptual mechanisms of spatial selection

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Abstract

Event-related potentials (ERPs) were recorded from volunteers performing a task requiring simple judgements about the spatial location of a single target that could appear with equal probability to the left or right of fixation. A robust finding in the ERP literature is a dichotomy between attentional selection for spatial and non-spatial features. Visual spatial selection is manifest as a modulation of early components (P1, N1) that reveal exogenous processes, while non-spatial selection is revealed by the presence of longer latency endogenous components (N2). We present an analysis of several conditions that require different degrees of visual analysis to confirm the location of the single target, and show that spatial selection can be manifest at early (N1) or later (N2) stages. Observers identified the location of targets that were more salient (2D line drawings with abrupt onset) or less salient (2D line drawings without abrupt onset or 3D objects embedded in random-dot stereograms). We examined differences in amplitude, latency, and topography of early ERP components (P1, N1, P2, N2), and compared responses measured over the left and right hemispheres in response to left and right targets. The results support the hypothesis that the processes involved in spatial selection can be manifest at early or late stages, dependent on the quality of the incoming data. Moreover, the iterative process by which the percept is established benefits from a change in the visual input that is specific to the target.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Spatial attention; Stereopsis; Reentry; Event-related potential; P1; N1; N115; N2

1. Introduction

Many studies have examined event-related potentials (ERP) to reveal the time course of visual attention. The tasks used have primarily been spatial cueing tasks in which attended and unattended stimuli are compared, or visual search tasks in which the target is presented in a visual array with one or more distractors. It is fairly well accepted that the mechanisms of attention for selection of spatial location are distinct from the mechanisms for selection of other cues such as colour, form, orientation, spatial frequency, and feature conjunctions [15,26]. A robust finding is that there are timing differences between spatial and non-spatial selection. Spatial selection appears to have precedence in processing over attentional selection based on non-spatial cues [11,17]. One way to characterize these differences is that spatial cues benefit from early attentional selection mechanisms and are more influenced by bottom-up exogenous input, whereas non-spatial cues rely on later mechanisms and are linked with top-down endogenous processes.

Although there is some evidence to suggest that it is possible to reverse the order of selection (e.g., colour prior to location) [17], the mechanisms which determine early or late selection of spatial location per se are not yet clear. This paper examines the nature of early perceptual and attentional processing of object information under conditions that make the spatial location of the target easy or difficult to extract from the visual display.

In Experiment 1, observers made simple decisions about the spatial location of object parts embedded in random-dot autostereograms. Extracting information about an

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object embedded in a random-dot stereogram requires processing that is additional to that needed to recognize a 2D line drawing of the same object. Form perception in random-dot stereograms is not available in the 2D representation of the image, but is based on the correlation between the information presented to each eye. Thus, the cyclopean object contours are defined by retinal disparity, and corresponding monocular dot patterns must be fused before the depth object can be identified [20].

Recent single cell work from monkeys suggests that, although V1 neurons respond to stereoscopic surfaces related to receptive field location [4,40], stereoscopic edges and edge orientation are explicitly represented in area V2 [40]. This is interesting in light of the evidence that V2 cells are also important in the response to illusory contours [30], for example, the contours of a Kanizsa triangle (but see [9]). Essentially, the contours of the cyclopean object embedded in a random-dot stereogram are illusory in the same sense that the contours of a Kanizsa triangle are illusory. In such cases, the second-order features depend on the configuration of first-order features. The first-order features of random-dot stereograms are the dots, and the second-order features are the contours of the object perceived once the correct correspondence has been attained between the dot patterns represented on the left and right retinae.

The results of Experiment 1 suggested that simple selection of spatial location is delayed in time when the stimulus is defined by second-order features. The results may provide insight into the interpretation of ERP components for which the generator sites are not easily localized. Note that cells in V2 are selective for complex shapes [13], and could be important to timing differences for object analysis.

2. Experiment 1 (cyclopean object)

2.1. Materials and methods

2.1.1. Participants

Twelve volunteers participated in a 2-h session. All had participated in previous experiments and training sessions that used the same stimuli [1] and were skilled at diverging their eyes to fuse the autostereograms. Two volunteers were eliminated from the final analysis due to excessive eye movements. An additional volunteer was eliminated from the ERP analysis due to excessive blinking which required discarding 40% of trials.

2.1.2. Stimuli

The stimuli used in Experiment 1 were single-image random-dot stereograms (autostereograms). The shape embedded in each autostereogram was a single disk (diameter=5.6 cm; visual angle of diameter=5.1 degrees) centred in the random-dot array. The disk was always in the same central *x*, *y* position and fixation was at the centre of the disk (see example in Fig. 1). Successful divergence and fusion resulted in the perception of the disk floating above a flat background. In total, five types of disk stimuli were created. Four of the five disk stimuli had a circular target (diameter=1.6 cm; visual angle of diameter=1.5 degrees) located at the inner edge (3, 6, 9, or 12 o'clock positions), which appeared as a hole in the edge of the larger disk. The fifth disk did not contain a target. The task was a 5-alternative forced choice to indicate the position of the target on each trial.

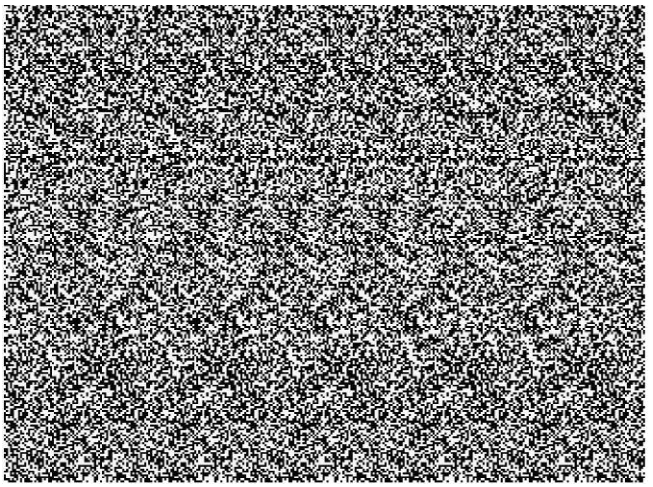
The random-dot images were computer generated directly from line drawings of the disks using a simple algorithm. For example, for each image, a random-dot field was generated with a horizontal repeating pattern width of 60 pixels, or 24 mm displayed on a 15″ VGA monitor at a resolution of 640×480 pixels (see Fig. 1), and the embedded object was created by an algorithmic manipulation of the dot periodicity [37]. At 630 mm between the eyes and the monitor, the pattern width subtended a visual angle of 2.2 degrees. The density of black dots on a white background was 50%. Construction of the random-dot stimuli and training of observers is described in detail elsewhere [1].

2.1.3. Procedure

All sessions were conducted in a dimly lit, sound attenuated room. A chin rest was used to maintain the eyes at a fixed distance from the display. Participants received instruction to maintain fixation and were monitored for compliance via a close-circuit video system. The experimenter reminded participants to withhold blinks and eye movements as was necessary. The session began with 4 practice blocks of 10 trials each, followed by 25 test blocks of 25 trials each. (An additional 25 blocks of trials examining attention switching in depth are not relevant and did not affect the results reported here.)

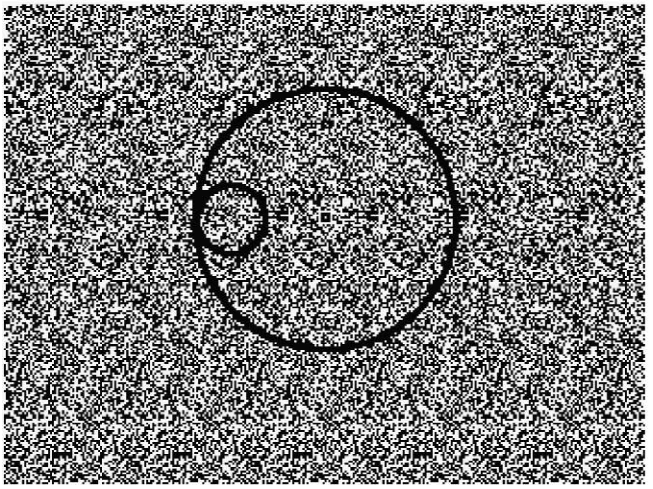
Observers initiated each block by pressing the spacebar, upon which there was a 1200 ms delay (blank screen), followed by a random-dot background without an embedded object which was displayed for 2 s to allow observers to achieve the correct divergence prior to the first trial. Each trial presented a new random-dot stimulus with embedded object which remained on the screen until 1000 ms after the behavioural response. At that point, the current random-dot stimulus was immediately replaced by the next stimulus (see Fig. 2 for stimulus timing). Responses were made as quickly and accurately as possible to the position of the target using the right hand placed over the 3×3 grid of the number pad keyboard. The mapping between target position and key was straight-forward (none=5, upper=8, right=6, lower=2, left=4).

