Unseen stimuli modulate conscious visual experience: evidence from inter-hemispheric summation

Beatrice de Gelder,[1,2,CA] Gilles Pourtois,[1,2] Monique van Raamsdonk,[1] Jean Vroomen[1] and Lawrence Weiskrantz[3]

[1]Cognitive Neuroscience Laboratory, Tilburg University, PO Box 90153, 5000 LE Tilburg, The Netherlands; [2]Neurophysiology Laboratory, Faculty of Medicine, Louvain University, Brussels, Belgium; [3]Department of Experimental Psychology, Oxford University, Oxford, UK

[CA]Corresponding Author

Received 9 October 2000; accepted 23 November 2000

Emotional facial expression can be discriminated despite extensive lesions of striate cortex. Here we report differential performance with recognition of facial stimuli in the intact visual field depending on simultaneous presentation of congruent or incongruent stimuli in the blind field. Three experiments were based on inter-hemispheric summation. Redundant stimulation in the blind field led to shorter latencies for stimulus detection in the intact field. Recognition of the expression of a half-face expression in the intact field was faster when the other half of the face presented to the blind field had a congruent expression. Finally, responses to the expression of whole faces to the intact field were delayed for incongruent facial expressions presented in the blind field. These results indicate that the neuro-anatomical pathways (extra-striate cortical and sub-cortical) sustaining inter-hemispheric summation can operate in the absence of striate cortex. *NeuroReport* 12:385–391 © 2001 Lippincott Williams & Wilkins.

Key words: Blindsight; Emotion; ERP; Inter-hemispheric summation; Redundant target effect; Vision; V1

INTRODUCTION

Damage to striate cortex produces blindness in the corresponding visual field. Earlier reports of animal studies indicated that residual visual abilities with striate cortex lesions (blindsight) did not include preserved discrimination of stimulus valence [1,2]. We recently reported the existence of this phenomenon in a human subject, which we called affective blindsight [3]. Affective blindsight refers to the ability of patients with damage to striate cortex to discriminate the valence of facial expressions presented to the blind field. There has, however, been some question whether evidence of blindsight based directly on measures of the patient's forced-choice guesses can unambiguously establish the phenomenon [4]. A major methodological drawback of some direct approaches is that they leave open the possibility of deliberate response strategy. More interestingly, direct methods may actually be less sensitive than indirect methods. For example, our previous study based on direct methods indicated that there was affective blindsight when dynamic stimuli (short video clips) were presented but not when still faces were used. In the present experiments using indirect methods, the existence of affective blindsight is suggested when static faces are used.

Inter-hemispheric summation represents a useful measure to test for blindsight in an indirect fashion [5,6]. With indirect procedures involving bilateral stimuli, conclusions about visual stimuli in the blind field are entirely based on the patient's performance to stimulation in the intact field. In the present study, we took advantage of this paradigm and used several indirect measures, none of which required the patient to make counterintuitive guesses about unseen events that might be subject to response biases. Three indirect testing paradigms were developed for testing for affective blindsight. The first experiment was conducted in order to obtain evidence of normal inter-hemispheric interaction in a stimulus detection task, by investigating the existence and the time course of inter-hemispheric summation in GY, using both behavioral and electro-physiological data. Positive evidence of inter-hemispheric transfer would set the stage for the second experiment in which chimeric faces were presented simultaneously to the intact and the blind field. Finally, in the third experiment summation across the vertical meridian was investigated for full faces presented concurrently to the two visual fields .

SUBJECT AND METHODS

Case report: We tested the well known blindsight patient GY (male, born in 1956) who sustained damage to the posterior part of his brain by head injury (a road accident) when he was 7 years old. The lesion (see [7] for an extensive structural and functional description of the lesion) invades the left striate cortex (i.e. medial aspect of the left occipital lobe, slightly anterior to the spared occipital pole, extending dorsally to the cuneus and ventrally to the lingual, but not the fusiform gyrus) and surrounding extra-striate cortex (inferior parietal lobule and supramarginal gyrus of the right parietal lobe). The location of the lesion is functionally confirmed by perimetry field tests (see [8] for a recent representation of GY's perimetric field and see [9] for a comparison).

General procedure Testing took place in three consecutive sessions with three months interval between them. Eye movements were reliably monitored either by closed circuit TV or by means of electrodes attached to the orbits of the eyes and calibrated to record deviations from fixation. In order to deal with the small area (2.5°) of macular sparing in the center of the retina, the relevant section on the screen was masked from view. No trial was rejected from the analysis because of eye movement. Stimuli, presentation parameters and results are described separately for each experiment.

