

Differential neural responses to overt and covert presentations of facial expressions of fear and disgust

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There is debate in cognitive neuroscience whether conscious versus unconscious processing represents a categorical or a quantitative distinction. The purpose of the study was to explore this matter using functional magnetic resonance imaging (fMRI). We first established objective thresholds of the critical temporal parameters for overt and covert presentations of fear and disgust. Next we applied these stimulus parameters in an fMRI experiment to determine whether non-consciously perceived (covert) facial expressions of fear and disgust show the same double dissociation (amygdala response to fear, insula to disgust) observed with consciously perceived (overt) stimuli. A backward masking paradigm was used. In the psychophysics experiment, the following parameters were established: 30-ms target duration for the covert condition, and 170-ms target duration for the overt condition. Results of the block-design fMRI study indicated substantial differences underlying the perception of fearful and disgusted facial expressions, with significant effects of both emotion and target duration. Findings for the overt condition (170 ms) confirm previous evidence of amygdala activation to fearful faces, and insula activation to disgusted faces, and a double dissociation between these two emotions. In the covert condition (30 ms), the amygdala was not activated to fear, nor was the insula activated to disgust. Overall, findings demonstrate significant differences between the neural responses to fear and to disgust, and between the covert presentations of these two emotions. These results therefore suggest distinct neural correlates of conscious and unconscious emotion perception.

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Introduction

The distinction between information processing in the brain that is accompanied or not by conscious experience is problematic for cognitive neuroscience. Opinions vary from the view that the distinction is spurious (Dennett, 1991; Dennett and Kinsbourne, 1992) to one that holds it to be profound (Gray, 2004; Penrose, 1989). Complex information processing can occur with no access to (reportable) conscious awareness (Velmans, 1991). Conversely, visual illusions may be reported in conscious experience while having no influence on accompanying visually guided (unreportable) behavior (Milner and Goodale, 1993). Such evidence supports a categorical distinction between information processing that does and does not reach conscious awareness. This distinction sometimes marks a permanent boundary between the two types of processing. For example, it is impossible to consciously experience the processes by which language achieves phonetic realization (Velmans, 1991); conversely, imagining music ‘in one’s head’ cannot be unconscious. In other cases, however, the same processing may occur either consciously or unconsciously, the difference depending, for example, upon the duration of exposure of the relevant stimuli. Here, we examined one such case: the discrimination of human facial emotional expression.

The judgement of facial expression as, for example, ‘fear’ or ‘disgust’ is normally made by verbal report. If such expressions are presented for short periods (c. 30 ms) in a backward masking procedure (Esteves and Öhman, 1993), verbal description of the stimulus is impossible. However, electrodermal (Öhman, 1992; Williams et al., 2004) and electromyographic (Dimberg et al., 2000) indices show that these faces are processed as emotional stimuli, and even as expressing a specific emotion. Using functional magnetic resonance imaging (fMRI) and exposure durations clearly above the threshold for conscious perception, we have previously demonstrated a double dissociation between activation

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patterns in normal human subjects to fear and disgust expressions. The former activated the amygdala (confirming other reports: Breiter et al., 1996; Morris et al., 1996) but not the insula, while the latter activated the insula but not the amygdala (Phillips et al., 1997, 1998), confirmed by others (Anderson et al., 2003; Sprengelmeyer et al., 1998). Here, we used fMRI to ask whether there would be similar or different activation patterns to these facial expressions presented *below* as well as *above* the level of fully conscious awareness.

In a related electroencephalographic (EEG) study (Williams et al., 2004) of event-related potentials (ERPs), we used a backward masking procedure, a mask displaying a neutral expression presented for 100 ms immediately after a target displaying the emotional expression (Esteves and Öhman, 1993), to establish two different objective thresholds of conscious versus non-conscious processing. In a *discrimination* threshold-setting task, we determined the point at which subjects could not discriminate fear from neutral expressions with above-chance accuracy; while, in a *detection* threshold-setting task, we determined the point at which subjects could not detect whether a face of any kind was presented or just a blank screen. In both cases, the objective criterion (Macmillan, 1986) for lack of conscious perception was set at the stimulus onset asynchrony (SOA) from target to mask at which performance accuracy does not differ significantly from chance performance, that is, 50%. The two thresholds were found to differ: the discrimination threshold occurred at an SOA of 30 ms, the detection threshold at 10 ms. Consistent accuracy was achieved for both face detection and discrimination of fear versus neutral expressions at an SOA of 170 ms. At all three SOAs, the emotional impact of the fear stimulus was verified by a faster rise time of the skin conductance response (SCR) than occurred to neutral expressions. The ERP data also demonstrated differential responding to the fear versus neutral expressions at all three SOAs, but taking in each case different forms. Non-conscious fear perception (both detection and discrimination, that is, at both the 10- and 30-ms SOAs) elicited greater responses for the negative-going N2 component, elicited around 200 ms post-stimulus. However, non-consciously detected (10-ms SOA) fear also evoked a relatively faster P1 response within 100 ms of stimulus onset. By contrast, conscious fear perception (SOA= 170 ms) was distinguished by a more prominent N4, peaking around 400 ms. The complex picture revealed by these results suggests that there may be no single correct answer to the question: how does brain activity differ in relation to the distinction between conscious and non-conscious processing?

In the present study, we employed the same psychophysical procedure as Williams et al. (2004) to establish objective thresholds for the discrimination of both fear and disgust, separately, from neutral expressions. We then used the same stimulus parameters in an fMRI experiment to determine whether non-consciously discriminated fear and disgust show the same double dissociation (amygdala activation to fear, insula activation to disgust, in both cases versus neutral) observed before (Phillips et al., 1997, 1998) for consciously discriminated fear and disgust.

Materials and methods

In a first psychophysical experiment in this study, we determined once again the threshold for the discrimination of fear from neutral expressions, and also that for disgust from neutral expres-

sions, investigating both the interval between onset of target and mask (SOA) and that between the termination of the target and mask (stimulus termination asynchrony, STA). Findings from humans and primates indicate that a critical value of 100 ms for the STA is necessary to render the target stimulus invisible to the observer (Macknik and Livingstone, 1998). In two experiments employing a backward masking paradigm, we showed right-handed healthy volunteers target–mask pairs, in which either fearful or neutral facial expressions, or disgust or neutral expressions, were masked with neutral expressions, and target or mask durations were varied. We determined the point at which participants did not perform significantly differently from chance in discriminating fear from neutral, or disgust from neutral, in the target expressions. A crucial feature of our design was that the objective identification thresholds determined were directly related to the structure of the subsequent fMRI study, in which target expressions alternated between emotional and neutral. These thresholds (fear versus neutral and disgust versus neutral, separately established) would be expected to constitute a more conservative criterion for unconscious discrimination of the target expression than a simple fear versus disgust threshold. We also ensured that the numbers of target–mask trials presented in each condition of the psychophysical and fMRI studies were similar (384 and 300, respectively), to avoid thresholds being rendered inaccurate through differential levels of practice across the different studies.

Psychophysical experiments: subjects and design

Two independent samples of 10 right-handed healthy volunteers (5 males in each sample) participated in two experiments determining critical values of SOA (mean age, 29.5 years, SD = 4.7) and STA (mean age, 28.4 years, SD = 6.2). Informed consent was obtained. Stimuli were photographs of eight different individuals depicting fear, disgust and mildly happy expressions (Ekman and Friesen, 1976), the latter employed as neutral baseline expressions for some targets and all masks. These mildly happy facial expressions are derived from morphing prototypical neutral and happy expressions to depict an expression 25% along the dimension from 100% neutral to 100% happy (Calder et al., 1997). They are labelled ‘neutral’ by normal subjects (Young et al., 1997) and have been employed in previous functional neuroimaging studies as a neutral expression, because of the tendency of the prototypical (100%) neutral expression to appear threatening (Phillips et al., 1997, 1998).