Feedback about accuracy and average response time (RT) was provided at the end of each block. Participants were allowed to rest as long as they wished between

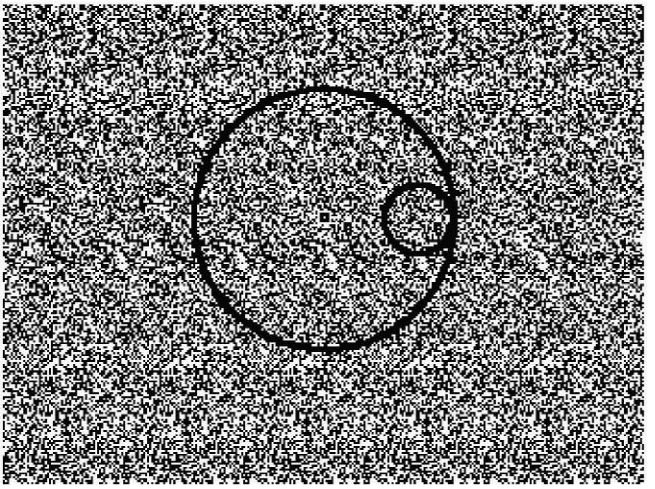


Embedded circle

Enlarged view of fixation point (white dot on black square on white square)



Circle with left target



Circle with right target

Fig. 1. Examples of random-dot fields to illustrate the embedded object (Experiment 1) and the superimposed line drawings with a left and a right target (Experiments 2b and 3). Also shown is an enlarged view of the centre of the random-dot array to show the fixation point designed to be easily seen within the dot array. Note that these illustrations are reduced in size relative to actual size on the computer monitor.

blocks. The stimulus presentation and response collection were programmed using MEL2 software [34].

2.1.4. Electrophysiological recording

Electrophysiological recording was conducted in the same way for all experiments. Participants were fitted with an elasticized cap mounted with 64 pure tin electrodes (Electro-Cap International Inc.). Saccadic and vergence eye movements and blink activity were monitored by leads placed supraorbitally and at the external ocular canthi of both eyes. A continuous EEG was recorded from the 64 channel montage, referenced to the right mastoid and amplified by a custom-built S.A. Instrumentation Bio-amplifier system. The recording bandwidth was 0.1–100 Hz and the signal was digitized at 400 Hz.

The EEG was segmented and averaged off-line. Only epochs associated with correct behavioural responses were included for further analysis. Epochs that contained eye blinks, saccades, vergence eye movements, or other eye or muscle movement artifacts were discarded, making up approximately 10% of the remaining epochs. The discarded trials were manually inspected and the rejection criteria were adjusted until satisfactory rejection performance was achieved for each individual. The data were digitally filtered off-line using a low-pass 30 Hz filter and re-referenced using a distance-weighted Laplacian algorithm [19]. The arrangement of electrodes in the custom-designed cap was such that each electrode was approximately equidistant from surrounding electrodes; the array is illustrated in Fig. 3, which shows a top view and a back view of electrode placement after locations were digitized and fitted to a sphere. Spherical splines were then used to interpolate the topographical voltage maps [29].

From the 64 electrodes, the following 4 pairs of left and

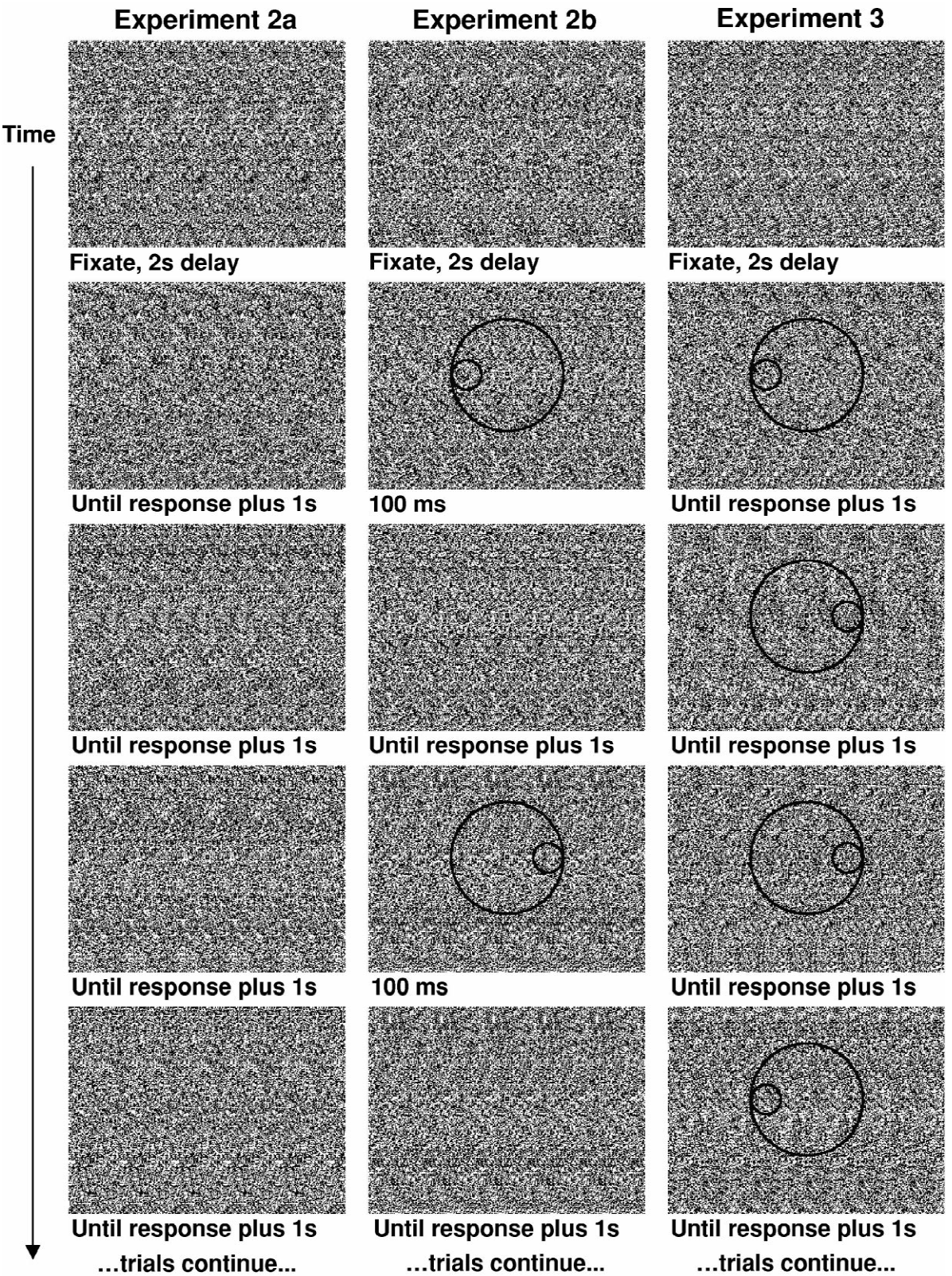


Fig. 2. For each experiment, a sequence of possible trials is shown. Note that the timing is different for the experiments (Experiment 1 is not illustrated but the timing of the display is identical to Experiment 3). The first display is a random-dot field with a fixation point (see Fig. 1 for an enlarged illustration of the fixation point). The first column is Experiment 2a, in which observers responded to a change in the random dot pattern on each trial. The second column is Experiment 2b, in which the line drawing of a stimulus with a left or right target was superimposed over a random-dot field for a duration of 100 ms. The third column is Experiment 3, in which the line drawing remained superimposed on the random-dot field for the duration of the trial.

