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Dissociable Neural Pathways Are Involved in the Recognition of Emotion in Static and Dynamic Facial Expressions

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Facial expressions of emotion powerfully influence social behavior. The distributed network of brain regions thought to decode these social signals has been empirically defined using static, usually photographic, displays of such expressions. Facial emotional expressions are however highly dynamic signals that encode the emotion message in facial action patterns. This study sought to determine whether the encoding of facial expressions of emotion by static or dynamic displays is associated with different neural correlates for their decoding. We used positron emission tomography to compare patterns of brain activity in healthy men and women during the explicit judgment of emotion intensity in static and dynamic facial expressions of anger and happiness. Compared to judgments of spatial orientation for moving neutral facial expressions, the judgment of anger in dynamic expressions was associated with increased right-lateralized activity in the medial, superior, middle, and inferior frontal cortex and cerebellum, while judgments of happiness were associated with relative activation of the cuneus, temporal cortex, and the middle, medial, and superior frontal cortex. In contrast, the perception of anger or happiness in static facial expressions activated a motor, prefrontal, and parietal cortical network previously shown to be involved in motor imagery. The direct contrast of dynamic and static expressions indicated differential activation of visual area V5, superior temporal sulcus, periamygdaloid cortex, and cerebellum for dynamic angry expressions and differential activation of area V5, extrastriate cortex, brain stem, and middle temporal cortical activations for dynamic happy expressions. Thus, a distribution of neural activations is related to the analysis of emotion messages in the nearly constant biological motion of the face and differ for angry and happy expressions. Static displays of facial emotional expression may represent noncanonical stimuli that are processed for emotion content by mental strategies and neural events distinct from their more ecologically relevant dynamic counterparts.

Key Words: **positron emission tomography (PET); facial expressions of emotion; dynamic and static stimuli; biological motion; social perception.**

INTRODUCTION

The human face represents a powerful medium for social signaling. Its highly contoured skeletal foundation supports over 100 anatomically and functionally distinct muscles that function with the spatially varying viscoelastic properties of the skin to form an enormous pose space (Waters and Terzopoulous, 1990). Using these rich physical features, the human face encodes numerous discrete emotions. The ability to decode these complex facial expressions is essential to social behavior (Ekman, 1982). Diverse psychiatric and neurologic disorders are associated with deficits in social cognition that have been empirically defined by deficits in the perception of emotion in facial expressions (Singh *et al.*, 1998; Kohler *et al.*, 2000; Hargrave *et al.*, 2002). The neural correlates of these perceptual tasks have been the recent focus of functional neuroimaging studies (see Calder *et al.*, 2001) as well as studies of the effects of brain damage (see Adolphs *et al.*, 2000). These studies have typically focused on the perception of emotion in static, usually photographic, displays of facial expressions of emotion. Such studies have implicated dissociable brain areas in the perception of different emotions. The perception of the most studied emotion of fear has been linked to the amygdala (Adolphs *et al.*, 1994; Morris *et al.*, 1996; Breiter *et al.*, 1996; Whalen, 1998; Calder *et al.*, 2001). The perception of anger in static facial displays is apparently less dependent on amygdala activity (Adolphs *et al.*, 1994; Blair *et al.*, 1999; Phillips *et al.*, 1999; Whalen *et al.*, 2001), and the amygdala is seldom implicated in the neural correlates of the recognition of disgust or happiness in static displays. The insula and basal ganglia appear to be involved in the perception of disgust (Phillips *et al.*, 1997), while recognition of happiness is associated with cingulate, medial frontal, and parietal activations (Phillips *et al.*, 1998). While the neural substrates of emotion perception in static facial expressions appear to be at least somewhat emotion-specific, the somatosensory cortex may have a more global role in the ability to comprehend the emotional significance of static facial expressions (Adolphs *et al.*, 2000).

Although typically studied as static displays, facial expressions of emotion are highly dynamic social signals that encode the emotion message in facial action patterns. In this regard, facial action patterns that encode emotions are an

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important subset of the phenomenon of biological motion. Biological motion refers to meaningful human body actions (Johansson, 1973), and the perception of actual as well implied motion has been linked to a distributed network involving the basal ganglia, the amygdala, the posterior superior temporal sulcus (STS), the intraparietal sulcus, and the inferofrontal cortex (Bonda *et al.,* 1996; Grèzes *et al.,* 2001; Binkofski *et al.,* 2000; Grossman *et al.,* 2000; Puce *et al.,* 2000). The dependence of the encoded emotion message on facial dynamics was supported by the observation that the onset of perception of happiness in a smile was related to the time of most rapid facial movement (Leonard *et al.,* 1991). A study of emotion perception for schematic facial expressions supported the contention that dynamic displays improved the recognition and discrimination of emotions compared to static displays (Werhle *et al.,* 2000). Moreover, the demonstration of a dissociation in the effects of brain damage (Humphreys *et al.,* 1993) or psychopathology (Archer *et al.,* 1994) on the ability to recognize emotion in static and dynamic facial expressions suggests that separable neural correlates are involved.

Haxby and colleagues (2000) have proposed a model of a distributed neural system for face perception that emphasizes a distinction between brain regions involved in the analysis of invariant aspects of faces (e.g., recognition) versus changeable aspects (e.g., eye gaze, expression). This study used positron emission tomography (PET) to test and extend this model by determining whether the emotion message encoded in static or fixed action patterns versus dynamic action patterns are decoded for emotion content by separable neural activations. Study design and analysis focused on the comparison of dynamic and static emotional expressions to a common face processing control task and on the direct comparison of static and dynamic expressions. We hypothesized that static and dynamic facial expressions of emotion are processed for emotion content by differing neural correlates and inferred strategies. As a specific hypothesis, it was proposed that emotion judgments in dynamic facial expressions would involve activations of the superior temporal gyrus and related structures (Haxby *et al.,* 2000; Allison *et al.,* 2000). Planned comparisons between stimulus conditions also sought to determine if the neural correlates of the perception of emotion in dynamically encoded facial expressions differ for expressions of anger and happiness, as has been demonstrated for static expressions.

MATERIALS AND METHODS

Subjects

The studied sample of research volunteers consisted of 13 right-handed and healthy Caucasian individuals (9 men and 4 women) between the ages of 22 and 26 years (mean 24.5 years). After describing the study in detail, all subjects gave written informed consent to participate in a research protocol approved by the Human Investigation and Radiation Safety Committees of the Emory University School of Medicine.