Two backward masking conditions were counterbalanced across subjects in each experiment (condition 1 = fear or neutral target, neutral mask; condition 2 = disgust or neutral target, neutral mask). Each condition comprised six blocks of 64 target/mask pairs, randomized within subjects. ‘Emotional’ and ‘neutral’ targets appeared with equal frequency. In one experiment, SOA was manipulated between the six blocks (20, 30, 50, 90, 170, or 330 ms) with an inter-stimulus interval between target and mask of 0 ms. Mask stimuli were presented for 100 ms and were spatially offset by 1° visual angle in the direction of the four diagonals of the target stimulus to avoid artefactual detection of facial expressions from apparent motion. As a result of this procedure, subjects could not employ motion detection strategies to discriminate short-duration emotional from neutral targets. The interval between successive target–mask pairs was 1 s. In the second experiment, the mask as well as the target duration was

varied; each six-block presentation of 64 target–mask trials for each condition (fear or disgust) was presented three times, once at each mask duration of 50, 100, or 150 ms. Following each target/mask trial, subjects made a forced-choice decision (objective identification threshold measurement) about the target face expression (fear versus neutral or disgust versus neutral) via button-press, and a corresponding confidence rating (1–9 scale; 1 = ‘not at all confident’ to 9 = ‘extremely confident’; subjective identification threshold measurement). The latter served as a strict criterion for confirming the target face duration necessary for fully conscious (overt) perception.

fMRI experiment: subjects and design

Eight right-handed male subjects (mean age, 31.9 years, range 25–36; mean no. years education, 22.1 years, range 15–25) participated in four 5-min experimental conditions comprising ten 30-s alternating blocks of target–mask stimuli: emotional (covert or overt fear or disgust) and neutral (covert

or overt neutral) targets, each followed by a neutral mask. Informed consent was obtained. The subjects were different from those in the behavioral experiment to avoid practice effects that might alter the discrimination thresholds from the values measured psychophysically. The facial expressions employed were the same as those in the psychophysical experiments, including the presentation rate, and the spatial offset (1° visual angle) of the mask. The target-plus-mask stimuli were presented at a rate of one pair per second. Stimuli subtended visual angles of 10° vertically and 8° horizontally. The position of consecutive target–mask stimuli varied over four positions on screen, and eight different facial identities were employed, each paired with two others to construct the target–mask stimuli. Four conditions were studied (Fig. 1), with stimuli varying in the target but always followed by a 100-ms neutral mask. (1) *Covert fear*: 30 ms 100% fearful facial expression, alternating with 30 ms neutral target. (2) *Overt fear*: 170 ms fear alternating with 170 ms neutral target. (3) *Covert disgust*: 30 ms 100% disgust alternating with 30 ms neutral target. (4)

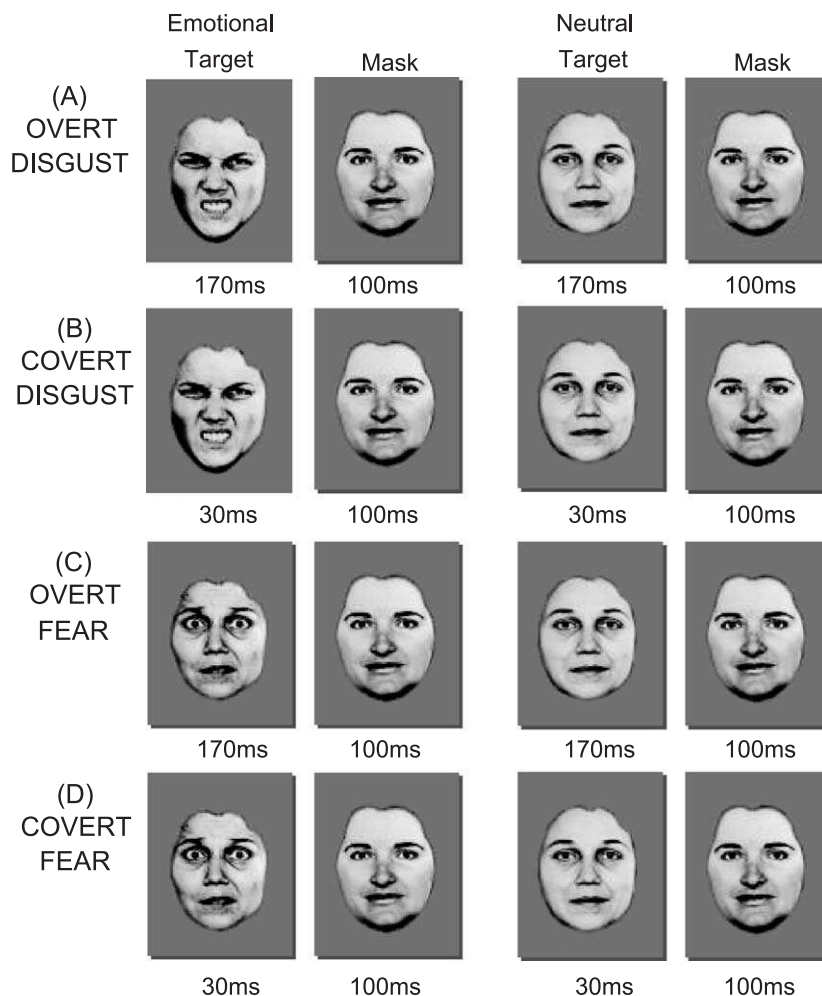


Fig. 1. Design of fMRI experiments. Subjects participated in four 5-min experimental conditions, each comprising ten 30-s alternating blocks of emotional (covert or overt fear or disgust) versus neutral (covert or overt neutral) targets, each paired with a neutral mask: (A) *overt disgust* (target, 170 ms 100% disgusted facial expressions; mask, 100 ms neutral face; alternating with 170 ms neutral target and 100 ms neutral mask pairs); (B) *covert disgust* (as for A, but 30 ms target); (C) *overt fear* (as for A, but fearful faces in place of disgusted faces for 170 ms); (D) *covert fear* (as for C, but 30 ms target). The stimulus pairs were presented at a rate of one pair per second. Eight different facial identities were employed, each paired with two others in the target–mask pairs. The orders of the four conditions, the identity pairs in each block, and the blocks (emotional or neutral first) were counterbalanced across subjects.

Overt disgust: 170 ms disgust alternating with 170 ms neutral target. To prevent determination of the nature of the study, subjects did not judge the target emotion or make any other response. The orders of the four conditions, the identity pairs in each phase, and the phases (emotional or neutral first) were counterbalanced across subjects. One subject was unable to complete a fourth condition (overt disgust). On debriefing after scanning, subjects reported awareness of the presence of fear or disgust expressions only in overt presentation conditions. After scanning, all subjects identified unmasked examples of the emotional facial expressions in the study, choosing one out of a total of seven different expressions (neutral, fear, disgust, happiness, sadness, anger, surprise). Mean accuracy scores for facial expressions of fear and disgust were 93% (range: 75–100%) and 86% (range: 75–100%), respectively.