EXPERIMENT 1: INTER-HEMISHERIC SUMMATION

Studies of stimulus summation across the vertical meridian have provided behavioral evidence for processing of unattended visual stimuli (the redundant target effect) [10]. Indeed, a response gain in latencies is obtained when normal viewers are required to detect the presence of a stimulus in one visual field when a second stimulus is also presented simultaneously in the other field [5–6]. Electrophysiological recordings (event-related brain potentials, ERPs) reveal that with bilateral stimulation two visual components corresponding to the earliest activity in extra-striate cortex (P1 and N1) are about 10 ms faster in the hemisphere involved in the detection task (10). This electrophysiological gain is thus the equivalent at the neuronal level of the redundant target effect.

Combining behavioral measures and electrophysiological recordings we tested GY and assessed whether specific electrophysiological changes (e.g. earlier time-course of visual ERPs) could indeed be associated with bilateral stimulation.

Materials and Methods: Rectangular black and white checkerboards (2.6 × 4.1 cm, sustaining a visual angle of 2.48° horizontally and 3.9° vertically) were presented unilaterally or bilaterally either in the upper or lower visual field for 200 ms (Fig. 1). Stimuli were presented 6 cm to the left (5.71°) or to the right of the fixation point and 4 cm (3.81°) above or below the horizontal meridian (e.g. bilateral stimuli were always symmetrical). ISI was randomly varied between 750 and 1000 ms. Mean stimulus luminance was 25 cd/m^2 and mean luminance of the white background was 40 cd/m^2. GY was seated in front of a video screen with the head restrained by a chin rest, eyes at 60 cm from the screen. Four blocks of 160 randomized trials (40 repetitions of each type of stimulus) were presented.

While fixating a central cross, GY was instructed to respond by pressing a button when he saw a stimulus. Reaction times were recorded from stimulus onset.

Horizontal and vertical EOG were monitored using four facial bipolar electrodes, one pair placed on the outer canthi of the eyes and the other placed on the inferior and superior edges of the orbit. Scalp EEG was recorded from 58 electrodes mounted in an electrode cap (10-20 System) with the left ear as reference, and amplified with a gain of 30K and bandpass filtered at 0.01–100 Hz. Impedance was kept below 5 kΩ. EEG and EOG were continuously acquired at a rate of 500 Hz. Epochs lasted from 100 ms prior to stimulus onset continuing for 924 ms after stimulus

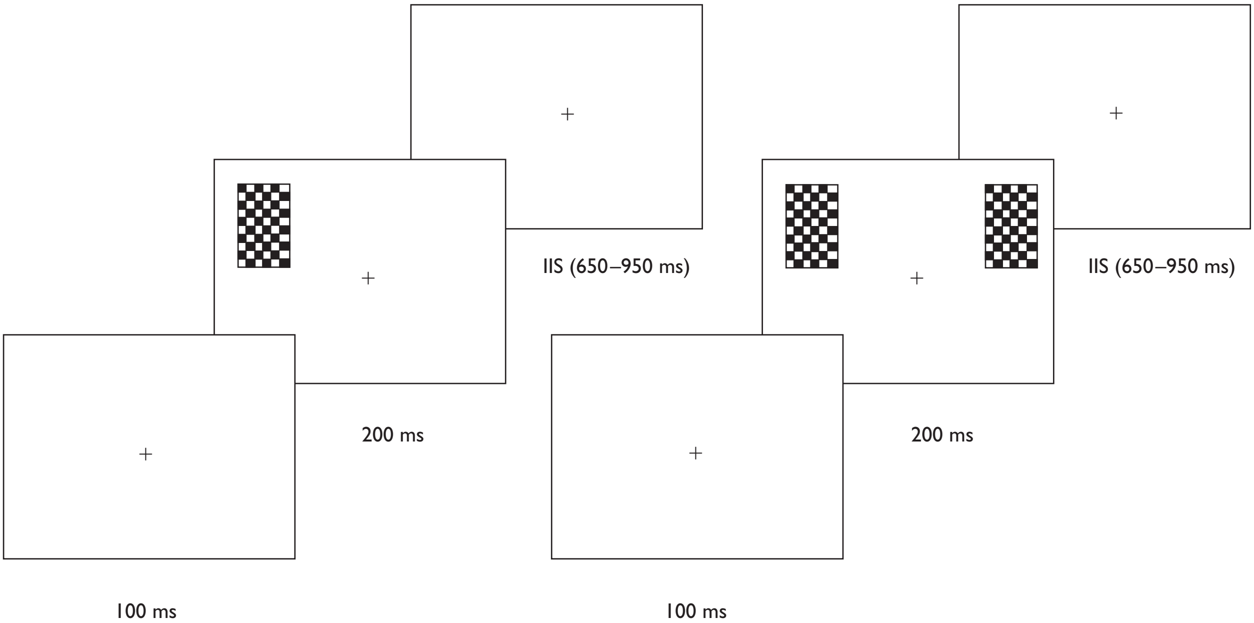


Fig. 1. Procedure and stimuli used in experiment 1 with unilateral trial (left) and bilateral trial (right).