Stimuli and Experimental Design

Facial expression stimuli were selected and edited from the dynamic angry, happy, and emotionally neutral video sequences (30 frames/s) of the face processing subtests of the Perception of Emotion Test (POET; available on request). Expressions involved horizontal, vertical, and diagonal facial and head motion displayed from the shoulders up for four Caucasian posers consisting of a young adult man and woman and a middle-aged man and woman (Fig. 1A). For dynamic expressions, the emotion waxed and waned over the video sequence (Fig. 1A). Static displays of each facial expression of emotion were assembled by a frame selection at the perceived apex of the expression. Dynamic and static displays of emotionally neutral faces for the same posers were similarly selected for face orientation that was exclusively (static) or predominantly (dynamic) in the viewers right, center, or left visual field. Nonface stimuli (Fig. 1C) were computer generated and, for the dynamic stimulus condition, were matched in diagonal, vertical, and horizontal motion to the head movement for emotional expressions by one of the posers. All face and nonface stimuli were matched for color and foreground and background illumination. Stimuli were presented on a 13-in., high-resolution color monitor positioned approximately 2 ft from the faces of the supine subjects.

Subjects performed four emotion perception tasks involving explicit judgments of emotion intensity in dynamic or static facial expressions of anger or happiness. Emotion intensity was rated as being low, medium, or high with responses recorded using a three-button, hand-held response pad. As a control face processing task, subjects were instructed to judge the viewer-observed spatial orientation (i.e., left, right, or center) of emotionally neutral faces using the same response pad. The selection of a visuospatial control task for face processing was based on the view of static displays of facial expressions of emotion as being spatially encoded and processed (Phillips and David, 1994; Wright *et al.,* 2002) and of dynamic facial expressions as being spatiotemporally encoded and decoded (Leonard *et al.,* 1991). An additional nonface visual processing task involved similar judgments of spatial orientation for static and dynamic abstract geometric shapes. Each task consisted of 12 stimuli and all stimuli were presented for 4 s followed by a 4 s interstimulus interval for recording of responses. The order of task presentation was counterbalanced between subjects using two task versions, and subjects saw each face emotion and motion condition once only to negate an influence of stimulus habituation (Breiter *et al.,* 1996; Whalen, 1998).

Image Acquisition, Processing, and Statistical Analysis

Head movement was minimized by a molded thermoplastic face mask (TruScan) attached to the head rest. The onset of stimulus display coincided with the bolus intravenous administration of 25 mCi (925 Mbq) of the freely diffusible blood flow tracer $[^{15}O]H_2$ (Mazziotta *et al.,* 1985). Image acquisition was performed with an ECAT 921 PET scanner (Siemens, Knoxville, TN) with the interdetector septa retracted. Three-dimensional image acquisition (Cherry *et al.,* 1993) was ini-

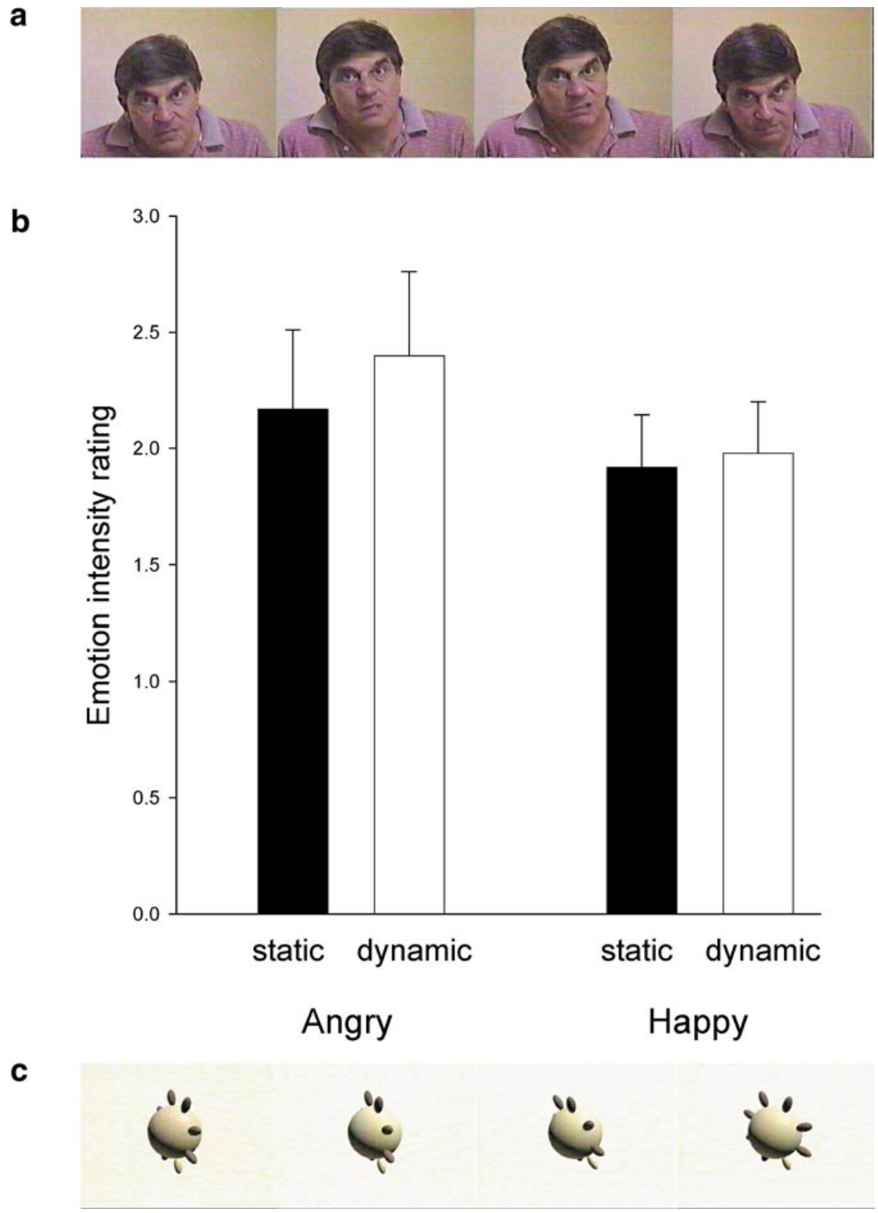
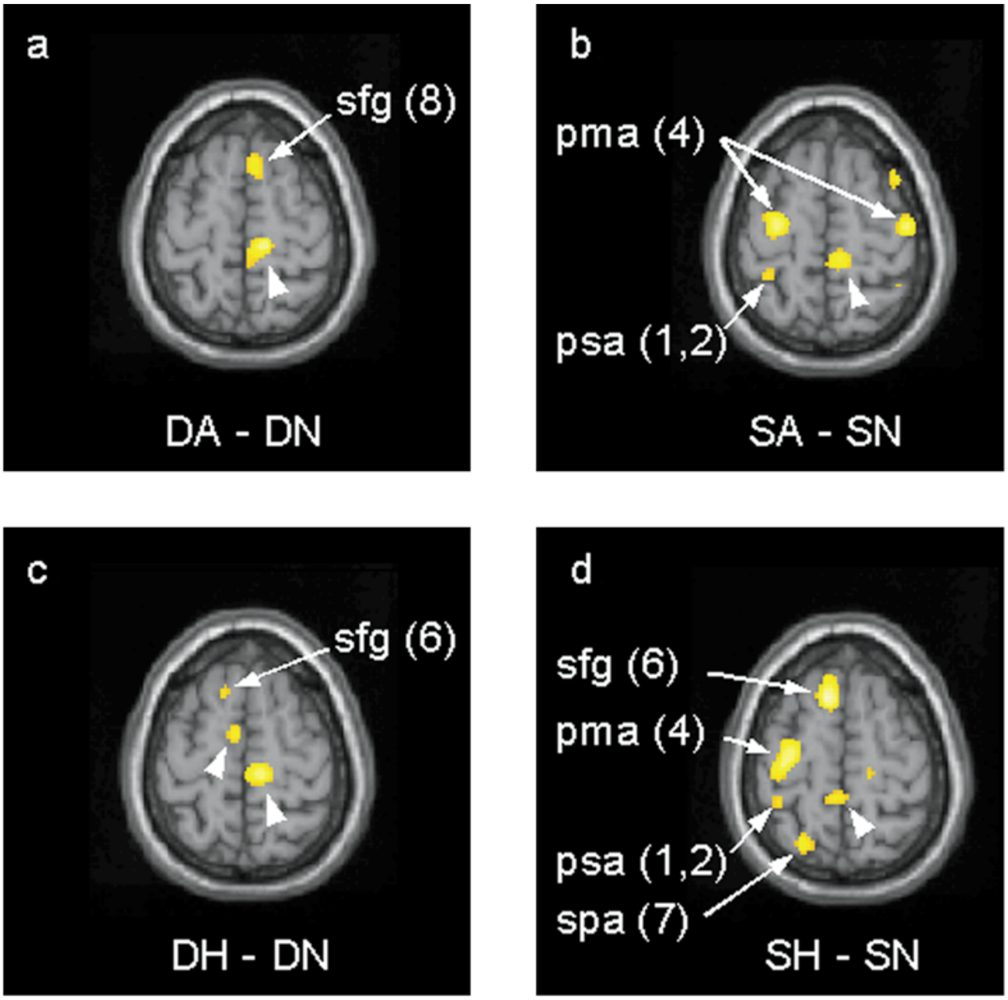