Image acquisition and analysis

Gradient echo echoplanar imaging (EPI) data were acquired on a GE Signa 1.5 T system (General Electric, Milwaukee WI) retrofitted with Advanced NMR hardware (ANMR, Woburn, MA) at the Maudsley Hospital, London. A quadrature birdcage headcoil was used for RF transmission and reception. One hundred T_2^* -weighted images depicting BOLD contrast (Kwong et al., 1992) were acquired over 5 min (for each task) at each of 14 near-axial non-contiguous 7-mm-thick planes parallel to the intercommissural (AC–PC) line: TE 40 ms, TR 3 s, in-plane resolution 7 mm, interslice gap 0.7 mm (Simmons et al., 1999). In the same scanning session, an inversion recovery EPI data set was acquired at 43 near-axial 3-mm-thick planes parallel to the AC–PC line: TE 80 ms, TI 180 ms, TR 16 s, in-plane resolution 1.5 mm, interslice gap 0.3 mm, no. signal averages = 8. This higher resolution EPI data set was later used to register the fMRI data sets acquired from each individual in standard stereotactic space (Brammer et al., 1997; Talairach and Tournoux, 1988).

The following analytical methods were chosen specifically to reflect (and to some extent accommodate) knowledge of the nature of changes in the BOLD signal seen in areas such as the amygdala and insula in response to emotional stimuli. These changes reflect both neural factors (rate of onset and delay in response following the presentation of stimuli) and hemodynamic factors. Both of these will also vary between individuals. In analysing block responses, techniques in which signal changes at each voxel are fitted to a model based on the convolution of the experimental design with a hemodynamic response function will lead to severe loss of power if the actual response differs markedly (as is likely) from the delayed and smoothed box-car function produced by the convolution. We therefore used instead a truncated Fourier model (Bullmore et al., 1996) in which the response is modelled by a Fourier series comprising the frequency of alternation of the two experimental conditions plus its first two harmonics. This allows the power and phase of the response at these frequencies to be estimated. The phase components allow shifts of timing to be accommodated by the analysis, and the different frequency terms permit the fitted curve shape to adapt to some extent to the characteristics of the response at each voxel. A number of previous studies (Phillips et al., 1997, 1998, 2001), focussing on amygdala and insula function, have shown that this method is effective in detecting responses in these regions, despite their deviating (neurally and

hemodynamically) from the simple box-car input function. We note also that serial autocorrelation (or more generally, colored noise) in fMRI data can lead to elevated type I error rates if not treated properly during the process of statistical inference. We have developed a series of methods for dealing with this problem, which we have described and validated in detail (see Bullmore et al., 1996, 2001).

Following motion correction (Bullmore et al., 1999a), periodic change in T_2^* -weighted signal intensity at the (fundamental) experimentally determined frequency of alternation between emotional and neutral stimulus blocks (=1/60 Hz) in each of the four experimental conditions was estimated by an iterated least squares fit of a sinusoidal regression model to the fMRI time series observed at each voxel (Bullmore et al., 1996). This model included sine and cosine waves at the fundamental frequency of the experimental input function (emotional versus neutral blocks), parameterised by coefficients $\{\gamma, \delta\}$. The power of periodic response to the input function was estimated by $\{\gamma^2 + \delta^2\}$; and this fundamental power divided by its standard error yielded a standardised test statistic, the fundamental power quotient (FPQ), at each voxel. Parametric maps representing FPQ observed at each intracerebral voxel were constructed. To sample the distribution of FPQ under the null hypothesis that observed values of FPQ were not determined by experimental design (with few assumptions), the 99 images observed in each anatomical plane were randomly permuted and FPQ was estimated exactly as above in each permuted time series. This process was repeated 10 times, resulting in 10 permuted parametric maps of FPQ at each plane for each subject.

Observed and randomised FPQ maps were transformed into standard space and smoothed by a 2D Gaussian filter with full-width half maximum (FWHM) = 11 mm. This filter size was chosen to accommodate regional differences in brain anatomy between subjects (Clark et al., 1996). The median observed FPQ at each intracerebral voxel in standard space was tested against a critical value of the permutation distribution for median FPQ ascertained from the permuted FPQ maps (Brammer et al., 1997). This yielded a generic brain activation map for each experimental condition, with a voxel-level threshold for activation of $P \leq 0.005$. This is a non-parametric and robust random-effects analysis using the median rather than the mean as a measure of central location to mitigate the potential impact of outlying observations in small samples (Brammer et al., 1997).

Comparison of the four experimental conditions

To estimate between-condition differences in mean power of functional activation, we fitted a saturated, two-way analysis of variance (ANOVA) model at each intracerebral voxel of the standardised power maps after their co-registration in standard space. In this analysis, we wished to determine the main effects of two factors—*Emotion* (fear versus disgust) and *Target Duration* (covert versus overt)—on the mean power of functional activation, and also the interaction between these factors. In this repeated-measures ANOVA, both emotion and target duration were treated as within-subject factors. The form of the model was:

$$\text{FPQ} = \mu + \beta_1 \text{Emotion} + \beta_2 \text{Duration} \\ + \beta_3 \text{Interaction} + \varepsilon$$

where FPQ is the standardised power of functional activation; μ is the overall mean power of response at a given voxel; Emotion, Duration and Interaction are the factors of the model; and ε denotes an error term.

To improve sensitivity of this analysis and to mitigate the multiple comparisons problem, we tested the null hypothesis that the coefficient for each factorial effect of interest was zero, for example, $\beta_1 = 0$, at cluster level rather than voxel level. To do this, maps of each coefficient were thresholded at $P < 0.05$ to generate a set of suprathreshold voxel clusters spatially contiguous in 3D. The sum of suprathreshold voxel statistics, or mass, of each 3D cluster was then tested against its permutation distribution, as previously described and validated (Bullmore et al., 1999b). For each such comparison, the P value for cluster testing was chosen such that the expected number of false-positive tests was less than one over the whole map, that is, $P < 0.02$.

To test a set of more specific null hypotheses of prior interest, namely that there would be zero difference in the power of functional activation between overt and covert fear, overt fear and overt disgust, covert fear and covert disgust, and overt and covert disgust, we then fitted one-way ANOVA models at each intracerebral voxel of the standardised power maps of the four conditions.

Results

Psychophysical data

In the first experiment (mask duration 100 ms), target expression recognition accuracy was not significantly above chance at the 30-ms SOA, and reached consistent, significantly above-chance accuracy at 170 ms (upper confidence level limit for chance responding = 67.6% correct) for both conditions, fear and disgust each versus neutral. The mean correct detection of the fear expression at 30-ms target and 100-ms mask durations (the parameters chosen for the subsequent fMRI experiment) was 59.9%, SD = 8.9, well below the 67.6% upper confidence limit for chance detection. The corresponding values for disgust were 54.95%, SD 9.38. Confidence ratings required an SOA of 170 ms or greater to be significantly above 5, the rating for the point halfway between total guess and certainty. In the second experiment (varying mask duration), the data for SOA confirmed those for the first experiment. At 50-ms mask durations, there was greater accuracy in identifying shorter duration target expressions. This suggested that the shorter STA provided insufficient masking, but that 100 ms would be an effective STA for the subsequent fMRI study (Fig. 2).