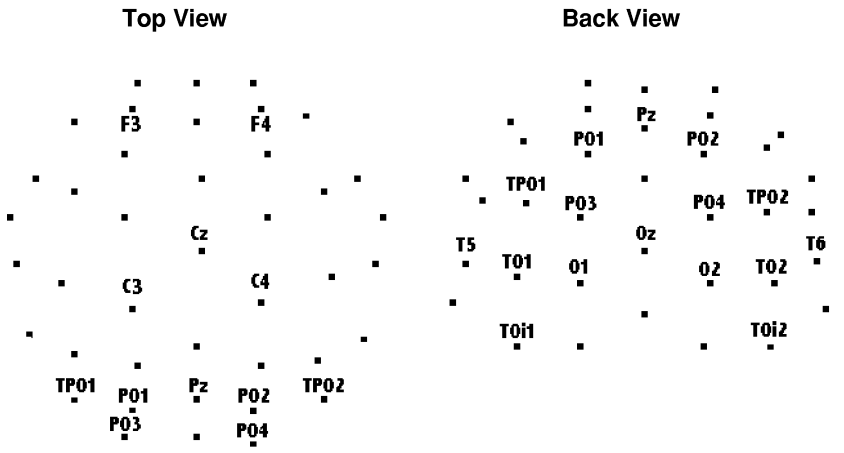


Fig. 3. Top View (left) and Back View (right) of 64 digitized electrode locations, fitted to a sphere. Note that locations near the edges of the sphere are not as close together as they appear, and that some of the lateral frontal electrode sites do not appear on these views. Electrodes were placed so that each electrode was as equidistant as possible from surrounding electrodes. Labelled electrodes referred to in the text and figures are shown here at the occipital (O1/O2), temporal-occipital (TO1/TO2), parietal-occipital (PO3/PO4), and temporal-parietal-occipital (TPO1/TPO2) sites.

right hemisphere electrode sites were selected for statistical analysis of component peaks and latencies. The labels shown in Fig. 3 correspond to the 10/20 system, including additional electrode sites named to reflect spatial relation to the 10/20 system sites. The 4 pairs of sites were chosen based on differences between the conditions in the averaged waveforms, to cover posterior regions of interest. They include occipital (O1/O2), temporal-occipital (TO1/TO2), temporal-parietal-occipital (TPO1/TPO2), and parietal-occipital (PO3/PO4) sites. Statistical tests were performed separately on peak amplitudes and latencies for the following components (ms time windows are shown in brackets for Experiments 1, 2a, 2b, and 3): P1 (2a: 40–120 ms; 1, 2b and 3: 40–140 ms), N1 (1: 60–160 ms; 2a: 80–180 ms; 2b and 3: 100–200 ms), P2 (1: 100–230 ms; 2a: 150–250 ms; 2b: 150–300 ms; 3: 150–200 ms), and N2 (1: 160–360 ms; 2a: 200–350 ms; 2b: 250–350 ms; 3: 200–250 ms). The time windows were chosen after manual inspection of each data set to ensure the peak of the component would fall within that window for all observers.

Repeated measures ANOVA was applied to behavioural and ERP analyses with $\alpha = 0.05$. Where appropriate when repeated measures factors had more than two levels, the Greenhouse–Geisser adjustment for possible violation of the assumption of compound symmetry was applied [8]. Post-hoc comparison of means used the Newman–Keuls test with $\alpha = 0.05$.

2.2. Results and discussion

The effect of the 5 Target Positions was examined on behavioural responses (accuracy and RT; Table 1) and on peak amplitude and latency for the N2 component at temporal-occipital electrode sites TO1/TO2 (bottom cells of Table 2). This component and electrode pair were chosen because of maximal differences in the grand averaged waveforms. Target position did not affect accuracy but did have a significant effect on behavioural RT (for correct responses) due to faster responses for left and right targets, and relatively slower responses for lower targets and for the no-target condition. This pattern of behavioural results is consistent with Arnott and Shedden [1], and is important to the current paper to show that responses to the left and right target positions did not differ behaviourally. There was no effect of Target Position on the latency of the N2, however, there were large effects on amplitude illustrating the sensitivity of the N2 to visual field location of the stimulus. The left target position (LTarg) produced a larger N2 over the right hemisphere (RH) and the right target position (RTarg) produced a larger N2 over the left hemisphere (LH). Differences between TO1 and TO2 electrode sites were examined for each of the 5 target positions revealing that contralateral enhancement occurred for the left and right target positions only ($P < 0.01$).

Table 2 presents the significant ANOVA results in tabular form, and Fig. 4 illustrates the pattern of effects for

Table 1
Experiment 1: Behavioural measures[a]

Target Position	Response time		Accuracy	
	Mean	Std. Err.	Mean	Std. Err.
Left	462	63	0.984	0.006
Right	462	25	0.989	0.005
Upper	499	29	0.985	0.009
Lower	549	36	0.975	0.010
None	542	30	0.974	0.008

[a] Means and standard errors for RT and accuracy (proportion correct) are presented. A repeated measures ANOVA showed that Target Position (left, right, upper, lower, and no target) did not affect accuracy but was significant for RT ($F(4,36) = 15.68$; $P < 0.0001$; $\epsilon = 0.60$). The original degrees of freedom are reported with the adjusted P-value and relevant Greenhouse–Geisser Epsilon value ϵ.

Table 2
Experiment 1: ERP ANOVA summary[a]

	Effect	ERP	O1/O2		TO1/TO2		TPO1/TPO2		PO3/PO4	
			$F(1,8)$	$P<$	$F(1,8)$	$P<$	$F(1,8)$	$P<$	$F(1,8)$	$P<$
Amplitude	P	P1			6.01	0.05				
	H	P1			10.29	0.05				
		N2	10.4	0.05						
	P×H	P2			22.4	0.01	16.77	0.01	17.82	0.01
		N2	30.41	0.001	27.67	0.001	23.78	0.01	24.58	0.01
Latency	P	P2							7.25	0.05
		N2							5.67	0.05

Analysis of the N2 component at TO1/TO2 for all 5 Target Positions.

	Effect	ERP	TO1/TO2		
			$F(4,32)$	$P<$	ϵ
Amplitude	P	N2	11.77	0.001	0.53
	H	N2	5.96	0.05	
	P×H	N2	15.22	0.001	0.61

[a] Summary table of ANOVA results from ERP analyses. Greenhouse–Geisser epsilon (ϵ) indicated when applicable (the original degrees of freedom are reported with the adjusted P-value and relevant Greenhouse–Geisser Epsilon value ϵ). Target Position (P: LTarg/RTarg) by Hemisphere (H: LH/RH). Bottom set of results described Target Position (P: left, right, upper, lower, none) by Hemisphere (H: LH/RH).

left and right target positions. Statistical analyses of the remaining ERP components focused on the left and right target positions only, in part to simplify the analysis and in part because electrophysiological responses to the left and right target positions held considerably more theoretical interest in the context of the goals of the current paper. The most important observations involved the interaction between Target Position and Hemisphere because the sensitivity to the location of the target tells us about the stage at which the cyclopean form is processed. The contralateral sensitivity of the visual N1, which usually peaks between 100 and 200 ms, is well known [22] and we would expect to see amplitude differences depending on whether the target was presented in the left or right visual field. However, the N1 peaked much earlier (115 ms) than the N1 that is usually observed in visual experiments. Moreover, there were no effects on the amplitude or latency of the N115 component at any electrode site. This is important, indicating that the contralateral response of the first negative component does not occur for these stimuli. This does not mean that target position did not have any effect on early components because there was a small effect of that factor on the amplitude of the P1 at temporal-occipital sites TO1/TO2. The important observation is that the response of the N115 is not what we would expect for the N1.

Critically, the later N2 at 220 ms was the first negative deflection sensitive to the position of the target in the visual field. There was a strong contralateral enhancement ($P<0.01$) in which the LTarg produced a larger N2 over the RH and the RTarg produced a larger N2 over the LH. This is in the direction expected if the N2 component is an index of target location processing and indicates that the response to the lateralized cyclopean form was delayed. This hypothesis is supported by comparing the topography of the N115 and the topography of the N2 (Fig. 4). They are highly distinct, and it is notable that the N2 topography is similar to the topography usually observed for the N1 produced by 2D stimuli. Although the N115 might be an index of processes related to disparity processing, which would be consistent with a model that disparity processing occurs prior to processing of the cyclopean form [38], there are some obvious questions about Experiment 1 that need to be addressed.

3. Experiment 2a (random-dot pattern detection) and 2b (2D target localization)

One question we addressed in Experiment 2 asked whether the early N115 component in Experiment 1 was related to disparity processing or whether it was a function of the high frequency and high contrast display of random dots. The latter hypothesis is consistent with a study by Zani and Proverbio [42], who showed a similar early component in response to high frequency high contrast checks. If so, then it is possible that the N115 is an index of an attentional filtering process. Recent work by Worden and colleagues [41] suggests there may be stimulus locked alpha-band activity that is localized to visual field locations where distracting information is expected. Such a filtering process may work to suppress the intensity of the field of dots to allow more focused processing of the embedded object. In a sense, that would mean suppressing the first-order features to better attend to the second-order features. In either case, the additional processing would result in a delay in the selection of the task-relevant features of the object.