FIG. 1. (a) Example of face and head motion encoding a dynamic expression of anger for the middle-aged male poser. From left to right, frames 1, 20, 60, and 100 are shown for a 4-s anger expression videotaped at 30 frames/s; frame 20 was selected as the static representation of this posed emotion. (b) Subjects ratings of the perceived intensity of emotional expression for static and dynamic expressions of anger and happiness. The mean and standard deviation for emotion intensity judgments for 13 subjects are displayed, with ratings of 1, 2, and 3 corresponding to judgments of low, medium, and high emotional intensity. (c) Example of abstract nonface stimuli corresponding to frames 1, 20, 60, and 100 for a dynamic (30 frames/s) display.

tiated with the detection of head radioactivity and continued for a single 90-s frame. Ten minutes elapsed between each of the eight scans comprising the PET imaging session. Image postprocessing and data analysis were performed using statistical parametric mapping software (SPM99; Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm). Images were reconstructed using measured attenuation correction. To control for head movement over the PET imaging session, images for each subject were aligned to the first scan acquired. A mean image for each subject was then spatially normalized to a reference standard centered in Talairach space (Talairach and Tournoux, 1988). The normalization parameters were applied to the individual scans and the scans were smoothed by Gaussian filtering to a final isotropic resolution of 9-mm full-width at half-maximum.

Task-related activations were identified by the use of a general linear model (Neter *et al.*, 1996) to calculate difference images reflecting the relative changes in regional cerebral blood flow (rCBF) between the conditions. Subject variability in global CBF was included in the model as a covariate. Simple effects were determined from contrasts between emotional [angry (A) or happy (H)] and neutral (N)



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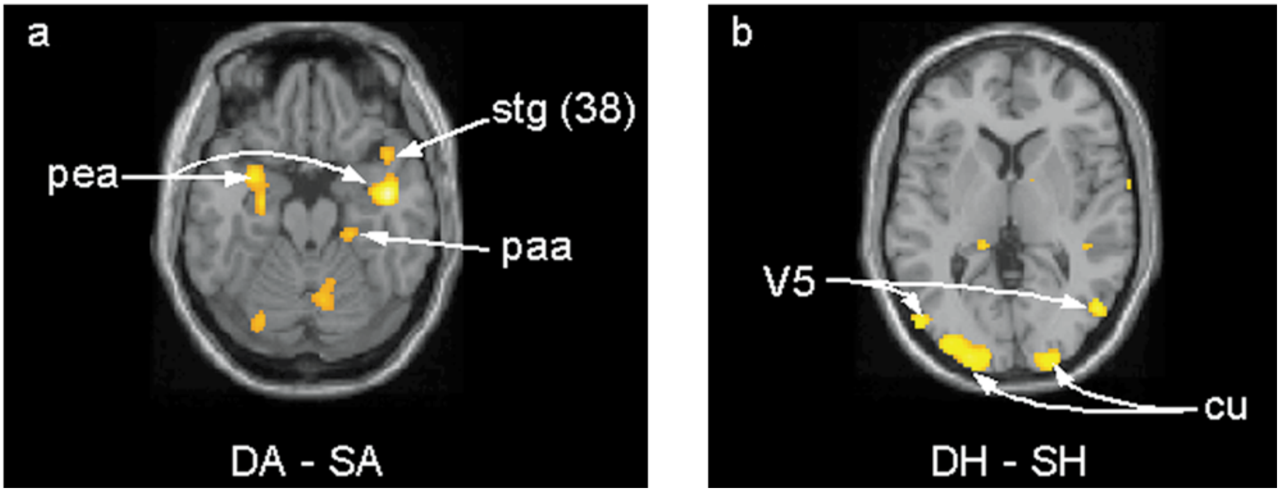

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FIG. 2. Cortical regions activated by anger (A) or happiness (H) judgments in expressive faces versus spatial orientation judgments in emotionally neutral faces for dynamic (D) and static (S) stimuli. (a) Dynamic angry > dynamic neutral. (b) Static angry > static neutral. (c) Dynamic happy > dynamic neutral. (d) Static happy > static neutral. Activations are superimposed on a dorsal ($z = +62$ mm) axial T1 anatomic image. White arrowheads indicate the stereotaxic location of the medial frontal cortex (BA 6) activations. Abbreviations [region (Brodmann's area)]: pma (4), the primary motor area, psa (1, 2), primary sensory area; sfg (8), superior frontal gyrus; spa (7), superior parietal area.