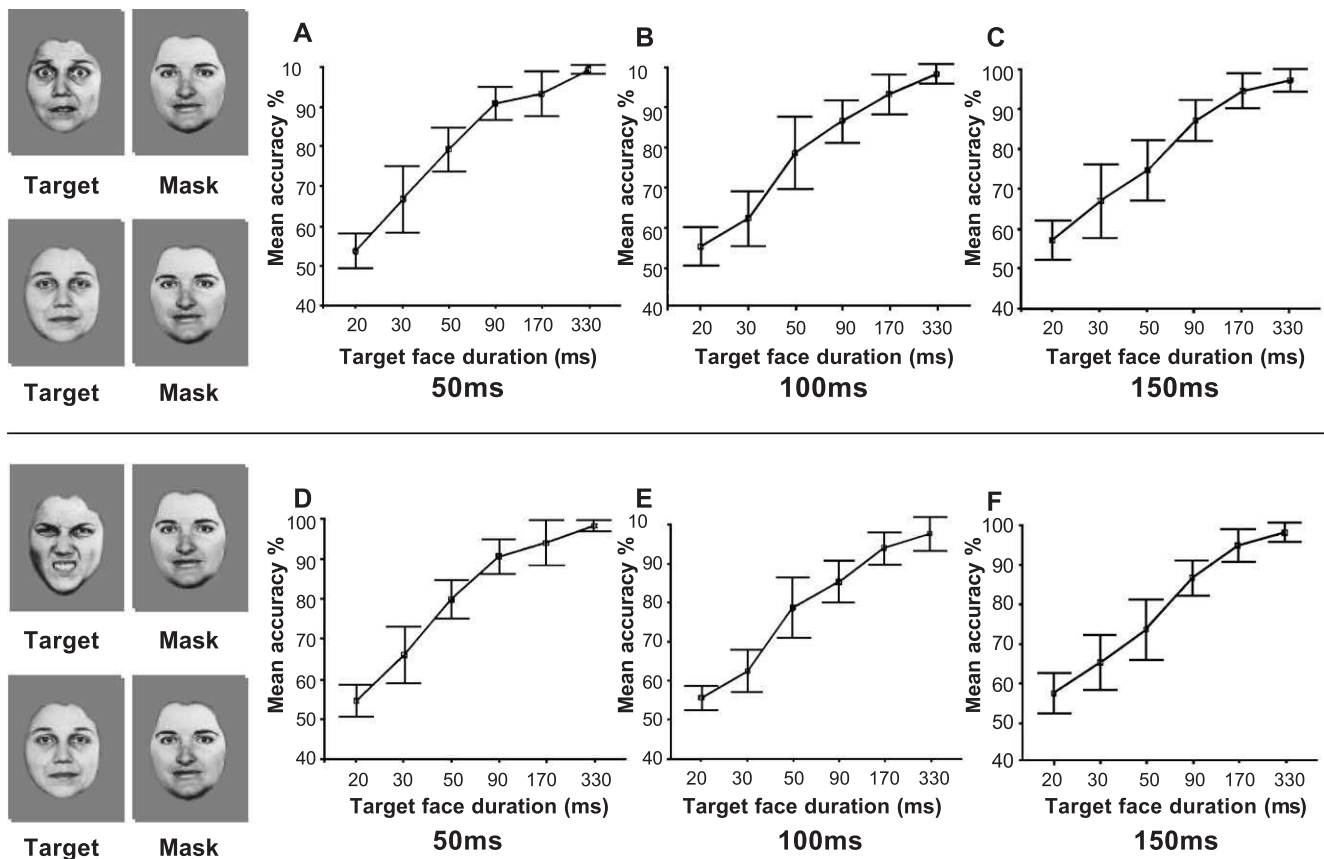


Fig. 2. Psychophysical results. Standardized facial stimuli (Ekman and Friesen, 1976) were employed, with 25% happy expressions as neutral expressions. Target–mask pairs are shown on the left: fear/neutral target and neutral mask (above, A–C); disgust/neutral target and neutral mask (below, D–F). (A) Mean percent accuracy (\pm SEM; above-chance accuracy $>67.6\%$) for discrimination of fear from neutral target expressions as a function of duration of target exposure (abscissa) with a 50-ms neutral mask; (B) as A but with a 100-ms mask; (C) as A but with a 150-ms mask; (D) as A but for discrimination of disgust from neutral target expressions; (E) as D but with a 100-ms mask; (F) as D but with a 150-ms mask. Accuracy was similar with 100-ms and 150-ms masks.

fMRI data

Generic brain activation maps

Covert and overt presentations of fear. Voxels with significant mean power of response ($P < 0.005$) to covert (30-ms target) and overt (170-ms target) presentations of fear are shown in Tables 1 and 2, respectively, and in Fig. 3. Significantly activated voxels were demonstrated in the right amygdala in response to overt but not covert presentations of fear. Overt presentations of fear also activated bilateral posterior cingulate gyri and the left putamen, while covert presentations of fear activated the left caudate nucleus. In response to both types of expression of fear, significantly activated voxels were demonstrated in regions involved in visual processing: the left precuneus, bilateral superior and the right middle temporal gyri in response to covert, and bilateral superior and the right middle temporal and lingual gyri and precuneus in response to overt presentations of fear. Other structures activated in response to both types of presented expression included the left inferior frontal and right anterior cingulate gyri, bilateral inferior parietal lobules, and the right cerebellum.

Covert and overt presentations of disgust. Voxels with significant mean power of response ($P < 0.005$) to covert and overt presentations of disgust are shown in Tables 3 and 4, respectively, and in Fig. 3. Significantly activated voxels were demonstrated in bilateral insulae in response to overt but not covert presentations of disgust. Covert presentations of disgust activated the right thalamus and putamen. Significantly activated voxels were demonstrated in response to both types of expression of disgust in visual processing regions: the right fusiform gyrus, precuneus and middle temporal gyrus in response to covert, and the right precuneus, left middle occipital, bilateral lingual, right superior

Table 1
Generically activated brain regions to covert expressions of fear

Region	Side	x^a	y^a	z^a	No. of voxels
(Approximate Brodmann Area)					
Cerebellum	R	28	-63	-18	21 ^{b,c}
	L	-11	-76	-13	15 ^b
Precuneus (7)	L	-32	-50	48	16
Inferior frontal gyrus (44)	L	-40	0	31	13 ^{b,c}
Caudate nucleus	L	-21	-30	20	10
Superior temporal gyrus (38/42)	R	43	4	-7	8 ^c
	L	-50	-26	15	9 ^c
Precentral gyrus (6)	R	43	10	9	8
	L	-40	-4	37	9
Anterior cingulate gyrus (32)	R	4	13	42	7
Inferior parietal lobule (40)	L	-40	-50	42	7 ^{b,c}
Middle temporal gyrus (21)	R	47	-33	4	6
Paracentral lobule (5)	R	4	-30	48	5
Supramarginal gyrus (40)	L	-36	-50	37	5

^a The cluster with the largest number of voxels within each region is reported. Talairach co-ordinates refer to the voxel with the maximum FPQ in each cluster. All voxels were identified by a one-tailed test of the null hypothesis that median FPQ is not determined by experimental design. The threshold for activation was $P \leq 0.005$.

^b Significantly greater mean power of response in these regions than to overt expressions of fear.

^c Significantly greater mean power of response in these regions than to covert expressions of disgust.

Table 2
Generically activated brain regions to overt expressions of fear

Region	Side	x^a	y^a	z^a	No. of voxels
(Approximate Brodmann Area)					
Posterior cingulate gyrus (31)	R	4	-63	20	62 ^{b,c}
	L	-4	-69	15	58 ^{b,c}
Putamen	L	-32	-13	-2	29 ^{b,c}
Inferior parietal lobule (40)	R	40	-26	42	22 ^b
Amygdala/Hippocampus	R	28	-13	-7	16 ^{b,c}
Amygdala		28	-10	-13	7
Anterior cingulate gyrus (32)	R	4	46	4	15 ^{b,c}
Lingual gyrus (18)	R	21	-69	-2	14 ^{b,c}
Medial frontal gyrus (9)	R	32	23	26	13 ^{b,c}
Precuneus (7)	R	7	-50	31	11 ^b
Cerebellum	R	28	-46	-18	9 ^c
Inferior frontal gyrus (45)	L	-40	23	15	9 ^c
Superior temporal gyrus (22/38)	R	47	10	-2	8
	L	-32	-4	-7	9
Middle temporal gyrus (38)	R	40	-56	26	7

^a As for Table 1.