presentation and recorded epochs were re-referenced off-line to a common average reference. Signals were low-pass filtered at 30 Hz. Maximum amplitudes and mean latencies of event-related potentials were measured relative to a 100 ms pre-stimulus baseline and assessed with repeated measures Analyses of Variance (ANOVAs). Visual stimuli in the left/normal visual hemifield give rise to a dipolar complex consisting of a left occipital positive component associated with a negative counterpart at right centro-lateral electrodes [11]. Statistical analyses were therefore computed on several posterior electrodes located in the left (lesioned) hemisphere (O1, P3P, CB1, T5, T3L, TCP1, P5 and P1P) and the midline occipital electrode (OZ) considered as a group in order to increase the signal to noise ratio. Analyses were focused on two early visual components known to be generated in extra-striate cortex [12,13], namely the P1 and N1 components. Measurements of peak amplitude were not analyzed because of volume conduction effects related to bilateral stimulation [10].

Behavioral results: Response time to bilateral was faster than to unilateral stimuli and this effect seems to be more marked for lower than upper-field stimuli. ANOVA conducted on mean reaction times for each block with two within-subjects factors: hemifield (lower *vs* upper) and condition (bilateral *vs* unilateral) yields a significant effect of hemifield ($F(1,3) = 237.71$, $p < 0.001$) and of condition ($F(1,3) = 241.59$, $p < 0.001$). The hemifield × condition interaction is also significant ($F(1,3) = 344.01$, $p < 0.001$) indicating that GY was faster with bilateral stimuli (257 ms) than unilateral stimuli (270 ms) only in his lower visual field (in his upper visual field, mean reaction times are 276 ms both for bilateral and unilateral). *Post-hoc* tests revealed a significant effect of condition only in the lower visual field ($F(1,3) = 607.99$, $pMO < 0.001$) as reported for normal subjects [10].

ERP results: Bilateral stimuli elicit an earlier P1 component for lower visual field presentations (Fig. 2). There seems to be no effect of condition on the latency of the N1 component whatever the position in the visual field. These observations were confirmed by several statistical analyses computed only on measurements of peak latency.

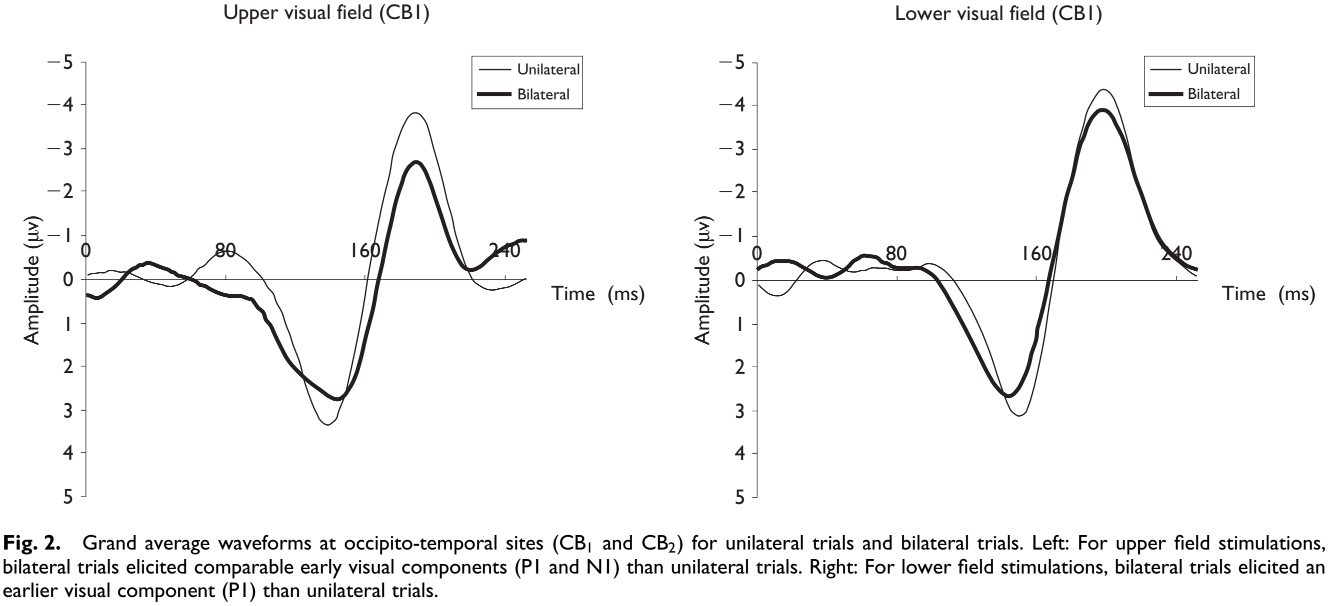
The latency of the P1 component showed a significant effect of hemifield ($F(1,35) = 5.4$, $p = 0.026$) and a significant Hemifield × condition interaction ($F(1,35) = 7.84$, $p = 0.008$), indicating shorter latencies for bilateral (mean latency 139 ms) than unilateral (mean latency 147 ms) stimuli in the lower visual field. *Post-hoc* tests confirmed the significant effect of condition only for lower visual field ($F(1,35) = 9.41$, $p = 0.004$).