FIG. 3. Activations related to the contrast of emotion judgments in dynamic (D) versus static (S) expressions of anger (A) or happiness (H). Activations are superimposed on axial T1 anatomic images for (a) anger ($z = -20$) and (b) happiness ($z = +4$) judgments. Abbreviations [region (Brodmann's area)]: pea, periamygdaloid cortex; paa, parahippocampal area; stg (38), superior temporal gyrus; cu (17), cuneus.

TABLE 1

Sites of Neural Activation Associated with the Spatial Processing of Dynamic and Static Faces and Nonface Objects

	Stereotaxic coordinates[a]			
Brain area (BA)[b]	x	y	z	Voxel T
Dynamic neutral faces-dynamic nonface objects				
Right inferior frontal gyrus (45)[c]	+61	+27	+6	5.12
Right superior temporal gyrus (38)	+53	+19	−13	4.46
Right middle temporal gyrus (21)	+44	−1	−13	4.02
Left superior temporal gyrus (38)	−30	+3	−25	4.81
Left superior temporal gyrus (38)	−38	+18	−29	3.23
Right amygdala	−20	−12	−8	3.42
Right cuneus	+22	−95	+5	4.19
Right lingual gyrus (18)	+16	−80	−1	3.72
Right superior frontal gyrus (9)	+6	+60	+34	3.81
Left inferior occipital gyrus (17)	−20	−94	−7	3.68
Right fusiform gyrus (20)	+46	−40	−22	3.64
Right superior temporal gyrus (38)	+32	+12	−38	3.48
Dynamic neutral faces-static neutral faces				
Right middle temporal gyrus (37), V5	+50	−60	+5	4.59
Right middle temporal gyrus (39)	+50	−71	+16	3.49
Cerebellum	−4	−59	−24	3.92
Left middle occipital gyrus (18)	−22	−90	+19	3.52
Left middle occipital gyrus (19)	−20	−20	−7	3.20
Left superior temporal gyrus (38)	−48	+20	−23	3.07

[a] Values represent the stereotaxic location of voxel maxima with coordinates in Talairach space in millimeters lateral to midline (x), anterior/posterior to the anterior commissure (y), and superior/inferior to the commissural line (z).

[b] BA, Brodmann designation for cortical areas.

[c] Activation sites satisfying ($P < 0.05$) a correction for multiple comparisons. All other sites satisfied a statistical threshold of $P < 0.001$ uncorrected for multiple spatial comparisons.

conditions for each of the expression motion conditions [static (S) or dynamic (D)]. Additional planned contrasts included comparisons within an emotional expression and across a motion condition (e.g., DA − SA) and between emotional expressions within a stimulus motion condition (e.g., SA − SH). Threshold for significance was set at $P < 0.001$ (uncorrected) or $P < 0.05$ (corrected), with a cluster threshold of 20 contiguous voxels exceeding these intensity thresholds. The main effects for brain regions related to the mental representation of anger or happiness were identified by an analysis of conjunction (Price and Friston, 1997) based on the model [(DA − DN) and (SA − SN)] for angry expressions and [(DH − DN) and (SH − SN)] for happy expressions. An analysis of conjunction based on the model [(DA − DH) and (SA − SH)] was also performed to identify differential neural activations related to anger recognition.

RESULTS

Behavioral Results

Dynamic and static displays of emotional expression were judged to be of overall moderate to high intensity that did not differ between motion conditions for either emotion (t_{14}'s < 1.1, P's > 0.29; Fig. 1B). Both static and dynamic expressions of anger were rated as being more intense than their corresponding motion condition for expressions of happiness ($t_{14} = 2.6$, $P < 0.01$, and $t_{14} = 3.8$, $P < 0.01$, respectively; Fig. 1).

PET Imaging Results

Sites of altered rCBF associated with processing faces versus nonface objects for dynamic stimuli. To initiate this study of the effects of expression dynamics on the neural correlates of emotion perception, we compared rCBF images acquired during the visuospatial processing of dynamic, emotionally neutral facial expressions and motion-matched nonface objects. Similar to the results of a recent fMRI study comparing face and nonface object processing for static stimuli (Pierce *et al.*, 2001), this contrast revealed relative activations in the bilateral anterior STS, inferior and superior frontal gyri, amygdala, fusiform gyrus, and occipital cortex (Table 1). The direct comparison of spatial processing for dynamic and static neutral faces indicated differential activations in the right occipital–temporal junction corresponding to motion-sensitive visual area V5 (Zeki *et al.*, 1991; Watson *et al.*, 1993; McCarthy *et al.*, 1995), the temporal and occipital visual cortex, and cerebellum (Table 1).

Effect of expression dynamics on rCBF changes related to emotion perception. Compared to judgments of spatial orientation of dynamic neutral expressions, judgment of anger intensity in dynamic expressions was associated with prominent right hemisphere-lateralized superior, medial, middle, and inferior frontal cortex and cerebellar activations (Fig. 2a; Table 2). In contrast, judgment of anger content in static expressions was associated with activations in the bilateral precentral and left postcentral gyri, left cuneus, posterior

TABLE 2

Sites of Neural Activation Related to the Judgment of Anger in Static and Dynamic Expressions