^b Significantly greater mean power of response in these regions than to covert expressions of fear.

^c Significantly greater mean power of response in these regions than to overt expressions of disgust.

and left middle temporal gyri in response to overt presentations of disgust. Significantly activated voxels were also demonstrated in response to both types of presented expression of disgust in bilateral posterior cingulate and right anterior cingulate gyri and the left cerebellum.

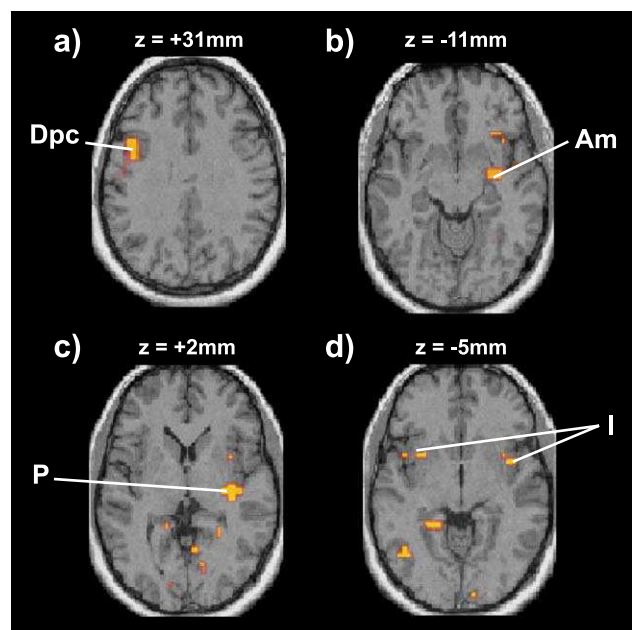


Fig. 3. Generic brain activation maps (GBAMs). Major regions of activation to the covert fear condition (a) are shown in the left dorsolateral prefrontal cortex BA 44 (Dpc); to the overt fear condition (b) in the right amygdala (Am); to the covert disgust condition (c) in the right putamen (P); and to the overt disgust condition (d) in bilateral insulae (I). The numbers above the transverse sections indicate the distance in millimeters from the transcassal line. The activation threshold at each voxel was $P < 0.005$.

Table 3
Generically activated brain regions to covert expressions of disgust

Region	Side	x^a	y^a	z^a	No. of voxels
(Approximate Brodmann Area)					
Thalamus (dorsomedial nucleus)	R	4	-20	15	79 ^{b,c}
		7	-17	9	46
Precuneus (7)	R	4	-63	26	25
Anterior cingulate gyrus (24)	R	7	-4	37	19 ^{b,c}
Posterior cingulate gyrus (31)	R	11	-63	15	14
Putamen	R	32	-17	-2	12 ^c
Fusiform gyrus (37)	R	25	-43	-7	10
Cerebellum	L	-28	-46	-13	6
Middle temporal gyrus (21/37)	R	47	-56	4	5 ^b

^a As for Table 1.

^b Significantly greater mean power of response in these regions than to overt expressions of disgust.

^c Significantly greater mean power of response in these regions than to covert expressions of fear.

Repeated-measures analysis of variance

Effect of emotion (fear versus disgust). There were three regions with greater mean power of response to both disgust compared with both fear conditions ($P = 0.02$; no. false-positive activated clusters <1; no. significantly activated voxels = 16): the left anterior cingulate gyrus (Brodmann Area, BA 24), the right posterior cingulate gyrus (BA 23/31), and the right inferior parietal lobule (BA 40). There were no regions with greater mean power of response to both fear conditions compared with both disgust conditions.

Effect of target duration (overt versus covert presentations). There were four regions with greater mean power of response to both overt compared with both covert conditions ($P = 0.02$; no. false-positive activated clusters <1; no. significantly activated voxels = 44): right-sided frontal regions (the right inferior frontal gyrus, BA 45/47; and the right anterior cingulate gyrus, BA 32), and left-sided visual processing regions (the left precuneus, BA 7; and the left cuneus, BA 19). There were no regions with greater mean power of response to both covert conditions compared with both overt conditions.

Interaction between emotion and target duration. There were nine regions in which there were significant changes in mean power of response associated with the interaction between Emotion (fear/disgust) and Target Duration (covert/overt) ($P = 0.02$; no. of false-positive activated clusters <1; no. of significantly activated voxels = 83). The complexity of the interaction precludes simple overall description and is best understood in the light of the following one-way analyses performed to examine whether non-consciously discriminated fear and disgust show the same double dissociation (amygdala activation to fear, insular activation to disgust, in both cases versus neutral) observed for consciously discriminated fear and disgust.

Specific comparisons

Overt versus covert presentations of fear. Voxels with significantly greater mean power of response ($P < 0.05$) to overt than covert presentations of fear were found in the right amygdala and left putamen, in addition to right-sided visual processing regions (right lingual gyrus and right precuneus), bilateral posterior cingulate gyri, the right inferior parietal lobule, and right-sided frontal

regions (anterior cingulate and medial frontal gyri), while voxels with significantly greater mean power of response to covert than overt presentations of fear were found primarily in the left inferior frontal gyrus, the left inferior parietal lobule and bilateral cerebellum (search volume = 763 voxels; $P = 0.05$; no. expected false-positive activated voxels = 38; observed no. activated voxels = 276; Tables 1 and 2).

Overt versus covert presentations of disgust. Voxels with significantly greater mean power of response ($P < 0.05$) to overt than covert presentations of disgust were found primarily in the right insula, bilateral occipitotemporal cortex (right lingual gyrus, right superior temporal gyrus, left middle temporal gyrus), left posterior cingulate gyrus and left inferior parietal lobule; while voxels with significantly greater mean power of response to covert than overt expressions of disgust were found in the right thalamus, right anterior cingulate gyrus and right middle temporal gyrus (search volume = 589 voxels; $P = 0.05$; no. expected false-positive activated voxels = 29; observed no. activated voxels = 182; Tables 3 and 4).

Covert presentations of fear versus disgust. Voxels with significantly greater mean power of response ($P < 0.05$) to covert presentations of fear than covert presentations of disgust were demonstrated in the left inferior frontal gyrus, right cerebellum, bilateral superior temporal gyri and left inferior parietal lobule; while voxels with significantly greater mean power of response to covert presentations of disgust than fear were found in the right thalamus, right anterior cingulate gyrus and right putamen (search volume = 554 voxels; $P = 0.05$; no. expected falsely activated voxels = 27; observed no. activated voxels = 167; Tables 1 and 3).

Overt presentations of fear versus disgust. Voxels with significantly greater mean power of response ($P < 0.05$) to overt presentations of fear than disgust were found in the left putamen, bilateral frontal regions (right anterior cingulate gyrus, right medial

Table 4
Generically activated brain regions to overt expressions of disgust

Region	Side	x^a	y^a	z^a	No. of voxels
(Approximate Brodmann Area)					
Middle temporal gyrus (19)	L	-28	-63	20	43 ^b
		-40	-67	15	31
Posterior cingulate gyrus (30/31)	R	7	-50	20	4
	L	-4	-37	31	24 ^{b,c}
Precuneus (7)	R	11	-60	37	21
Cerebellum	R	32	-63	-13	12
	L	-17	-43	-7	7
Postcentral gyrus (40)	L	-53	-20	15	9 ^c
Inferior parietal lobule (40)	L	-25	-30	37	8 ^{b,c}
Insula	R	40	-10	4	7 ^b
	R	36	0	-7	3
	L	-28	4	-7	3
Anterior cingulate gyrus (32)	R	7	43	-2	7
Lingual gyrus (18)	R	4	-80	4	5 ^b
	L	-15	-50	-2	4
Superior temporal gyrus (22)	R	47	-7	-2	4 ^b
Middle occipital gyrus (37)	L	-40	-56	-7	4

^a As for Table 1.