The latency of the N1 component showed a significant effect of hemifield ($F(1,35) = 13.05$, $p < 0.001$) indicating shorter latencies for upper than lower (mean latency 184 ms *vs* 193 ms) presentations. There is no significant effect of condition and no significant interaction between these two variables for the N1 component.

GY has a pattern of behavioral and electro-physiological results comparable to that observed with normal subjects [10]. This overall advantage for the lower hemifield in ERP and behavioural responses fits well with evidence of an overall greater sensitivity and representation of the lower hemifield [14,15]. He is faster with bilateral stimuli and this behavioral effect is corroborated by the ERPs results showing an earlier P1 component for lower bilateral stimuli. There is thus a strong correlation between the ability of GY correct performance of the task (in terms of RTs) and the electro-physiological recordings. These results clearly indicate that despite his cortical blindness a spatial summation occurred and stimuli presented in his lower blind hemifield facilitate detection in his intact field. This effect seems to take place as early as 140 ms in the intact extra-striate regions.

EXPERIMENT 2: STIMULUS COMPLETION ACROSS HEMIFIELDS USING CHIMERIC FACES

Studies of commissurotomy patients have illustrated how partial stimulus presentation to the two hemifields sepa-


Upper visual field (CB1)

Lower visual field (CB1)

Fig. 2. Grand average waveforms at occipito-temporal sites (CB$_1$ and CB$_2$) for unilateral trials and bilateral trials. Left: For upper field stimulations, bilateral trials elicited comparable early visual components (P1 and N1) than unilateral trials. Right: For lower field stimulations, bilateral trials elicited an earlier visual component (P1) than unilateral trials.

rately facilitates completion across the vertical meridian [16]. When the information provided to the two hemispheres is inconsistent as, for example, when one facial expression is shown in one hemifield and a different one in the other, a conflict is generated which translates as an inhibition on naming latencies in the good field. This procedure is useful as an indirect measure of affective blindsight because the patient is exclusively questioned about the stimulus in the intact field.

Materials and procedure: Twelve photographs (two female actors and one male actor with either an angry, a sad, a neutral or a fearful expression) [17] were cropped, cut along the vertical midline and then re-assembled in pairs such as to make for a whole face stimulus. In this procedure personal identity was respected, but the resulting facial expression could be either possible (congruent) or impossible (incongruent; Figure 3). In one block the expression in the left field was either anger or fear combined with a congruent (angry or afraid) or incongruent expression. When different expressions were combined, for example angry/afraid, this was designated as incongruent type I; when one expression was combined with a neutral expression (e.g. angry/neutral or fear/neutral) it was designated incongruent type II. In another block similar combinations were made with the target expressions angry and sad. Stimuli were presented centrally on a computer monitor with face halves separated by a white gap of 2 centimeters corresponding to 1.9° of visual angle. The image size was 12.35 cm in width and 17.4 cm in height (sustaining a visual angle of 13.52 × 16.17° 60 cm from the screen). GY was tested in a dimly lit room with the head restrained by a chin rest at 60 cm of the screen fixating a central cross and instructed with the forced choice alternatives. Each trial began with the presentation of a fixation cross for 500 ms, followed by presentation of the picture for 300 ms followed by a white background. The inter-trial interval was 2000 ms. A block consisted of 36 trials (two presentations of 18 combinations with 3 actors × 6 types of trials) and was repeated twice. Reaction times faster than 350 ms and slower than 950 ms were excluded from statistical analyses. GY was instructed to judge the expression (angry/sad or angry/fear) of the chimere presented in his intact visual field. The macular spared part (2.5°) of the blind field was blanked out.