Brain area (BA)[b]	Stereotaxic coordinates[a] x	y	z	Voxel T
Static angry-static neutral expressions				
Left precentral gyrus (4)	−28	−13	+50	4.86
Left precentral gyrus (4/6)	−55	+2	+44	3.94
Right precentral gyrus (4)	+46	−11	+59	3.79
Right medial frontal cortex (6)	+10	−26	+66	4.36
Right middle frontal gyrus (9)	+24	+21	+30	4.22
Right superior frontal gyrus (8)	+12	+26	+47	3.73
Left superior frontal gyrus (6)	−2	+13	+62	3.76
Right posterior cingulate gyrus (31)	+12	−18	+29	3.58
Left cuneus (17)	−10	−83	+6	3.51
Left inferior frontal gyrus (44)	−48	+14	+14	3.46
Left inferior frontal gyrus (45)	−51	+33	+0	3.36
Left middle frontal gyrus (10)	−24	+51	+10	3.37
Left postcentral gyrus (1,2)	−32	−36	+57	2.80
Dynamic angry-dynamic neutral expressions				
Right medial frontal cortex (6)	+14	−24	+62	4.83
Right superior frontal gyrus (8)	+20	+35	+44	4.18
Right anterior cerebellum	+26	−37	−32	3.82
Right posterior cerebellum	+30	−85	−24	3.52
Right middle frontal gyrus (8)	+44	+23	+39	3.71
Right superior frontal gyrus (10)	+42	+50	+25	3.56
Left superior frontal gyrus (9)	−8	+54	+30	3.31
Left inferior frontal gyrus (45)	−55	+31	+0	3.23
Conjunction [(DA − DN) and (SA − SN)]				
Right medial frontal cortex (6)[c]	+12	−26	+64	4.31
Right superior frontal gyrus (8)[c]	+12	+26	+48	3.61
Left inferior frontal gyrus (45)	−53	+31	+0	3.05
Left superior frontal gyrus (10)	−22	+49	+10	3.02
Right middle frontal gyrus (8)	+36	+22	+43	2.53
Right middle frontal gyrus (10)	+38	+56	−4	2.72
Right middle frontal gyrus (10)	+40	+44	+25	2.67
Left medial frontal gyrus (8)	−8	+43	+38	2.43
Left superior frontal gyrus (6)	−6	+1	+63	2.52
Dynamic angry-static angry expressions				
Right middle occipital gyrus (37),[c] V5	+55	−72	+4	5.71
Right middle temporal gyrus (21)[c]	+46	−7	−18	5.35
Right superior temporal sulcus (22)	+61	−54	+10	4.22
Right superior temporal gyrus (38)	+46	+12	−24	4.19
Left superior temporal sulcus (22)	−63	−42	+8	3.76
Right periamygdaloid cortex	+30	−6	−8	3.09
Left periamygdaloid cortex	−28	+3	−14	3.84
Left parahippocampal gyrus (28)	−26	−12	−15	3.56
Cerebellum	+8	−59	−7	3.39
Right parahippocampal gyrus (36)	+22	−34	−10	3.27
Left fusiform gyrus (18/19)	−28	−76	−11	3.12

[a] Values represent the stereotaxic location of voxel maxima with coordinates in Talairach space in millimeters lateral to midline (*x*), anterior/posterior to the anterior commissure (*y*), and superior/inferior to the commissural line (*z*).

[b] BA, Brodmann designation for cortical areas.

[c] Activation sites satisfying ($P < 0.05$) a correction for multiple comparisons. All other sites satisfied a statistical threshold of $P < 0.001$ uncorrected for multiple spatial comparisons.

cingulate cortex, and superior, middle, medial, and inferior frontal cortex compared to the judgment of orientation of static neutral expressions (Fig. 2b; Table 2). An analysis of conjunction between these two contrasts revealed conjoint activations for many of the medial, superior, middle, and inferior frontal sites (Table 2). The direct contrast of images acquired during anger recognition in dynamic versus static expressions was associated with activations in the right occipital–temporal junction corresponding to area V5 and in the periamygdaloid cortex, parahippocampal gyrus, STS, and cerebellum (Fig. 3a; Table 2).

Compared to the spatial orientation judgment of dynamic neutral expressions, intensity judgment of happiness in dynamic expressions was associated with bilateral activations in the cuneus; the middle, medial, and superior frontal cortex; and superior and middle temporal gyri (Fig. 2c; Table 3). Similar to difference images related to anger perception, intensity judgment of happiness in static displays was associated with activations (relative to orientation judgments for neutral faces) in the bilateral precentral and left postcentral gyri, posterior cingulate cortex, and superior, middle, medial, and inferior frontal cortex (Fig. 2d; Table 3). The analysis of conjunction between these two contrasts indicated common activations for many of the medial, superior, middle, and inferior frontal sites, as well as the posterior cingulate and precentral gyrus sites (Table 3). Difference images comparing intensity judgments in dynamic happy versus static happy expressions indicated relative bilateral activations in the area of V5, as well as bilaterally in the cuneus, left lingual gyrus, and brain stem and right middle temporal and medial frontal cortex for dynamic expressions (Fig. 3b; Table 3).

Comparative alterations in rCBF related to the judgment of anger or happiness. Activations related to the emotion-specific processing of facial expressions (Adolphs *et al.*, 1994, 1999; Morris *et al.*, 1996; Whalen *et al.*, 2001) were here similarly identified by comparison of PET images related to emotion perception in angry and happy expressions (Table 4). Directly contrasting static displays of angry and happy facial expressions indicated a differential activation of the right caudate/putamen and middle frontal gyrus and the left lingual and middle occipital gyri for anger judgments; judgments of happiness were associated with differential right-lateralized activity in the anterior STS, the right parahippocampal and supramarginal gyri, and the right premotor cortex (Table 4). For dynamic expressions, differential activations in the cerebellum, left inferior temporal and frontal gyri, left parahippocampal gyrus and periamygdaloid cortex, and right STS were noted for anger judgments; judgments of happiness were associated with differential activations in the occipital–temporal cortex and right caudate nucleus. Conjunction analysis indicated that anger, relative to happiness, perception was associated with differential activation of the right amygdala and gyrus rectus, left fusiform gyrus, and cerebellum.

DISCUSSION

Emotional messages are conveyed in complex action patterns involving head and body movement, eye gaze, and facial expressions. Rapid and accurate decoding of these messages of intent is essential to effective social cognition. Personal experience and a large experimental literature show that we can readily recognize emotions in static photographic images of faces and even from their minimal configural features (Ekman, 1982; Aronoff *et al.*, 1992; Wright *et al.*, 2002). So what, if any, additional information does dynamic expressive motion of the face and head impart to such messages? It is increasingly recognized that the human brain possesses neural mechanisms specialized for the analysis of meaningful motion conveyed by body action patterns (Grossman *et al.*, 2000). The biological motion of the face and head encodes information related to identity and gender (Hill and Johnston, 2001) and aids emotion identification (Lemay *et al.*, 1995; Wehrle *et al.*, 2000). Studies of the effects of brain damage and psychopathology suggest that emotions encoded by static and dynamic facial displays are decoded by separate neural substrates. The possibility therefore exists that subtle differences in the social information encoded by dynamic and static expressions may be associated with larger differences in the neural and mental strategies involved in decoding these expressions. The emerging functional anatomy of emotion perception in facial expressions has been defined almost exclusively by the study of static stimuli, with the attendant assumption that such displays are ecologically valid in that they convey the emotion message by implied action patterns. This study sought to determine whether the neural events involved in decoding expressions of emotion are indeed similarly sensitive to actual and implied action patterns.