^b Significantly greater mean power of response in these regions than to covert expressions of disgust.

^c Significantly greater mean power of response in these regions than to overt expressions of fear.

frontal gyrus, left inferior frontal gyrus), bilateral posterior cingulate gyri, right lingual gyrus, right cerebellum and right amygdala; while voxels with significantly greater mean power of response to overt expressions of disgust than fear were found primarily in the left inferior parietal lobule, right precuneus and left postcentral gyrus (search volume = 767 voxels; $P = 0.05$; no. expected false-positive activated voxels = 38; observed no. activated voxels = 166; Tables 2 and 4).

Discussion

In the psychophysical experiments, we used objective discrimination thresholds (Williams et al., 2004) to establish critical temporal parameters, with respect to both SOA and STA, for overt and covert presentations of masked facial expressions of fear and disgust. Our results for fear agree in detail with those reported by Williams et al. (2004) using identical stimuli but in a different laboratory. Our results for disgust (not studied by Williams et al., 2004) are essentially identical to those for fear (Fig. 2). In both cases, we observed chance discrimination of emotional from neutral expressions at a 30-ms SOA and 100-ms STA, and clear conscious perception of the target emotional expression at a 170-ms SOA. Using these parameters, Williams et al. (2004) found faster SCR rise time for fear than neutral targets at the 30-ms SOA, confirming other reports (Dimberg et al., 2000; Öhman, 1992) that unconscious emotional response can occur under these conditions in the absence of verbal report. It is reasonable to suppose, therefore, that this was also the case in the present experiments, at least with regard to the fear expressions.

We demonstrated substantial differences in the neural substrates underlying perception of these facial expressions, consistent with theories that posit a small number of fundamental emotions (here, fear and disgust), each dependent upon a separate brain system (Calder et al., 2001). Furthermore, the overall analysis of variance indicates significant effects, not only of the factor Emotion (fear versus disgust), but also of Target Duration (covert versus overt) upon neural responses to target–mask stimuli. Predominantly right-sided frontal and left-sided visual regions were activated significantly more by both overt compared with both covert conditions; while predominantly left-sided frontal and right sided posterior and parietal regions were activated significantly more by both disgust compared with both fearful conditions. The involvement of right-sided frontal regions in the neural response to overt but not covert presentations of emotional stimuli is consistent with the proposed role of the right hemisphere in the conscious perception of emotion (Adolphs et al., 1996; Davidson and Irwin, 1999). Increased activation of extrastriate visual cortical regions by emotional compared with neutral expressions has been demonstrated previously (Morris et al., 1998; Surguladze et al., 2003). Our results indicate that this effect is greater for overt than covert presentation (although it occurred in both conditions) for both fear and disgust (see Tables 2 and 4, footnote b).

We did not necessarily expect activation in the fusiform gyrus (where the fusiform face area is located; Haxby et al., 2000). Although such activation has been reported previously in contrasts between emotional and neutral facial expressions, overall the results of such experiments are mixed. Increased fusiform gyrus activation to fearful versus neutral expressions was observed by Vuilleumier et al. (2001) and Pessoa et al. (2002), but not by Morris et al. (1998). Anderson et al. (2003) reported fusiform

activation to fearful versus neutral expressions, but only when subjects were instructed to attend to faces (our subjects had no attentional instructions). In studies of multiple emotional expressions, fusiform activation has been reported variously to angry but not fearful, sad or happy expressions (Kesler-West et al., 2001); to fearful but not disgusted or angry expressions (Sprengelmeyer et al., 1998); and to all of fearful, disgusted, happy and sad expressions (Surguladze et al., 2003). In the present study, we did not observe activation in the fusiform gyrus to either overt fear or overt disgust. A major difference between our procedure and that used by others, including Surguladze et al. (2003) in our own laboratory, is that all presentations of either emotional or neutral expressions were immediately followed by the neutral expression used here as a mask. This manipulation decreases the difference between the facial stimuli entering into the fear versus neutral and disgust versus neutral contrasts and so may account for the absence of detectable fusiform gyral activation. Surprisingly, despite this absence of activation in the overt conditions, we did see fusiform gyral activation in the contrast between covert disgust (but not covert fear) versus neutral expressions. Given the variability in the literature noted above, this finding stands in need of replication.

Our results when presenting fully conscious (170 ms SOA) facial expressions confirm previous evidence that fear activates the amygdala (Breiter et al., 1996; Morris et al., 1996; and see reviews by Phan et al., 2002 and Zald, 2003). The center of this activation lay at the amygdala/hippocampus border, but within the range of coordinates described elsewhere as amygdala responses to fear (e.g., Breiter et al., 1996; Hariri et al., 2002; Lange et al., 2003; Morris et al., 1998; Phelps et al., 2001; Phillips et al., 1997, 1998). This location may indicate activity in both the amygdala and the hippocampus, consistent with evidence that interactions between these two structures are of especial importance in mediating aversive emotions (Gray and McNaughton, 2000; Lange et al., 2003). We also confirm the finding that fully conscious facial expressions of disgust activate the insula (Anderson et al., 2003; Phillips et al., 1997, 1998; Sprengelmeyer et al., 1998), as well as the double dissociation (fear not activating the insula, nor disgust the amygdala) reported by Phillips et al. (1998) (but see Gorno-Tempini et al., 2001). This dissociation received further confirmation in respect of amygdalar (but not insular) activation to fear in the direct statistical comparison of overt fear versus overt disgust conditions; this analysis, however, failed to provide additional statistical support for greater insular activation to overt disgust than to overt fear.

The overall analysis of variance disclosed, in addition, a strong and complex interaction between Emotion and Target Duration. To analyse this further, we performed specific statistical comparisons between neural responses to overt and covert presentations of fear and disgust. These revealed that, unlike overt presentation, covert presentations of fear did not activate the amygdala; and, also unlike overt presentation, covert presentations of disgust did not activate the insula. This pattern of results was confirmed by the analyses of variance comparing activation to covert fear and disgust expressions, respectively. These did not reveal any greater activity in the amygdala for fear relative to disgust, nor in the insula for disgust relative to fear. These negative statistical results for the amygdala and insula in the covert condition occurred, moreover, in a context of significant differences between the neural responses to covert fear and disgust, but in other regions.

It is difficult to rely upon negative results (here, in the covert condition, absence of activation of the amygdala to fear and of the

insula to disgust expressions). Furthermore, we employed a relatively large voxel size ($3 \times 3 \times 7$ mm) and a block design paradigm with a small set of facial stimuli, the latter potentially leading to within and/or between block habituation. Either or both of these factors may have led to loss of BOLD signal. However, were this to have had a major influence on our findings, it is surprising that we nonetheless observed clear amygdala activation to fear (as well as insula activation to disgust) in the overt condition, especially since habituation of the amygdalar response has been demonstrated in a similar block design with overt (3 s) presentation of fear expressions (Phillips et al., 2001). A further possibility is that our analytical methods were inappropriate for the detection of signals of low strength and/or small volume. To exclude this possibility, we repeated our analyses using two less conservative thresholds for voxel level activation ($P < 0.01$ and < 0.02 , as opposed to the initial $P < 0.005$), and also with FWHM set at 7.2 as opposed to 11 mm. Neither of these manipulations disclosed any activation in either the amygdala or insula in response to covertly presented fear or disgust expressions. Note that, at the statistical threshold of activation of $P < 0.02$, we expect about 220 false-positive activated voxels in the whole brain (approximately 11,000 voxels), that is, 1 in 50 voxels is expected to be activated by chance alone. Assuming the amygdala to be a sphere of diameter 1 cm and given the voxel dimensions of our standard space template (54 mm^3), each amygdala consists of ~ 10 voxels. There is therefore a 40% chance that one voxel will be activated in one of the two amygdalae. In response to the covert fear stimulus, we saw no amygdalar activation at all. It is reasonable to conclude, therefore, that in our covert fear condition the amygdala was not activated.