Results: Data were analyzed by ANOVA with the reaction times for correct responses as the dependent variable and two factors as repeated measures, congruency (congruent, incongruent type I, and incongruent type II) and combination (angry-fear *vs* angry-sad). There is a significant main effect of congruency ($F(2,102) = 46.72$, $p < 0.001$), a significant main effect of combination ($F(1,51) = 11.82$, $p < 0.001$) and a significant interaction between these two variables ($F(2,102) = 25.69$, $p < 0.001$), indicating that the effect of congruency (i.e. faster responses in the congruent condition than in the incongruent conditions) is stronger in the angry-fear combination than the angry-sad combination (Fig. 4). *Post-hoc* comparisons between the three types of trials computed separately for the two combinations confirmed this conclusion. In the angry-fear combination, the comparison between congruent and incongruent type I ($F(1,51) = 84.45$, $p < 0.001$; indicating faster reaction times in the congruent condition) and between incongruent type I and incongruent type II ($F(1,51) = 102.25$, $p < 0.001$; indicating faster reaction times in the Incongruent type II condition) are statistically significant. In this latter combination, the quadratic component was statistically significant ($F(1,51) = 112.99$, $p < 0.001$). In the other combination, the comparison between congruent and incongruent type I ($F(1,51) = 67.10$, $p < 0.001$; indicating faster reaction times in the congruent condition) and between congruent and incongruent type II ($F(1,51) = 6.75$, $p = 0.012$; indicating faster reaction times in the congruent condition) are

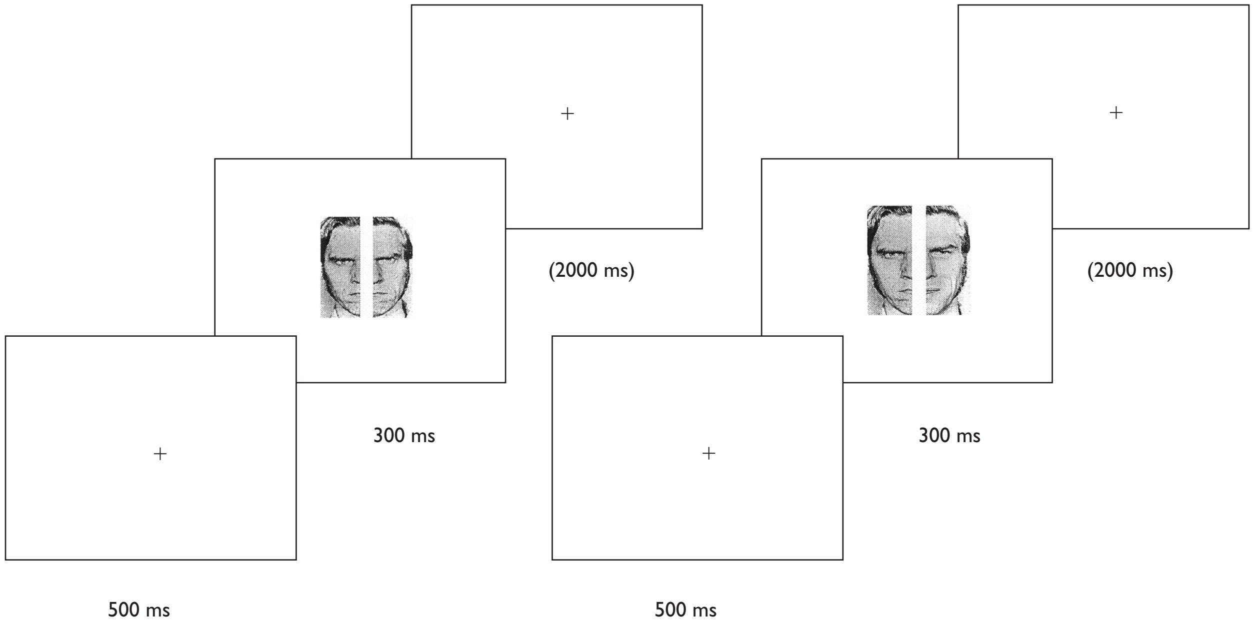


Fig. 3. Procedure and stimuli used in experiment 2 with congruent trial (left) and incongruent (type I) trial (right).