Comparative Neural Activations Related to the Perception of Emotion in Static and Dynamic Expressions

Angry facial expressions powerfully modulate social interactions. When corrected for activations related to the processing of face and head motion, explicit judgments of intensity of anger in expressions incorporating dynamic face and head movement activated widely distributed frontal cortical areas and the cerebellum. Similar judgments in static displays by the same posers revealed anger-related activations in motor and extrastriate cortex and in a distribution of both shared and distinct frontal areas. A conjunction analysis confirmed that the recognition of anger in dynamic and static expressions activated a common network of neocortical sites in the medial, superior, middle, and inferior frontal cortex. The intent of this analysis of conjoint activations was to identify the neural correlates of anger recognition irrespective of the dynamics of its expression. As these frontal activations were also identified by an analysis of conjunction related to the recognition of happiness in static and dynamic expressions (Table 3), they would appear to be related to another property of the task other than specific emotion recognition, such as selective attention. Middle and superior frontal cortex mediates attentional influences on visual processing in extrastriate cortex (Chawla *et al.*, 1999; Barceló *et al.*, 2000). These conjoint frontal activations may thus relate to a putative mechanism for visual attention (Desimone and Duncan, 1995; Miller, 1999) by acting to hold the mental representation of emotions in working memory to guide the top-down selection of facial and body features encoding an emotion. Other explanations, such as mental state interpretation, may however underlie these conjoint activations.

Uncommon activations related to the judgment of anger in static and dynamic expressions suggest that their perception is associated with separable neural correlates. A limitation of

TABLE 3

Sites of Neural Activation Related to the Judgment of Happiness in Static and Dynamic Expressions

	Stereotaxic coordinates[a]			
Brain area (BA)[b]	x	y	z	Voxel T
Static happy-static neutral expressions				
Left precentral gyrus (4)	−30	−13	+50	4.90
Right precentral gyrus (6)	+61	−8	+41	3.65
Left superior frontal gyrus (6)	−8	+20	+58	4.50
Right medial frontal gyrus (32)	+6	+8	+44	3.23
Left medial frontal gyrus (10)	−22	+47	+12	4.14
Posterior cingulate gyrus (23)	+0	−20	+21	4.13
Left middle frontal gyrus (8)	−30	+29	+43	3.96
Left inferior frontal gyrus (45)	−51	+31	+0	3.86
Paracentral lobule (4)	+0	−36	+64	3.64
Right medial frontal gyrus (6)	+8	−12	+69	3.44
Left superior parietal cortex (7)	−22	−57	+62	3.59
Left postcentral gyrus (1/2)	−36	−36	+55	3.27
Dynamic happy-dynamic neutral expressions				
Right cuneus (17)	+12	−99	−2	4.79
Right cuneus (18)	+20	−69	+16	3.24
Left cuneus (17)	−14	−97	+9	3.52
Right middle frontal gyrus (9)	+44	+29	+28	4.30
Right inferior frontal gyrus (10)	+44	+43	+0	3.29
Right superior temporal gyrus (22)	+44	−33	+7	4.19
Right medial frontal gyrus (6)	+10	−22	+60	4.09
Left superior frontal gyrus (6)	−12	+21	+62	3.65
Left medial frontal gyrus (10)	−20	+47	+11	3.57
Right superior frontal gyrus (8)	+16	+28	+48	3.51
Anterior cingulate gyrus (32)	+6	+6	+36	3.10
Left middle temporal gyrus (21,22)	−44	−37	+2	3.50
Left medial frontal gyrus (6)	−6	−1	+61	3.36
Conjunction [(DA − DN) and (SH − SN)]				
Left superior frontal gyrus (6)[c]	−12	+20	+60	3.52
Left medial frontal gyrus (8)[c]	−22	+47	+11	3.50
Posterior cingulate gyrus (23)	+2	−22	+25	3.15
Right middle frontal gyrus (9)	+40	+23	+39	2.98
Right medial frontal gyrus (6)	+6	−22	+67	2.96
Right superior frontal gyrus (8)	+16	+26	+45	2.64
Left precentral gyrus (4)	−28	−11	+43	2.69
Left inferior frontal gyrus (45/47)	−55	−23	−3	2.66
Left superior frontal gyrus (6)	−6	−4	−67	2.61
Dynamic happy-static happy expressions				
Right cuneus (17)[c]	+12	−95	+0	5.13
Left cuneus (17)	−22	−95	+3	4.05
Right middle occipital gyrus (19), V5	+51	−68	+7	3.84
Left middle occipital gyrus (19), V	−50	−75	+6	3.58
Left lingual gyrus (18)	−14	−88	−1	3.92
Left brain stem	−8	−24	−4	3.67
Right middle temporal gyrus (38)	+36	+2	−42	3.52
Right medial frontal gyrus (6)	+8	−20	+60	3.23

[a] Values represent the stereotaxic location of voxel maxima with coordinates in Talairach space in millimeters lateral to midline (x), anterior/posterior to the anterior commissure (y), and superior/inferior to the commissural line (z).

[b] BA, Brodmann designation for cortical areas.

[c] Activation sites satisfying ($P < 0.05$) a correction for multiple comparisons. All other sites satisfied a statistical threshold of $P < 0.001$ uncorrected for multiple spatial comparisons.