Nonetheless, our observations of the responses to covert fear and disgust are less easy to situate in relation to the previous literature than are the responses to overt presentation of these expressions. Most of the relevant studies have considered only fear. Until recently, the consensus has been that amygdala activation by fear expressions is present, and indeed undiminished, when these do not attract full conscious processing. The approaches employed in these studies to present fear expressions under conditions of reduced conscious awareness have varied, including backward masking as here (Rauch et al., 2000; Sheline et al., 2001; Whalen et al., 1998), manipulations of attention (Anderson et al., 2003; Vuilleumier et al., 2001), and investigations of single patients with 'blindsight' (Morris et al., 2001a) or 'extinction' upon bilateral stimulus presentation in hemifield neglect consequent upon right parietal damage (Vuilleumier et al., 2002). Often cited as part of this consensus is the report by Morris et al. (1998) of amygdala activation to backwardly masked, 30-ms presentations of facial expressions. However, this activation was to angry, not fearful, expressions, and it was observed only if the face had previously been made a conditioned aversive stimulus. Thus, the relation of this study to the present results is unclear. The consensus, however, has been disturbed by a recent report (Pessoa et al., 2002) of the complete abolition of amygdala activation to fear expressions by a competing task that made substantially greater demands upon attentional resources than attentional manipulations used in similar studies (Anderson et al., 2003; Vuilleumier et al., 2001). This suggests a possible general explanation for the survival of amygdala activation when attention or awareness has been reduced in the studies reviewed above: that this reduction has been insufficiently complete (Pessoa et al., 2002, 2003).

Our data fit comfortably with this generalisation. Compared to earlier studies in which backward masking left amygdala activation to fear expressions essentially unchanged, we took greater care to ensure that our stimuli were below the objective threshold at which fear and disgust can be distinguished from neutral. In all three of these earlier studies (Rauch et al., 2000; Sheline et al., 2001; Whalen et al., 1998), the determination of whether targets were discriminated was based only upon subject debriefing after the experiment. We can be more confident that our subjects were unable consciously to discriminate the expressions we presented covertly, for four reasons. First, we employed conservative thresholds for stimulus discrimination in the psychophysical study, with stimuli presented in a manner directly related to the structure of the subsequent fMRI study. Second, we used an objective procedure to ensure that subjects could not discriminate covert target stimuli, rather than relying on subjective report only. Third, we presented a similar number of target-mask trials in each condition of the psychophysical and fMRI studies to ensure optimal application of the psychophysical criteria. Fourth, we offset all target faces, neutral as well as emotional, by 1° visual angle in the direction of the four diagonals to avoid artefactual detection of emotional facial expressions from apparent motion. To our knowledge, this is the first time in which such a robust procedure has been employed in this type of study.

Nonetheless, given the lack of theoretical understanding of either the psychological or the neural basis of the conscious/unconscious distinction, these experimental precautions do not fully clarify the nature of the experiential contrast corresponding to our operational definition of 'covert' and 'overt' stimuli. In the covert case, we cannot distinguish between two possibilities: (1) that our subjects had no conscious experience of the target expressions; or (2) that they had some conscious experience, but not of sufficient clarity or intensity to permit discrimination of the specific expression (Williams et al., 2004). The latter possibility is suggested by the observed mean accuracies of identification of the 30-ms targets: between 50% chance expectation and the 67.6% upper confidence limit.

With regard to disgust, we are aware of only one previous attempt to measure fMRI responses to expressions of this emotion under conditions of reduced awareness. Anderson et al. (2003) used an attentional manipulation in which subjects were instructed to attend either to a face or to a place superimposed in one display. Instructions to attend to place eliminated the activation of the insula observed when disgust faces were focally attended. This result is consistent with the observation here that covert (30-ms SOA) presentation of disgust did not activate the insula, although overt (170-ms SOA) did. Note, however, that Anderson et al. (2003) found no effect of the identical manipulation upon the amygdala response to fear faces, implying that the latter is more robust under conditions of reduced awareness than is the insula response to disgust. The masking procedure we used here, in contrast, was equally effective in eliminating the amygdala response to fear and the insula response to disgust, suggesting that it was a more effective manipulation of awareness than that of Anderson et al. A further discrepancy between our results and those of Anderson et al. is that they observed a response in the amygdala to disgust expressions when the subject was instructed to attend to places, whereas we saw no activation in the amygdala in response to disgust with either overt or covert presentations. It seems likely that this difference between our results and those of

Anderson et al. can also be attributed to our use of a stronger manipulation of awareness.

Our results, taken together with those of Pessoa et al. (2002), suggest then that a sufficiently powerful manipulation of awareness can eliminate both the insula response to disgust and the amygdala response to fear; although this concept cannot readily be applied to the patterns of amygdala response to fear in cases of blindsight (Morris et al., 2001a) or unilateral neglect (Vuilleumier et al., 2002). Assuming that this inference is indeed correct, what are the general implications of our findings for the relationship of brain activity to the distinction between conscious and unconscious processing?

Different predictions may be derived from current general views of the neural basis of conscious experience (Weiskrantz, 1997). First, both theories (see Introduction) holding the conscious/unconscious distinction to be spurious (Dennett, 1991; Dennett and Kinsbourne, 1992) and some holding it to be real (Greenfield, 1998) predict that, if unconsciously presented expressions of fear and disgust elicit different activation patterns, these will be qualitatively the same as those to consciously perceived presentations of the same stimuli. These authors treat the conscious/unconscious distinction as quantitative, with conscious experience associated with a stronger or more widespread activation pattern than that to stimuli presented below the threshold of conscious perception. A second type of theory, lampooned (Dennett, 1991) as the ‘Cartesian Theater’, is that conscious experience depends upon activity in a specialized brain region/system. We would then predict a region(s) of activation to consciously perceived facial expressions that is additional to regions activated by the stimuli presented unconsciously; furthermore, the added region(s) should be the same for expressions of both fear and disgust. A third type of theory has been less explicitly stated, but may be inferred from attempts to define brain regions crucial for, for example, ‘visual awareness’ (Koch, 1998) or ‘episodic’ (i.e., conscious) memory (Lepage et al., 2000). Implicit here is that there are several specialized brain regions/systems (‘Cartesian multiplexes’), one for each separate domain of conscious information processing. Within one domain (e.g., facial expression processing), the predictions are the same as those of the single ‘Theater’ model. The two types of theory can be distinguished only by examining activation patterns characterizing conscious and unconscious processing across multiple domains.

Our data clearly establish differences in the patterns of brain activation elicited by overt and covert stimuli. Thus, even if there were a form of degraded conscious experience of the covert expressions (rather than none at all; see above), this experience depended upon different activation patterns from those associated with fully conscious percepts (see Saharie et al., 1998). We can therefore address the major issues regarding the neural basis of consciousness to which the experiments were directed, and use the word ‘unconscious’ to cover both of the possibilities distinguished above.

The quantitative theory of the neural basis of the conscious/unconscious processing distinction (Dennett, 1991; Dennett and Kinsbourne, 1992; Greenfield, 1998) predicts stronger and/or more widespread activation patterns to facial expressions of fear and disgust discriminated consciously than to the same expressions presented unconsciously. The Cartesian Theater theory predicts that the activation pattern for conscious perception should contain an additional region or system not present in the pattern for unconscious discrimination, and that this area should be the same

for fear and disgust. Neither of these theories is supported by our data.