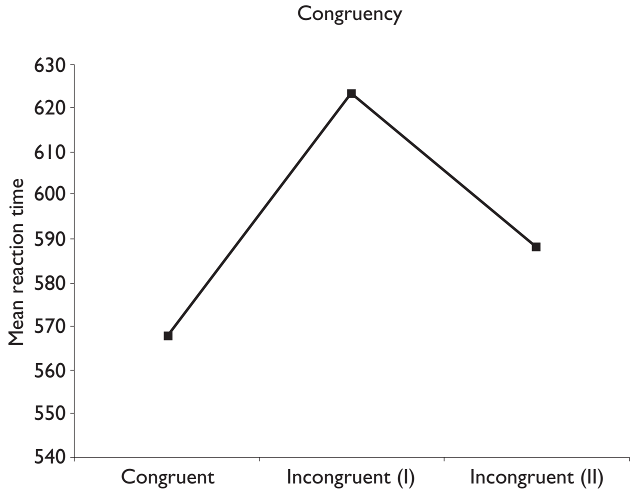


Fig. 4 Mean reaction times for congruent, incongruent (I) and incongruent (II) trials.

statistically significant (Fig. 4). In this latter combination, the linear component was statistically significant (F(1,51) = 6.75, $p = 0.012$).

In order to clarify the significant interaction between congruency and combination and to understand the relationship between the three emotions manipulated, the responses of GY were assessed (ANOVA) separately for each combination of emotions with the reaction times for correct responses as dependent variable and two factors as repeated measures: emotion (angry/fear *vs* angry/sad) and congruency (congruent, incongruent type I, incongruent type II). In the angry-fear combination, the analysis revealed a significant effect of congruency (F(2,44) = 29.17, $p < 0.001$) and a significant emotion × congruency interaction (F(2,44) = 5.33, $p = 0.008$) indicating that the congruency effect was higher for angry trials than for fearful trials. In the angry-sad continuum, the same analysis also revealed a significant emotion × congruency interaction (F(2,48) = 3.22, $p = 0.049$) with angry trials eliciting a significant congruency effect, absent for sad trials.

Errors were normally distributed across the different conditions (14.8% in the congruent condition, 10.1% in the incongruent type I and 17.5% in the incongruent type II) and the different stimulus pairs (18.9% in the angry-fear and 14.8% in the angry-sad) allowing us to rule out any interpretation in terms of speed/accuracy trade-off.

Throughout the whole of the experiment, when questioned GY reported being aware that something happened at the offset of the stimuli, but never reported being able to see any faces as such.

Using the paradigm of inter-hemispheric competition we showed the impact of the half face presented to the blind field on the rating of the half facial expression in the intact field. As predicted, pairs with incongruent expressions led to a response cost slowing down recognition in the intact field. This effect was bigger for combinations with a contrasting than with a neutral expression in the blind field and it was stronger for the combinations showing an angry expression than for those with sad expression in the blind field.

EXPERIMENT 3: INTER-HEMISPHERIC COMPETITION USING FULL FACIAL EXPRESSIONS

Materials and methods: The material consisted of 10 black and white photographs presented against a dark background and showing the faces of five different actors, two female and three male, each expressing either sadness or fear. On each trial, one of the photographs was presented in GY's intact left visual field together in the right field with either the photograph of the same actor with the same expression in the right field (congruent condition) or the other expression (incongruent condition) or no photograph (Fig. 5). The different types of trials appeared once each in random order in each block of 30 trials. Each photograph (6.2° wide × 8.4° high) was presented with its center at 6.2° left or right from the fixation point.

The task was of the go/no-go type, consisting of pressing a response key when the left, seen face was one of the two pre-specified expressions. The target expression was fixed for each block of trials, and was indicated on the screen at the beginning of the block. In total, 16 blocks were run, with the target expression the same of every group of four successive blocks. The first block of each group was considered as practice and discarded from the analysis.

Each trial involved the presentation first of a central fixation cross for an unpredictable 500–1000 ms period, and then of the photograph(s) for 150 ms. Next trial started upon press of the response key or after 2000 ms.

Results: An analysis of variance was computed of reaction times with congruency (congruent, incongruent and alone) and emotion (fearful or sad) as repeated factors. Trials slower or faster than the mean ± 2.5 s.d. were removed from the analysis. There was a significant main effect of congruency (F(2,154) = 4.28, $p < 0.02$), indicating faster reaction times in the congruent condition (Fig. 6) than in the alone condition. Errors were normally distributed across the different conditions (16% in the congruent condition, 10.5% in the Incongruent condition and 14.5% in the condition with face only in the good field) and the different emotions (15.7% with fearful faces and 11% with sad faces).

As in the previous experiments, GY did not report seeing any faces as such.

DISCUSSION

These results extend our previous report of affective blindsight [3] and show interesting parallels with data from healthy volunteers [18] and other categories of brain damaged patients (e.g. prosopagnosic patient). The major difference from our previous study is that the stimuli used here were not dynamic but still photographs. As still images can lead to affective blindsight, we can rule out that non-conscious emotion recognition critically depended on the presence of movement in the facial expressions.