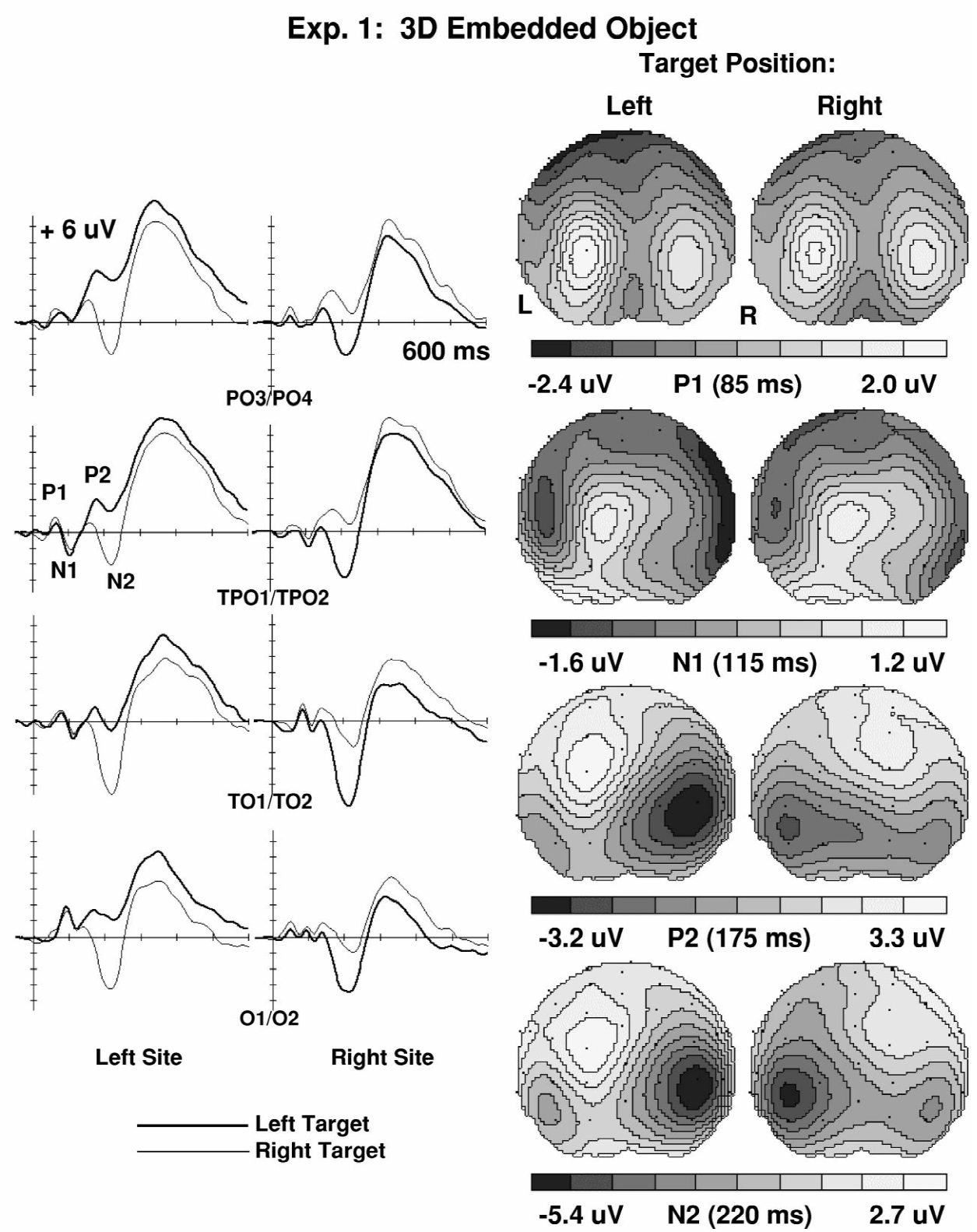


Fig. 4. Results from Experiment 1: ERP waveforms and topographic voltage maps elicited in response to left and right target features of objects embedded in random-dot stereograms.

An alternative hypothesis is that the early N115 indicates active processing of the dots, but is not part of a filtering mechanism. To test the response to the surface properties of the dots (Experiment 2a), we used the identical random-dot stimuli used in Experiment 1 and asked participants to simply respond each time one field of

dots was replaced by another. Thus, attention was directed to the surface features and the results should reveal processing that is related to the dot field itself, independent of the embedded object. If the N115 is observed in Experiment 2a, then it is not likely a result of suppression of the dots, which are now task-relevant.

Another important question from Experiment 1 is related to the delayed selection of target location, indicated by the late lateralized negativity (N220). The N220 may be an index of the same process usually revealed by the N1, but the reason for the delay is not clear. In Experiment 2b we tested responses to 2D line drawings superimposed for 100 ms on the same random-dot arrays that were used in Experiment 1. If the delay in the lateralized negative response to the target location in Experiment 1 was due to interference from the random-dot field, then we should see the same delay for line drawings superimposed on the random-dot field. If, however, the delay was related to extraction of object form from second-order features, then the same object defined by first-order features should produce a lateralized negative component with a much earlier latency (N1).

3.1. Materials and methods

3.1.1. Participants

Each of 10 volunteers participated in a two-hour session. All volunteers had normal or corrected to normal vision. Each volunteer gave informed consent to participate, and received $10 as remuneration.

3.1.2. Stimuli and procedure

The general procedure was the same as described for Experiment 1. In Experiment 2a, the stimuli consisted of the same random-dot patterns, however, given that our participants did not diverge and fuse the autostereograms but maintained a focal point at the plane of the monitor screen, the random-dot arrays appeared simply as horizontally repeating patterns of dots. In Experiment 2b, a line drawing of a large circle with a smaller target circle at the left or right edge was superimposed on the random-dot field for 100 ms at the same dimensions, visual angle, and x,y position described for Experiment 1. A small fixation point which subtended 0.17 degrees was also superimposed on each image (see enlarged illustration Fig. 1).

Experiment 2a was performed prior to Experiment 2b for all participants, and each was about 30 min in duration. Both experiments began with a practice block of 10 trials, followed by 25 test blocks of 25 trials each. The task was simply to indicate with a key press the onset of each new random-dot array (Experiment 2a), or to identify the location of the target which appeared equally often to the left or right (Experiment 2b). Timing of trials and displays is illustrated in the first two columns of Fig. 2. For both experiments, the display was turned off at the beginning of each trial for a duration of 2 screen refreshes (approximately 33 ms) while the new bitmap was drawn.

3.2. Results and discussion

Table 3 shows the means and standard errors for the behavioural results from Experiments 2a and 2b. The behavioural results are not particularly interesting for Experiment 2a because it was a simple detection task with above threshold stimuli (there were no errors), and we were primarily interested in the ERP. We performed a simple *t*-test for dependent samples on RT, comparing left and right target positions. Given that these target positions were detectable only if observers diverged and fused the random-dot patterns as autostereograms, and given that the task required analysis of the 2D dot pattern and not the embedded object, it was not surprising that there was no effect of target position ($P>0.7$). The target position was task-relevant in Experiment 2b and responses were slower relative to responses in Experiment 2a, however, observers were equally fast and accurate for LTarg and RTarg positions ($P>0.7$).

Table 4 displays a summary of the ANOVA results from the ERP analysis, and Figs. 5 and 6 illustrate the waveforms and topographical maps. Table 4 also shows the results of planned contrasts which directly examined the interaction between Target Position (LTarg/RTarg) and Hemisphere (LH/RH) on the N1 amplitude, contrasting contralateral (LTarg-RH and RTarg-LH) with ipsilateral (LTarg-LH and RTarg-RH) responses.

Our prediction for Experiment 2a was that there would

Table 3
Experiments 2a and 2b: Behavioural measures[a]

Target Position	Experiment 2a				Experiment 2b			
	Response time		Accuracy		Response time		Accuracy	
	Mean	Std. Err.	Mean	Std. Err.	Mean	Std. Err.	Mean	Std. Err.
LTarg	269	13	–	–	332	8	0.96	0.01
RTarg	267	13	–	–	329	11	0.97	0.01

[a] Means and standard errors are displayed for RT for Experiments 2a and 2b, and for accuracy (proportion correct) for Experiment 2b (Experiment 2a was a simple above threshold detection task and there were no errors). Note that Experiment 2b required detection of the left (LTarg) vs. right (RTarg) target whereas target position was not perceived in Experiment 2a. A *t*-test analysis revealed that Target Position did not affect RT or accuracy for either experiment ($P>0.7$).