Regarding the quantitative theory, there was, overall, a more widespread pattern of activation to overt than to covert stimuli, as supported statistically by the main effect of Target Duration in the ANOVA. However, the neural response to overt stimuli (both fear and disgust) was not merely an amplification of that to covert stimuli. The significant interaction term in the two-way ANOVA indicated that these responses differed radically. This result is particularly surprising given that the 30-ms duration of covert stimulus presentation is contained within the 170-ms overt presentation. A difference in the intensity of response might have been predicted on these grounds alone.

Regarding the Cartesian Theater theory, a number of regions were more strongly activated by overt than covert stimuli (and none showed the reverse pattern). However, in contradiction of this theory, no single region was activated both by overt fear and disgust and absent from activation patterns to covert fear and disgust. This failure to confirm the ‘Theater’ prediction is striking in that the stimuli employed were restricted: facial expressions of two aversive emotions differing only slightly visually.

The third theoretical approach, ‘Cartesian multiplexes’, envisages a single substrate of conscious perception for a given modality, for example, one for visual awareness (Koch, 1998). This approach might also predict a single substrate of conscious perception of emotion in general. Our data reveal a more complex picture: a 4-fold dissociation between activation patterns elicited by consciously and unconsciously discriminated expressions of fear and disgust respectively. Cartesian multiplexes fractionated to this degree (one for each specific emotion) will pose a formidable problem for empirical investigation. However, just such a state of affairs appears to be emerging in relation to vision: there is increasing evidence in support of the hypothesis (Ffytche et al., 1998; Zeki and Bartels, 1998) that activity in a particular ‘module’ of the visual system (e.g., V4 subserving colour perception, V5 subserving motion perception) is sufficient (provided—in line with the quantitative hypothesis—that it is also sufficiently intense; ffytche, 2002; Moutoussis and Zeki, 2002) to give rise to conscious awareness of the corresponding visual feature (colour or motion). Our results for fear and disgust appear to fit this kind of model.

Our intention is to bring these issues into the laboratory. We do not believe that a single experiment can resolve them. We are confident that our psychophysical procedures allowed us to construct stimuli that meet the best available criterion of the conscious/unconscious distinction, that is, reportability. The parameters we established for presentation below the threshold of discrimination were similar to those used in a study of facial mimicry of unconsciously detected expressions of anger or happiness (Dimberg et al., 2000) which demonstrated psychophysiological discrimination between two emotional expressions under conditions in which verbal report was at chance; and identical to those which showed greater SCR responses to fear than to neutral expressions (Williams et al., 2001, 2004). We have demonstrated that a discrimination occurs also in brain activation patterns to these stimuli. However, we made no predictions as to specific activation patterns by specific covert stimuli, so those observed must be treated as tentative until replicated.

There is an alternative account of our results. We have so far assumed that the same information processing ‘domain’ was invoked by consciously and unconsciously discriminated facial

expressions. However, emotional facial expression processing may have occurred only to consciously perceived stimuli, with short-duration targets eliciting processing either as faces devoid of emotional expression or as non-facial visual patterns. There are, however, features of our experimental design and results that render this alternative account unlikely. If the short-duration faces were processed as emotion-free, it is surprising that different brain regions were activated by what would then be random sets of either non-emotional faces or non-facial visual patterns. Furthermore, in our previous ERP study using identical face stimuli, we observed enhanced N2 responses to below-awareness perception of emotion (versus neutral) stimuli. This ERP component is preferentially elicited by faces, including the changeable aspects of faces, such as expressions and eye gaze (Bentin et al., 2002; Sokolov and Boucsein, 2000). Nonetheless, this important issue warrants further investigation, for example, by electromyographic recording during scanning. Technical limitations precluded such measurements during our study. A further control would be to present inverted stimuli in the expectation that this would impair their recognition as emotional facial expressions and eliminate differences between activation patterns to fear, disgust and neutral faces.

Another methodological concern is the temporal resolution of fMRI. It is possible that during the first 30 ms of presentation of the 170-ms stimuli, the same activation patterns occurred as to the 30-ms stimuli, but that these patterns were subsequently 'overwritten' by changes over the next 140 ms, in a manner akin to the process referred to by Dennett (1991) and Dennett and Kinsbourne (1992) as 'multiple drafts'. Evidence for this possibility comes from studies of cell recordings in non-human primates, which have demonstrated that inferior temporal cortical neurons show a graded response to masked as well as unmasked facial stimuli, which declines sharply at 30 ms following stimulus onset (Rolls, 2000; Rolls and Tovee, 1994). Further evidence comes from our study of ERPs elicited by fear and neutral faces identical to the ones used here. In this study (Williams et al., 2004), when fear expressions were presented below the level of conscious awareness (at SOAs of 10 and 30 ms), only the 10-ms SOA elicited a faster (relative to neutral expressions) positive P1 response within 100 ms of stimulus onset, whereas both the 10- and 30-ms SOAs gave rise to a greater negative N2 component, elicited around 200 ms post-stimulus. In contrast, conscious fear perception (SOA = 170 ms) was not accompanied by differential P1 or N2 activity, but rather by a more prominent N4, peaking around 400 ms post-stimulus. Further research is required to determine how these differences in the timing of ERP responses to unconsciously detected or discriminated and consciously perceived facial expressions, respectively, are related to the differences in regional location of BOLD activity observed in the present study. However, direct comparison between fMRI and ERP data is problematic: the temporal and spatial scales upon which the two methods operate differ by orders of magnitude; ERPs do not measure activity in subcortical structures such as the amygdala that can be reached by fMRI; and ERPs reflect electrical activity in neurons more directly than does fMRI.

Many regions important for face, facial feature and object perception, including the fusiform, superior and middle temporal gyri (Puce et al., 1996, 1998), were activated by covert and overt expressions of fear and disgust (Tables 1–4). There have been previous reports of emotional visual stimuli activating occipito-temporal cortex, including the fusiform gyrus, more than neutral visual stimuli (e.g., Lang et al., 1998; Morris et al., 1998). Our results are consistent with these reports: we demonstrated activa-

tion in the precuneus (BA 7), the inferior parietal lobule, previously shown to be activated by emotional stimuli (Puce et al., 1998), and the posterior cingulate gyrus, important in visual memory (Swartz et al., 1994), to emotion target–neutral mask stimuli in the majority of conditions. The anterior cingulate gyrus was activated by all emotion target–neutral mask stimuli, consistent with its proposed role in the mediation of arousal (Pribram and McGuiness, 1975), attention (Posner and Petersen, 1990) and novelty detection (Berns et al., 1997). Note, however, that we observed responses of this kind in response to disgust, both overt and covert, as well as covert presentations of fear, and there was no discernable activation of the amygdala under any of these conditions. Thus, suggestions that there is a neuromodulatory effect of the amygdala upon visual regions during processing of visual, emotionally salient stimuli (Morris et al., 2001b) probably require extension to other regions involved in emotion processing. Many of our stimuli (Tables 1–3) also activated components of basal ganglia-thalamocortical circuits directing flow of information to and from the cortex (Alexander et al., 1990).

In conclusion, our data demonstrate significant differences between neural responses to overt and covert presentations of two specific emotions, and between neural responses to expressions of fear and disgust during both covert and overt presentations. We provide further support for specific neural substrates underlying perception of different basic emotions, and suggest distinct neural correlates of unconscious and conscious perception of emotional stimuli. Most importantly, our findings demonstrate that it is possible to submit to experimental scrutiny issues in consciousness theory previously left largely to philosophical debate.

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