The finding that despite cortical damage unseen and unattended visual stimuli can be detected and discriminated is compatible with previous evidence obtained in normal subjects [19,20] and in hemianopic patients [5,6]. Our results from EEG recordings underscore the role of

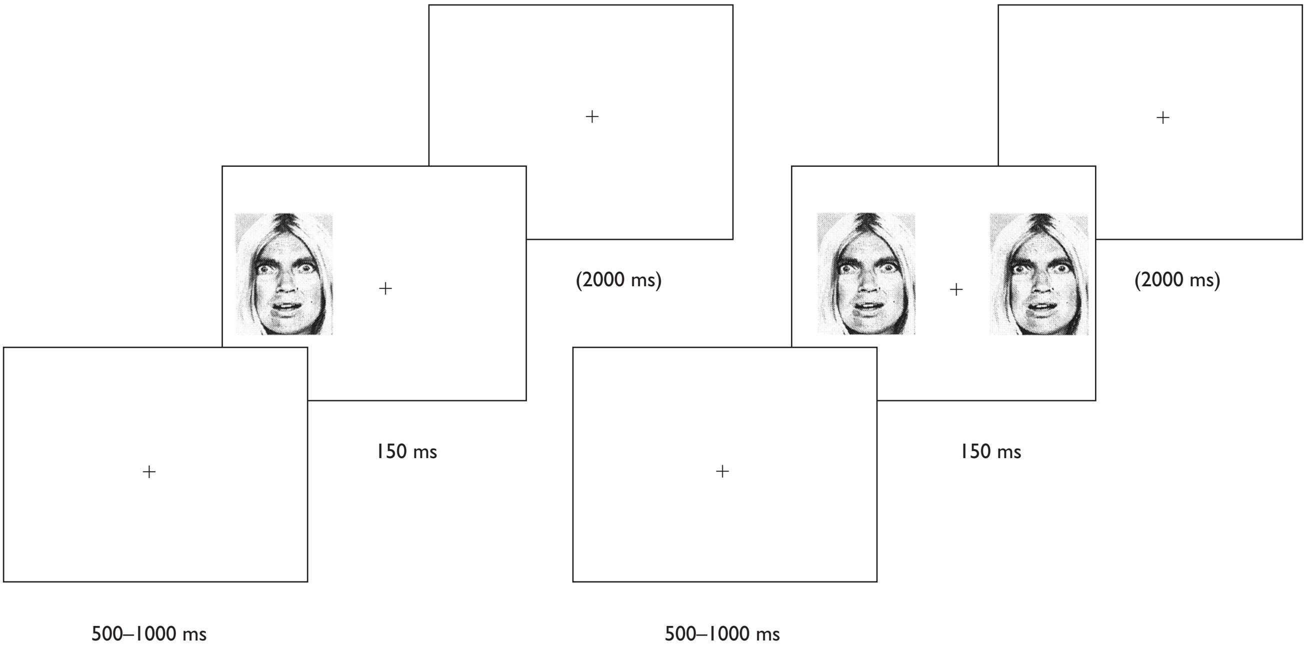


Fig. 5. Procedure and stimuli used in experiment 3 with unilateral trial (left) and bilateral trial (right).

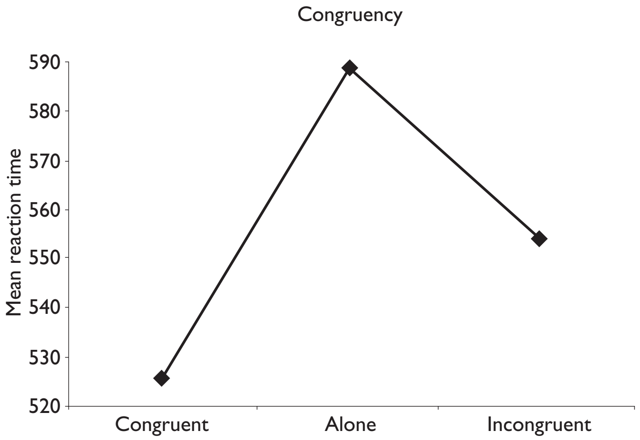


Fig. 6. Mean reaction times for congruent, alone and incongruent trials.

extra-striate processes for inter-hemispheric summation [10].

Residual visual ability for non-conscious recognition of facial expressions indicates the role of sub-cortical processes in processing affective images. This is consistent with neuro-imaging studies that have shown amygdala activation to unseen (backward masked) emotional stimuli in neurologically intact subjects [19] and with non-conscious recognition of facial expressions in patients with visual agnosia due to occipito-temporal lesions [21].