Table 4
Experiments 2a and 2b: ERP ANOVA summary[a]

	Effect	ERP	O1/O2		TO1/TO2		TPO1/TPO2		PO3/PO4	
			$F(1,9)$	$P<$	$F(1,9)$	$P<$	$F(1,9)$	$P<$	$F(1,9)$	$P<$
Amplitude	E	P1			20.2	0.01	9.1	0.05	5.8	0.05
		N1	16.8	0.01	14.4	0.01	10.6	0.01		
	P	P2	7.1	0.05	9.6	0.02				
	P×H	P1			12.5	0.01				
		N1	5.5	0.05	11.5	0.01	8.6	0.02	5.4	0.05
		P2	6.7	0.05					6.6	0.05
	E×P×H	N1	6.1	0.05	13.4	0.01	10.2	0.02	6.5	0.05
		P2	6.6	0.05					7.8	0.05
Latency	E	P1	22.7	0.01						
		N1	7.9	0.05	20.7	0.01	24.7	0.001	5.5	0.05
		P2			10.9	0.01	12.8	0.01	5.3	0.05
	H	P2					8.2	0.01		
	E×H	P1					11.6	0.01		
	E×P	P2	6.0	0.05						
	P×H	N1					10.8	0.01		
		P2	5.8	0.05					9.9	0.02
	E×P×H	N1	6.5	0.05	10.0	0.02	16.5	0.01		
		P2							7.2	0.05

Planned contrasts, component N1.

	Effect	ERP	O1/O2		TO1/TO2		TPO1/TPO2		PO3/PO4	
			$F(1,9)$	$P<$	$F(1,9)$	$P<$	$F(1,9)$	$P<$	$F(1,9)$	$P<$
Amplitude		N1	5.8	0.05	12.7	0.01	9.5	0.05	6.0	0.05

[a] Summary table of ANOVA results from ERP analyses for amplitude and latency. Experiment (E: 2a/2b) by Target Position (P: LTarg/RTarg) by Hemisphere (H: LH/RH). Planned contrasts examine contralateral enhancement, comparing LTarg-RH and RTarg-LH with LTarg-LH and RTarg-RH.

be no significant effects of Target Position on RT, accuracy, or the amplitude or latency of the ERP components, and that is exactly what occurred. The most important result from Experiment 2a is the latency of the N115 component (115 ms, although the peak was a little later at 123 ms at temporal-occipital sites). We acknowledge that the N115 may be produced by different sets of generators active in the two experiments due to the possibility that different neural populations are activate in V1 under different conditions of retinal disparity. In Experiment 2a, the retinal images are in correspondence which changes the low-level input to V1. It is fairly well accepted that the early P1 component is generated in extrastriate cortex [27], therefore the later N115 does not reflect initial processing in V1. However, differences in low-level input can have a dramatic effect on later stages. Despite this possibility, we are confident that the N115 is not simply an early N1; they differ in latency, topography, and sensitivity to target location. Moreover, the topography of the N115 in Experiment 2a was similar to the N115 in Experiment 1 (bilateral temporal focus). We conclude that the occurrence of the early N115 is not affected by attention in this task. It looks very much the same whether the task-relevant features are the 2D surface features of the dot pattern or the second-order features of the 3D object defined by disparity.

We suggested earlier that the N115 in Experiment 1 may be a result of an increase in stimulus-locked alpha-band activity related to a filtering or gating process [41]. In the current context, the effect would be to suppress the visual response to surface features of the random-dot field when attending to the second-order features of the embedded object. However, Experiment 2a provided some evidence against that hypothesis for the current experiments because the dots were task relevant. It may be that the N115 is simply an early visual response to an intense visual stimulus, consistent with the N115 observed by Zani and Proverbio [32,42].

In contrast to Experiment 2a, Target Position was a strong factor for Experiment 2b, producing ipsilateral enhancement of the P2 and contralateral enhancement of the N1. The amplitude of the N1 was large, peaking at 140 ms at TO1/TO2 and at about 130 ms at occipital and parietal sites. The general pattern of the interactions on amplitude describes an enhanced contralateral response such that LTarg was greater over the RH, and RTarg was greater over the LH ($P<0.01$). This was confirmed by the planned contrasts which examined the enhanced contralateral response directly. The topography of the N1 in Experiment 2b was strikingly similar to that of the N2 component in Experiment 1. We interpret these observations about the N1 and the N2 in the different experiments (similar topography, same contralateral sensitivity) to suggest that they may be reflecting the same underlying process. It is important to note, however, that drawing conclusions about contributing generators based solely on scalp topography should be done with caution.

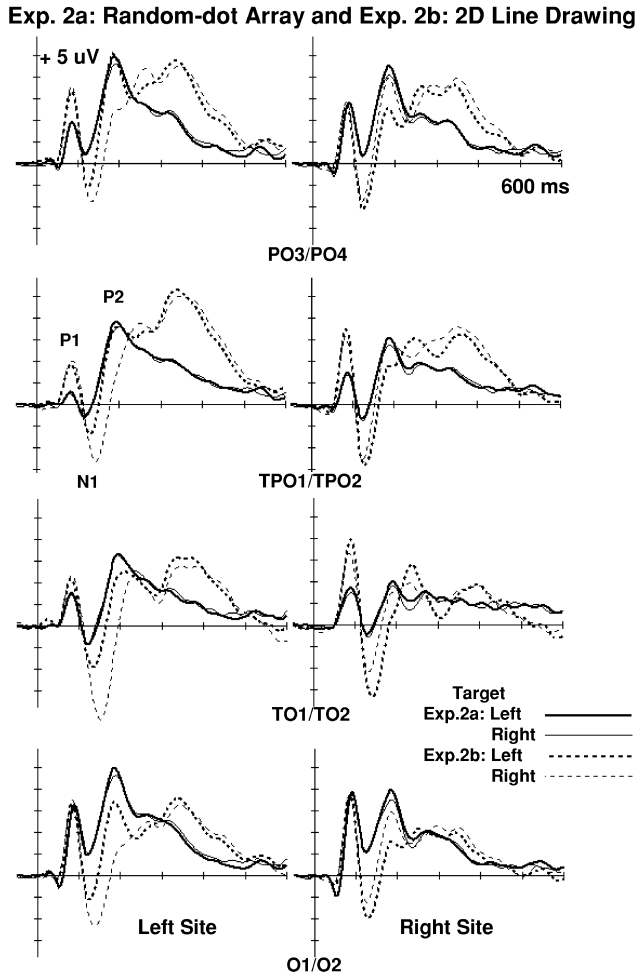


Fig. 5. ERP waveforms for Experiments 2a and 2b.

If the N1 in Experiment 2b and the N2 in Experiment 1 do reflect the same underlying process, then why such radical latency differences? Although the N2 in Experiment 1 looks much like what others have described as a selection negativity (SN) [11], our task is very different from the tasks which usually produce the SN, particularly in terms of spatial vs. non-spatial selection. It is important to point out that our experiments are not cueing experiments. The contrasts are between left and right hemispheres for left and right targets; they are not contrasts between attended and unattended locations. According to Harter and Aine [11], our tasks involve interlocation as opposed to intralocation selection. In Experiments 1 and 2b, the targets were identified based on location in the visual field, and it was not the case that feature selection was necessary once the target location had been determined. Therefore, it is somewhat unexpected that the timing of the selection (N1 vs. N2) is so different. We propose that the salience of the onset of the 2D object facilitates the iterative process that is necessary to establish the percept [5]. Presumably, additional processing was required in Experiment 1 to extract the object location information, leading to a delay in the process that establishes the percept.

We further propose that when the object is difficult to extract because the salience of its onset has been reduced, the iterative process requires longer (e.g., a greater number of iterations) to complete. This fits well with the reentrant model of Di Lollo, Enns, and Rensink [5] in which information about the visual stimulus is built up iteratively via information flow through cortico-cortical connections between early sensory areas and higher visual areas. Their model, which is based on metacontrast masking phenomena, suggests that the visual percept cannot be recognized until the iterative process completes, and that if the stimulus changes before that time (as it does in metacontrast masking experiments), the masked stimulus is not perceived.