TABLE 4

Sites of Differential Neural Activation Associated with the Judgment of Emotion in Angry and Happy Expressions

Brain area (BA)[b]	Stereotaxic coordinates[a] x	y	z	Voxel T
Static angry > static happy expressions				
Right caudate/putamen	+14	+2	+11	3.80
Right middle frontal gyrus (10)	+32	+54	−9	3.24
Left middle occipital gyrus (18)	−22	−95	+5	3.21
Left lingual gyrus (17)	−16	−81	+4	3.08
Right middle frontal gyrus (9)	+26	+21	+28	3.13
Right middle temporal gyrus (39)	+48	−63	+23	3.10
Dynamic angry > dynamic happy expressions				
Cerebellum	+4	−59	−19	4.38
Left inferior temporal gyrus (20)	−46	−9	−31	4.12
Left parahippocampal gyrus (28)	−26	−11	−16	3.88
Left periamygdaloid cortex	−30	+1	−15	3.81
Left inferior frontal gyrus (47)	−34	+17	−13	3.34
Right superior temporal sulcus (22)	+65	−58	+12	3.70
Right superior temporal gyrus (38)	+42	+12	−22	3.46
Right periamygdaloid cortex	+26	+3	−10	3.19
Left fusiform gyrus (20)	−42	−34	−18	3.13
Static happy > static angry expressions				
Right middle temporal gyrus (21)	+48	−8	−10	3.85
Left superior temporal gyrus (22)	−50	−10	+2	3.51
Right middle temporal gyrus (21)	+51	−29	−7	3.39
Right parahippocampal gyrus (35)	+20	−34	−10	3.23
Right supramarginal gyrus (40)	+59	−49	+23	3.15
Right precentral gyrus (6)	+61	−8	−10	3.12
Dynamic happy > dynamic angry expressions				
Right lingual gyrus (17)[c]	+10	−95	−4	5.61
Left lingual gyrus (17)	−12	−90	−6	3.33
Left cuneus (18)	−14	−93	+8	3.31
Right middle occipital gyrus (19)	+28	−92	+18	3.22
Right supramarginal gyrus (40)	+38	−51	+34	3.09
Right caudate	+14	+1	+15	3.01

[a] Values represent the stereotaxic location of voxel maxima with coordinates in Talairach space in millimeters lateral to midline (x), anterior/posterior to the anterior commissure (y), and superior/inferior to the commissural line (z).

[b] BA, Brodmann designation for cortical areas.

[c] Activation sites satisfying ($P < 0.05$) a correction for multiple comparisons. All other sites satisfied a statistical threshold of $P < 0.001$ uncorrected for multiple spatial comparisons.

these pairwise contrasts to emotionally neutral expressions is that the difference image also reflects differences in the explicitly processed stimulus feature (i.e., emotion intensity versus spatial orientation) for the two compared conditions. A direct comparison of dynamic and static stimuli sought to control for task effects and define further the effects of expression dynamics on the neural correlates of anger perception. Compared to static displays, the perception of anger in dynamic expressions was associated with prominent activations in brain regions specialized for the visual processing of coherent stimulus motion (V5; Zeki *et al.*, 1991; Watson *et al.*, 1993; Tootell and Taylor, 1995; Rees *et al.*, 2000) and facial and body actions related to social signaling (STS; Puce *et al.*, 1998; Allison *et al.*, 2000). The differential activation of the STS associated with dynamic versus static expressions of anger is not consistent with the contention (Allison *et al.*, 2000) that this region is similarly sensitive to actual and implied biological motion when supporting social perceptions. Alternatively, differential STS activation may result from a greater ability of dynamic expressions to signal the intentions of the viewed subjects, as the STS is sensitive to stimuli that signal intentions (Gallagher *et al.*, 2000). The explicit spatial processing of moving, emotionally neutral faces versus nonfacial objects was also associated with activation of regions (amygdala, STS, Broca's area, extrastriate cortex; Table 1) consistent with the perception of biological motion in social stimuli (Bonda *et al.*, 1996; Kawashima *et al.*, 1999; Allison *et al.*, 2000). Thus, these activations do not appear to be specifically related to perceptions of emotion, but rather contribute to more general aspects of the processing of dynamic social signals.

Activations in periamygdaloid and perihippocampal cortex during anger perception in dynamic versus static expressions suggest their involvement in decoding anger messages encoded in complex face and body movements. The persistence of these medial temporal activations when the dynamic anger condition was also compared to dynamic happy expressions (Table 4) suggests that these activations are related to anger recognition in dynamic expressions and are not attributable to idiosyncratic features of the control tasks (e.g., spatial processing of static stimuli). Furthermore, differential medial temporal lobe activations were not observed for judgments of happiness in dynamic expressions irrespective of the contrasted control condition. Why then are they not observed in contrasts of dynamic anger perceptions to dynamic neutral face processing tasks (Table 2)? Perhaps neutral expressions are themselves associated with medial temporal lobe activations, a contention consistent with the observed activation of the right amygdala when the dynamic neutral face and nonfacial object conditions were contrasted (Table 1). This amygdala activation associated with neutral expressions may relate to their ambiguity (Whalen, 1998), the implicit processing of emotion (Critchley *et al.*, 2000a), or gaze direction (Kawashima *et al.*, 1999).

A Role for Implicit Mental Imagery in the Perception of Emotion in Static Expressions?

Differences in activation sites related to emotion perception in static and dynamic expressions implicate different mental strategies in solving the emotion conveyed by static and dynamic expressions. Interestingly, the judgment of emotion content in both angry and happy static expressions was associated with activation (relative to neutral expressions) of the motor and premotor cortex (Tables 2 and 3). The sensory decoding of emotion and intent in others may be dependent on the same neural activations involved in motor encoding the same emotion. Such a link between the sensory and motor systems in elaborating a motor theory for the perception of human actions has been proposed (Decety and Grèzes, 1999). We suggest that static images of facial expressions represent degraded social stimuli and that their decoding for emotion content is accomplished by the covert motor simulation of the expression prior to attempts to match the static percept to its dynamic mental representation. If so, then the neural correlates of emotion perception should share a localization of neural activations with those related to implicit motor imagery, which refers to a dynamic state in which a motor act is subconsciously simulated within working memory without any overt motor output (Decety and Grèzes, 1999). This motor knowledge may provide the interpretive rules for recognizing biological motion and anticipating future sequences of action (Jeannerod and Decety, 1995; Jeannerod and Frak, 1999). The distributed neural substrates of motor imagery have been shown to include the primary and premotor cortex, supplementary motor area, Broca's area, prefrontal cortex, parietal cortex, cingulate gyrus, and basal ganglia (Bonda *et al.*, 1995; Parsons *et al.*, 1995; Cohen *et al.*, 1996; Lotze *et al.*, 1999; Gerardin *et al.*, 2000; Binkofski *et al.*, 2000). Relative to the visuospatial processing of emotionally neutral faces, the judgment of emotion intensity in both angry and happy static facial expressions was similarly associated with activations in the primary motor and premotor cortices, prefrontal cortex (BA 44/45, 8, 9,10), posterior cingulate cortex, and superior parietal cortex; these activations were not observed when static angry and happy expressions were directly compared (Table 4). Significant, although weaker, activations in the left primary sensory cortex (BA 1,2) suggest that decoding angry and happy signals in static images may involve the internal generation of a somatosensory (Adolphs *et al.*, 2000; Adolphs, 2002), as well as motor, representation of the emotional state. The results of this study suggest that the decoding of emotion messages in static, but not dynamic, expressions is solved by the activation of a network of brain regions that link by covert simulation the static percept to the mental representation of the emotion. Emotion perception in dynamic expressions apparently involves a lesser reliance on motor simulation. Electromyographic evidence of facial mimicry of facial expressions of emotion by others (Dimberg *et al.*, 2000) is consistent with a motor simulation mechanism.