As our procedures did not require the patient to make guesses about unseen events, the results are not likely to have been contaminated by response strategies. We can also rule out that the effects are due to implicit learning of the relationship between the forced-choice response alternatives provided by the experimenter. Interestingly, results of inter-hemispheric competition (experiment 3) are consistent with studies showing detrimental effects of irrelevant stimuli in normal viewers, which is the opposite of the summation advantage observed in this study and in others where viewers are not aware of the redundant stimulus. In normal subjects, however, when in addition to the target stimulus another stimulus is presented of which the subject is aware, performance suffers specifically when target stimulus and distractor stimulus are identical [22]. The usual interpretation of this effect assumes that attentional resources are limited and that the unattended stimulus competes with the target stimulus, leading to an impoverished performance on the latter. Such attentional competition does not appear to exist between the intact and the blind field suggesting that as a consequence there is no attentional competition at the level of attention and that signal summation at the neuronal level takes place unhibited by higher order systems.

A major question in blindsight concerns the pathways that sustain unaware processes. Previous studies reporting blindsight for elementary visual attributes have named collicular and pulvinar routes as the most likely alternatives in case of striate cortex lesions. Independently of this, studies of non-conscious affective processes have reported amygdala activation as well as modulation of fusiform gyrus and amygdala [18] for fearful faces. Our results indicate that despite damage to striate cortex, the extra-striate pathways implicated in inter-hemispheric summation interacts normally with the sub-cortical pathways implicated in non-conscious affect recognition [18,23–25].

REFERENCES

1. Cowey A. *Q J Exp Psychol* **19**, 232–245 (1967).
2. Cowey A and Weiskrantz L. *Q J Exp Psychol* **15**, 91–115 (1963).

3. de Gelder B, Vroomen J, Pourtois G and Weiskrantz L. *Neuroreport* **10**, 3759–3763 (1999).
4. Azzopardi P and Cowey A. *Proc Natl Acad Sci USA* **94**, 14190–14194 (1997).
5. Marzi CA, Tassinari G, Aglioti S and Lutzemberger L. *Neuropsychologia* **24**, 749–58 (1986).
6. Corbetta M, Marzi CA, Tassinari G and Aglioti S. *Brain* **113**, 603–616 (1990).
7. Baseler HA, Morland AB and Wandell BA. *J Neurosci* **19**, 2619–2627 (1999).
8. Barbur, JL, Watson JDG, Frackowiak RSJ and Zeki S. *Brain* **116**, 1293–1302 (1993).
9. Barbur JL, Ruddock KH and Waterfield VA. *Brain* **103**, 905–928 (1980).
10. Miniussi C, Girelli M and Marzi CA. *J Cogn Neurosci* **10**, 216–230 (1998).
11. Rossion B, de Gelder B, Pourtois G *et al. Neurosci Lett* **279**, 1–4 (2000).
12. Clark VP, Fan S and Hillyard SA. *Hum Brain Mapp* **2**, 170–187 (1995).
13. Martinez A, Anllo-Vento L, Sereno MI *et al. Nature Neurosci* **2**, 364–369 (1999).
14. Van Essen DC, Newsome WT and Maunsell JH. *Vis Res* **24**, 429–448 (1984).
15. Skrandies W. The upper and lower visual field of man: Electrophysiological and functional differences. In: Autrum H, Ottoson D, Perl ER *et al.*, eds. *Progress in Sensory Physiology* Berlin: Springer Verlag; 1987, pp. 1–93.
16. Levy J, Trevarthen C and Sperry RW. *Brain* **95**, 61–78 (1972).
17. Ekman P and Friesen WV. *J Environ Psychol Non-verbal Behav* **1**, 56–75 (1976).
18. Morris JS, Ohman A and Dolan RJ. *Proc Natl Acad Sci USA* **96**, 1680–1685 (1999).
19. Whalen PJ, Rauch SL, Etcoff NL *et al. J Neurosci* **18**, 411–418 (1998).
20. Morris JS, Ohman A and Dolan RJ. *Nature* **393**, 467–470 (1998).
21. de Gelder B, Pourtois G, Vroomen J and Bachoud-Le̦vi A-C. Brain Cogn (in press).
22. Desimone R and Duncan J. *Annu Rev Neurosci* **18**, 193–222 (1995).
23. de Gelder B, Vroomen J, Pourtois G and Weiskrantz L. *Trends Cogn Sci* **4**, 126–127 (2000).
24. de Gelder B. Recognizing emotions by ear and by eye. In: Lane R and Nadel L, eds. *Cognitive Neuroscience of Emotions*. Oxford: Oxford University Press; 1999, pp. 84–105.
25. Tomaiuolo F, Ptito M, Marzi CA *et al. Brain* **120**, 795–803 (1997).