In Experiment 1, the object was difficult to extract for a couple of reasons. First, it was not defined by first-order features. Calculation of retinal disparities of dot patterns was necessary to perceive the contours of the target, and thus determine its location. Second (and related), the onset of each new dot pattern was really an onset of 2D surface features that did not directly define the target, therefore the salient visual onset could not be used to facilitate the cortico-cortical iterative process. Contrast these conditions with Experiment 2b, in which the salient onset of the line drawing could be used to trigger and drive the iterative mechanism.

Then we should be able to make the following prediction. By reducing the salience of the onset of the line drawing, the contralateral enhancement of the negative component should occur later in time, similar to the response observed in Experiment 1. Importantly, this should occur even when there is a clear visual signal that a new trial has begun by a change in the background pattern of random dots. In other words, it is not uncertainty as to whether a new target has appeared, rather, the late spatial selection negativity results from reduced stimulus input to the iterative perceptual process. Experiment 3 addressed this question.

4. Experiment 3: Target onset salience

The task in Experiment 3 was identical to the task in Experiments 1 and 2b in that a response was required to indicate the location of a single target. We used the same stimuli as we did in Experiment 2b, with only one procedural difference. The line drawing remained visible for the entire trial rather than a duration of 100 ms, and was immediately replaced by a new random-dot background and a new line drawing at the beginning of the next trial.

The result of the extended duration was to produce two kinds of targets which differed in onset properties and thus in perceptual salience. For the Target Onset trials, the new

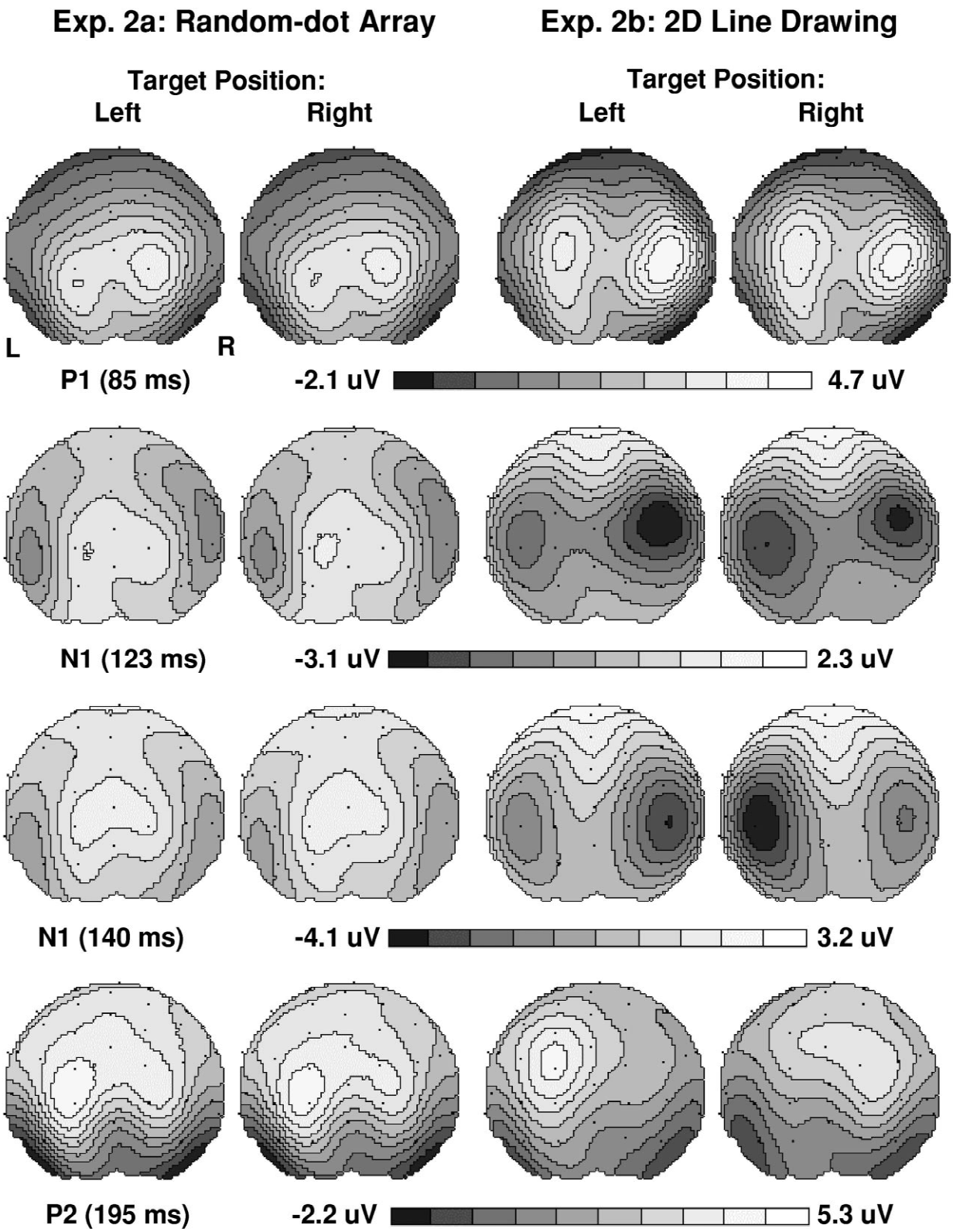


Fig. 6. Topographic voltage maps for Experiments 2a and 2b. Note that the palette scale is optimized for each set of topographic maps so it is important to note the minimum and maximum of each range.

target replaced the previous target in the opposite location, producing a salient visual onset (e.g., a left target replaced a right target, or a right target replaced a left target). In contrast, for the Target Repeat trials, the new target replaced the previous target in the same location (e.g., a left target replaced a left target, or a right target replaced a right target). The background random-dot pattern changed on every trial and the display was turned off for 2 screen refresh cycles (33 ms) between trials, so there was always a clear visual signal that the new trial had commenced. Despite these clear signals, the effect of repeating the target location in Target Repeat trials was to substantially reduce the perception of target onset compared to Target Onset trials.

4.1. Materials and methods

4.1.1. Participants, stimuli and procedure

Nine volunteers participated for $10 each in a 2 h session, which included time for ERP setup. All had normal or corrected to normal vision, and provided informed consent. The only difference between Experiment 2b and Experiment 3 was the duration of the 2D line drawing superimposed over the random-dot array as described above (see Fig. 2, third column).

4.2. Results and discussion

As indicated in Table 5, the salience manipulation had a small effect (12 ms) on the behavioural RT, whereby the response was slower when the previous trial was the same target position (target repeat) than when it was a different target position (target onset).

Similar to our examination of the N1 amplitude in Experiments 2a and 2b, planned contrasts examined the interaction between target position and contralateral/ipsilateral hemisphere response for the amplitude and latency of the N1, P2 and N2. Contralateral responses (LTarg-RH and RTarg-LH) were contrasted with the ipsilateral responses (LTarg-LH and RTarg-RH) separately for Target Onset and Target Repeat trials. Note that for the P2 and the N2, the peak of the response in the Target Onset condition was problematic, because there was no identifiable P2 or N2 peak over the contralateral hemisphere for Target Onset trials, although these components were identifiable over the ipsilateral hemisphere. Therefore, for the P2 and the N2, the planned contrasts were performed only for the Target Repeat condition. Table 6 displays a summary of the ANOVA results and planned comparisons, and Fig. 7 and Fig. 8 illustrate the waveforms and topographical maps.

The contrast between the Target Repeat and Target Onset conditions was striking. Reducing the perceptual salience of the target by repeating location and thus reducing the effect of target onset produced the predicted late negativity. In contrast, when the target appeared in a new location there was a strong contralateral response of the early N1 component. The topographic voltage maps shown in Fig. 8 are revealing. The early P1, which peaked at 85 ms, appeared highly similar in topography for all conditions and likely represents the response to the high contrast random-dot array. The N1 component peaked at 130 ms for the Target Repeat condition but was not significantly larger contralaterally. In contrast, the N1 component peaked at 168 ms for the Target Onset condition and the contralateral response to target position was highly significant. Finally, at 225 ms the N2 component showed a significant contralateral response to target position for Target Repeat only, and although the extent of the negativity across the scalp was not as large, the topography of the negative peak was similar to Target Onset at 168 ms.