Distinct Neural Correlates for Judgment of Emotion in Angry and Happy Expressions

The possibility that perception of different emotions are subserved by separate neural correlates has been the subject of much recent neuroscience research. Angry and happy facial expressions are thought to be recognized by separate neural correlates (Blair *et al.*, 1999; Phillips *et al.*, 1999; Whalen *et al.*, 2001). Activations related to the emotion-specific processing of dynamic social signals were similarly identified by direct comparison of PET images related to emotion perception in angry and happy expressions. Relative to the judgment of happiness, anger judgments were associated with differential activations in areas related to object recognition (inferior temporal gyrus), face processing (fusiform gyrus; Gauthier *et al.*, 1999; Kanwisher *et al.*, 1997), social signaling (STS; Allison *et al.*, 2000), assessing the incentive value of a stimulus (inferior frontal cortex; Rolls, 2000; Berns *et al.*, 2001), and assessing threat or danger (periamygdaloid cortex; Adolphs *et al.*, 1999). A conjunction analysis revealed the conjoint activation of the right amygdala and left fusiform gyrus for judgments related to angry versus happy expressions. The differential amygdala activation may reflect the composite effect of the relatively small amygdala activation (Whalen *et al.*, 2001) and deactivation (Calder *et al.*, 2001) associated with anger and happiness perceptions, respectively. The differential left fusiform activation may reflect a greater social expertise or familiarity (Gauthier *et al.*, 1999) with angry versus happy expressions (Whalen, 1998). When contrasted to angry expressions, judgments of happiness were associated with a differential activation of extrastriate areas and the caudate nucleus, suggesting that the recognition of happiness is subserved by neural mechanisms at early stages of visual processing. These comparisons further support the involvement of sepa-

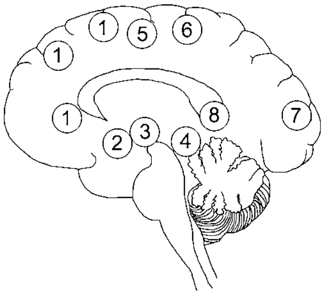

FIG. 4. Schematic model of a functional neuroanatomy related to decoding emotional messages in facial and body expressions. Numbers refer to activation sites subserving subcomponent processes related to emotion processing (see text).

rate neural pathways in decoding the emotion messages encoded in angry and happy expressions.

Significance and Limitations of This Study

A rapidly growing neuroscience literature has generated a draft version of a functional anatomy of emotion perception in static facial expressions. The findings of this study, integrated with those of prior studies, suggest further additions to this draft of the functional anatomy of social perception related to decoding emotion signals in facial and body expressions (Fig. 4). Selective attention to the recognition of emotional expressions in either static or dynamic displays activates a distributed frontal cortical network (Fig. 4, circle 1) that optimizes their detection by extrastriate mechanisms. The STS (Fig. 4, circle 8) activations support the integration of visual information related to the specialized biological motion that encodes dynamic expressions of emotion. As the perception of anger or happiness in static expressions was associated with the activation of regions implicated in implicit motor imagery (Fig. 4, circle 5), we propose that solving the emotion conveyed in such displays involves the performance of imagined spatial transformations of one's egocentric or object-based perspective, a strategy used in solving other spatial reasoning problems (Zacks *et al.*, 1999). Activations in the postcentral gyrus (Fig. 4, circle 6) may additionally support the judgment of emotion in static displays by providing a somatosensory referent for the emotion. Some evidence was also generated in support of emotion-specific neural correlates of perception. Dynamic expressions of anger, but not happiness, appear to be solved for emotion content by a neural pathway involving the periamygdaloid cortex (Fig. 4, circle 2), while dynamic expressions of happiness appear however to be solved by divergent neural processes beyond area V5 and largely subserved by extrastriate cortical mechanisms (Fig. 4, circle 7). The right amygdala (Fig. 4, circle 3) may serve roles related to the detection of an ambiguity of intentions conveyed by neutral facial expressions, and in differentiating angry and happy emotional expressions. Finally, the left fusiform gyrus (Fig. 4, circle 4) may be involved in detecting emotions associated with greater social familiarity or expertise (e.g., anger).

Limitations of this study prelude a definitive comparison and characterization of the influence of expression dynamics on the neural correlates of emotion perception. First, these findings are relevant only to perceptions based on selective attention to expressive stimuli. The neural representations of perception for incidentally or implicitly processed expressions apparently differ from those related to explicitly processed expressions (Critchley *et al.*, 2000b; Gorno-Tempini *et al.*, 2001). Second, the concern for behavioral adaptation and neural habituation to repeated emotional stimulus presentations (Breiter *et al.*, 1996; Whalen, 1998) precluded multiple presentations of stimuli and thus weakened the statistical power of the study. The longer integration time, relative to fMRI studies, for defining functional signals in this PET study may have also introduced type II error related to signal habituation.

While these collective findings do not yield a definitive picture, they do provide evidence for neural pathways dedicated to the analysis of emotions and their conveyed intentions in the nearly constant motion of the face and body used in social interactions. Importantly, static displays of emotional expressions commonly used in empirical studies of social signal perception do not appear to be substrates for these pathways. The ability to make accurate assessments of emotion messages in static displays speaks to the immense social, and perhaps evolutionary, salience of such expressions; however, diminished ability to judge static displays may result from generalized deficits that impair implicit mental imagery rather than specific emotion-processing deficits. A conclusion from this work is that the predominant use of static facial expressions of emotion as stimuli to characterize the effects of brain damage or psychiatric or neurologic disorders on social signal perception (see Archer *et al.*, 1992; Borod *et al.*, 1993; Kerr and Neale, 1993) should be reevaluated with more ecologically relevant dynamic expressions.

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