With respect to the stimulus, the Target Repeat condition provided the same information as the Target Onset condition, including a clear visual signal that the new target had appeared. The only difference was that in the Target Repeat condition the perceptual process did not benefit from the abrupt onset of the target. The endogenous processes may be similar for both conditions, but the exogenous processes specific to the target location would have differed. One hypothesis is that the iterative process necessary to establish the percept did not benefit from the abrupt onset at the input level and required additional processing at higher levels to reach completion.

Looking across the experiments, the relation between the P2 and the N1/N2 was suggestive. The P2 showed the same parietal-occipital peak in all the experiments, at approximately the same latencies (Experiment 1: 175 ms;

Table 5
Experiment 3: Behavioural measures[a]

Target	Target repeat				Target onset			
Position	Response time		Accuracy		Response time		Accuracy	
	Mean	Std. Err.	Mean	Std. Err.	Mean	Std. Err.	Mean	Std. Err.
LTarg	397	17	0.98	0.01	388	18	0.97	0.01
RTarg	401	18	0.98	0.01	386	17	0.98	0.00

[a] Means and standard errors for RT and accuracy (proportion correct): Repeated measures ANOVA (target position by target salience) indicated that there were no significant effects of Target Position (LTarg/RTarg) and only a small difference in RT due to Target Salience (target repeat=399 ms vs. target onset=387 ms) that approached significance ($F(1,8)=5.3$; $P=0.051$).

Table 6
Experiment 3: ERP ANOVA summary[a]

	Effect	ERP	O1/O2		TO1/TO2		TPO1/TPO2		PO3/PO4	
			$F(1,8)$	$P<$	$F(1,8)$	$P<$	$F(1,8)$	$P<$	$F(1,8)$	$P<$
Amplitude	P	N2					9.5	0.02		
	S	N1			10.6	0.02				
		P2	10.7	0.02	31.7	0.001	15.6	0.01	10.1	0.02
	P×H	P1			22.6	0.01	9.9	0.02		
		N1	7.7	0.05	12.3	0.01	7.1	0.05		
		P2	14.6	0.01	29.4	0.001	11.9	0.01	8.1	0.05
		N2	25.1	0.01	26.6	0.001	10.4	0.02	8.5	0.02
	S×H	N1							6.3	0.05
		P2	12.5	0.01					11.1	0.02
	P×S×H	P1	26.7	0.001	8.5	0.02				
		N1	9.4	0.02	6.5	0.05				
Latency	P	N1					10.2	0.02		
	S	N1			11.8	0.01	7.4	0.05		
	P×H	N1	13.1	0.01	32.6	0.001	16.1	0.01	30.2	0.001
	P×S×H	N1			36.5	0.001	13.7	0.01	14.3	0.01

Planned contrasts, components N1, P2, and N2 for Target Onset Condition

	Effect	ERP	O1/O2		TO1/TO2		TPO1/TPO2		PO3/PO4	
			$F(1,8)$	$P<$	$F(1,8)$	$P<$	$F(1,8)$	$P<$	$F(1,8)$	$P<$
Amplitude		N1	9.1	0.05	11.6	0.01	6.2	0.05		
		P2	12.05	0.01	26.53	0.001	58.71	0.001	20.02	0.01
		N2	48.6	0.001	39.21	0.001	11.03	0.01	7.05	0.05
Latency		N1	12.3	0.01	46.5	0.001	20.6	0.001	21.2	0.01
		P2	7.82	0.05	8.99	0.05	6.39	0.05	7.36	0.05

[a] Summary table of ANOVA results from ERP analyses on amplitude and latency. Target Position (P: LTarg/RTarg) by Target Salience (S: Onset/Repeat) by Hemisphere (H: LH/RH). Planned contrasts of enhanced contralateral response compare LTarg-RH and RTarg-LH with LTarg-LH and RTarg-RH for the Target Onset condition.

Experiment 2: 195 ms; Experiment 3: 187 ms). The negative deflection sensitive to target location was very similar in topography, but highly variable in latency across the experiments (Experiment 1 N2: 220 ms; Experiment 2b N1: 140 ms; Experiment 3 Target Onset N1: 168 ms; Experiment 3 Target Repeat N2: 225 ms). It is important that the spatial location selection negativity peaked prior to the P2 when the target location was salient, and subsequent to the P2 when the target location was not perceptually salient. This suggests a dissociation between the P2 and the spatial selection negativity, and that the same mechanisms producing the early spatial selection negativity might engage later in time under the right conditions.

5. General discussion

The results reported in this paper distinguish between two different kinds of visuospatial selection. We presented simple stimuli that required simple location detection of a single target, under conditions that required different degrees of visual analysis. Experiment 2a showed that the N115 observed in Experiment 1 was not related to spatial selection. When the targets appeared with abrupt onset, as they did in Experiment 2b and the Target Onset condition in Experiment 3, early spatial selection was revealed as an amplitude modulation of the exogenous N1 component (140 ms and 168 ms, respectively). This is consistent with many studies of spatial selection [7,10,14,18,21,23–25]. In contrast, when the target was defined by features other than those that occurred with abrupt onset, either because the edges were defined by second-order features in Experiment 1 or because there was no abrupt onset in the Target Repeat condition in Experiment 3, there was no effect of spatial selection on the N1 component. Instead, a later indication of spatial selection occurred that was most evident at the N2 component (220 ms and 225 ms, respectively). This is a most interesting result because the N2 is usually associated with endogenous selection that is not spatial in nature [11,12,16,31].

Electrophysiological studies have demonstrated P1 and N1 responses to 2D stimuli, particularly their sensitivity to the location of the target in the visual field, and sensitivity to manipulations of spatial attention [7,10,14,18,21,23–25]. For example, when processing stimuli in 2D space the P1 and N1 are robust components measured with a latency of approximately 80–100 ms and 160–180 ms, respectively. When unilateral stimuli are presented to the left or right of fixation, the N1 is larger in amplitude over the lateral occipital cortex contralateral to the location of the stimulus in the visual field. The amplitude can be modulated by selective attention to spatial location (e.g., attend to stimuli

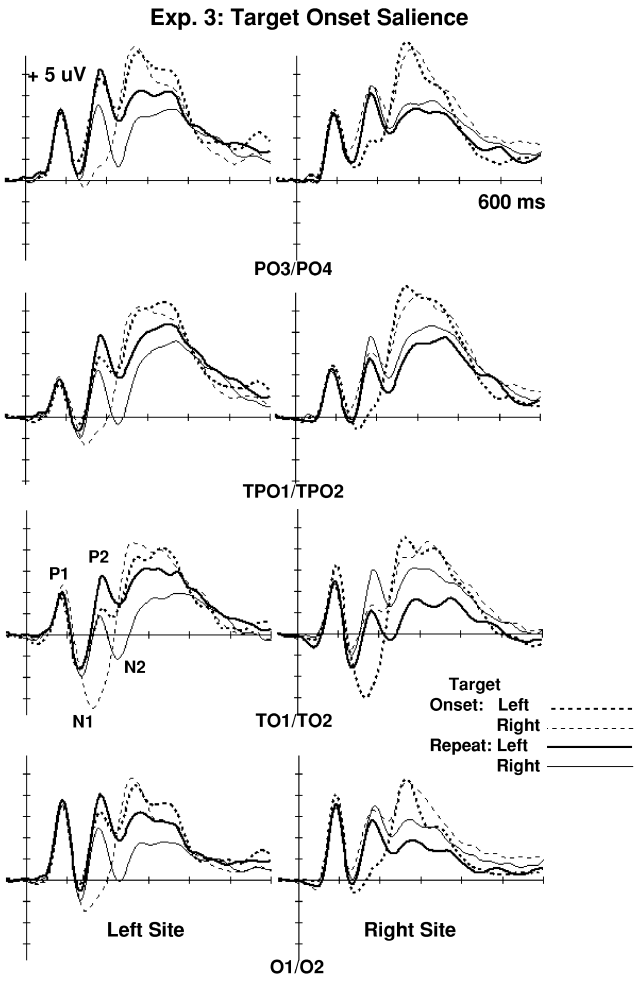


Fig. 7. ERP waveforms for Experiment 3.

in one visual hemifield while ignoring stimuli presented to the other) [6,10,39]. Based on the results of the spatial attention studies, the N1 has come to be understood as reflecting the initial selection of the location of the stimulus. The N1 component is thought to reflect exogenous processes; the amplitude but not the topography is affected by attention.

In contrast to the N1, the N2 has been associated with processes related to stimulus evaluation or classification, and may be a member of a family of relatively late occurring negative ERP components associated with non-spatial selection including the N200, mismatch negativity, and the selection negativity (SN) [11,22,28,33]. For example, the SN was identified by Harter and colleagues as a broad negativity (range approximately 150–300 ms) elicited by selective attention to stimulus properties other than location [11,12,31]. Similar to the N2 described by Hillyard and Mangun [16], the SN occurred for attended stimuli only, and was not detectable for unattended stimuli. The interpretation is that the SN and the N2 are not modulations of exogenous components like the P1 and the N1 attention effects, but rather they are thought to be endogenous components [16,23]. In other words, the topography of the N2 changes between attended and unattended conditions suggesting the engagement of an endogenous process, whereas the topography of the N1 component does not change suggesting attentional modulation of an exogenous process.

In this paper, the contralateral enhanced negativity observed at the N1 for salient targets or the N2 for less salient targets did not depend on previously directed attention and did not contrast between spatial and non-spatial selection. A single target was presented with equal probability at one of two possible locations, requiring a simple response to indicate the location of the target. The spatial locations were highly distinguishable and no other discriminations were required. It is important to note that in the Target Repeat condition in Experiment 3 there were clear visual signals that the display contained a new target. This, in addition to the fact that there was a full second delay between the behavioural response and the onset of the next target, argues against the possibility that the delay in the selection negativity could be due to confusion about whether a new trial had begun.

One critical factor for understanding the late negativity may be target discriminability. Hillyard and Mangun suggest discriminability of attended and unattended stimulus classes is critical for the time to select [15], and other ERP studies have shown that cue difficulty does in fact affect which of the early ERP components (P1, N1, N2) will show selection effects [17]. In our experiments, the delay in spatial selection of target location may be related to a kind of discriminability, that is the second-order nature of the stimulus — the fact that the contours which defined the location of the target feature were defined only by retinal disparity.

Hillyard and Munte [17] have demonstrated that the unique status of location as a selection cue is not mandatory, and that the order of cue selection can be manipulated by varying the discriminability within the attended and/or unattended stimulus sets. They made spatial selection difficult by placing stimuli close together, and were able to produce earlier selection for easily distinguishable colours. In that case, the ERP indices of spatial attention did not occur as modulations of the amplitudes of the early P1 or N1 components, but were manifest as longer-latency negativities with different topographic signatures and much diminished effects. These results were taken as evidence that the mechanisms involved were different from those usually engaged for early spatial selection [26].

Our task and results are much different in that the relevant locations were not in close proximity, target locations were distinct, and no other discriminations had to be made. Our indices of spatial attention at the longer latencies were not diminished in effect, but were quite large. In addition, the topographic maps we observed for the N1 (Experiments 2b and 3) and the N2 (Experiments 1 and 3) were remarkably similar. One interpretation is that

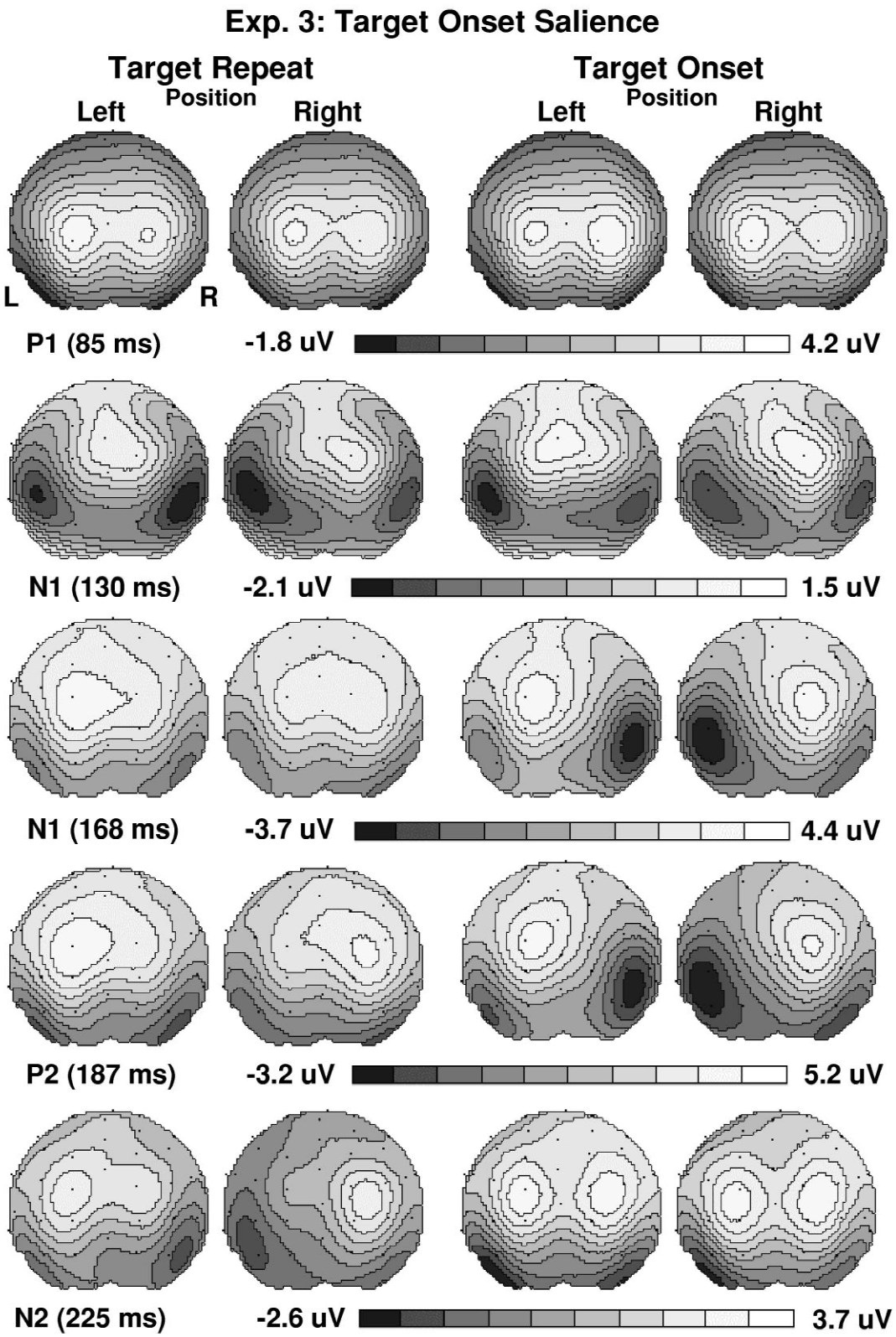


Fig. 8. Topographic voltage maps for Experiment 3. Note that the palette scale is optimized for each set of topographic maps so it is important to note the minimum and maximum of each range.

we are looking at the same mechanism engaged at an early and a late stage. This suggests two influences on spatial selection which may correspond to exogenous and endogenous attentional processes.

When a stimulus is more difficult to analyze, usually more analysis time is required. What is involved in this extended analysis? One hypothesis is that additional time is necessary to integrate information from a weak or noisy signal. A model like this has been proposed by Carpenter and Williams to account for variation in latency between the appearance of a visual target and the start of the saccadic eye movement due to decision processes [3]. A similar hypothesis is that visual perceptions emerge from an iterative exchange of information that takes place between populations of cells in early sensory cortices and populations later in the visual stream, refining the analysis until the visual percept is established [2,5,35,36]. If this process is interrupted before it can be completed, such as occurs with metacontrast masking, the masked object is not perceived [5]. The selection negativity, whether it be a reflection of spatial or non-spatial selection, may be an index of such a process by which information reenters sensory cortices as part of a reentrant process from higher levels, as described by the model put forth by Di Lollo, Enns, and Rensink [5].

One might imagine that the reentrant process is iterative, and that a salient stimulus onset drives the process. The sudden appearance of a new object facilitates the iterative process because the object is well represented at the input level and provides energy toward the completion of the process. However, confirmation of the location of an object that does not change, or of an object defined by second-order features, must be driven to a greater extent by endogenous processes, and additional iterations may be required to complete the process. One might hypothesize that the endogenous processes in the Target Repeat condition were the same as they were for the Target Onset condition, but the iterative process necessary to establish the percept could not benefit from the onset of the exogenous data input, leading to a later engagement of the endogenous attentional process.

6. Human subject ethics statement

All participants were volunteers and all experimental procedures and protocols were approved by the Human Ethics Board of McMaster University. Experiments were undertaken with the understanding and written consent of each volunteer.

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