The emotion–action link? Naturalistic emotional stimuli preferentially activate the human dorsal visual stream

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A B S T R A C T
A large body of brain imaging research highlights a set of specific regions in the limbic, insular and prefrontal cortex as sensitive to static visual images of high emotional content. Here we report that when using more naturalistic stimuli (short audio–visual video clips) the most selective cortical loci demonstrating preferential activation to emotional content were centered on the dorsal, action related, stream of visual areas. Subjects underwent fMRI scanning while watching a set of highly emotional as well as neutral video clips. Following the scan, clips were rated by each subject for emotional arousal and valence. Surprisingly, activity in dorsal stream visual areas (such as IPS and SPL) showed the highest preference to emotional arousal compared to all other brain areas. In contrast, ventral stream visual areas showed a significantly weaker emotional preference. Control experiments ruled out low level visual or auditory cues as contributing factors to this effect. Furthermore, the specific spatial pattern of emotion-related activations was incompatible with general arousal or attentional effects. Given the established role of dorsal stream visual areas in action-related functions, these results support the long held hypothesis associating emotion with preparation for action.

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Introduction

Emotional events constitute one of the most significant components of human mental life. A major effort in brain imaging research focuses on understanding the neuronal basis of emotional processing in the human brain. A large body of brain imaging research has identified specific cortical regions, as preferentially related to emotional processing. The most consistent network of cortical brain areas that has been associating emotion with preparation for action.

The emotion–action coupling also has some evidence in the neuroimaging literature, for instance some of the functional networks that were shown to be involved in processing of emotional stimuli (including medial temporal lobe, anterior cingulate cortex, medial orbitofrontal cortex, preSMA and insula) (Kober et al., 2008; Lindquist and Barrett, 2012) appear to also have a motor-related function.

Similarly, emotional processing has been linked to the mirror neuron system in human and primates, which has an important role in action understanding and imitation (Rizzolatti and Craighero, 2004). Imaging studies have shown an activation of the mirror neuron system — right

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superior parietal lobule (SPL) and left inferior frontal gyrus (IFG) (Iacoboni et al., 1999), in emotion recognition and more strongly in emotion imitation (Carr et al., 2003; Dapretto et al., 2005; Gallese, 2001; Leslie et al., 2004).

However, to date, the main body of brain imaging research of emotion-related responses relied on static and highly controlled stimuli such as pictures of emotional faces (Ekman, 1992, 1999) or emotional images (Lang et al., 1997a). In such paradigms, images are typically presented briefly, using a single sensory modality and subjects are often asked to assess the emotional content of the images. Clearly, the emotional effects of such static stimuli are very different from naturally induced emotional experiences. Thus, a more ecological approach to the study of the action–emotion link could rely on naturalistic and dynamic sensory stimulation conditions.

Films and movie clips present an appealing alternative to static presentations; due to their vividness, narrative and context such naturalistic stimuli may better reflect the nature of emotional experience in real life. Furthermore, movies are known to elicit emotions with greater intensity than still images (Gross and Levenson, 1995). There is indeed a primary visual cortex and high order areas in occipito-temporal and temporal regions of the brain known for their involvement in emotional processing such as amygdala, thalamus and medial PFC, as well as dorsolateral PFC, inferior frontal gyrus (IFG) midbrain and lateral cerebellum. Adding musical compositions of different valences (fear or joy), to neutral movie clips resulted in increased activity in the amygdala, hippocampus, and lateral prefrontal regions, pointing to the enhanced emotional impact of multi-sensory stimuli (Eldar et al., 2007).

A recently introduced approach used movie episodes to examine the dynamics of network coherence while watching sadness-inducing movies (Raz et al., 2012).

With regards to visual areas these studies showed preferential activation to emotional movie scenes throughout the visual system including primary visual cortex and high order areas in occipito-temporal and parietal lobes (Davidson et al., 1990; Eldar et al., 2007; Goldin et al., 2005; J skel inen et al., 2008; Paradiso et al., 1997; Raz et al., 2012; Reiman et al., 1997). Commonly these studies used very short movie scenes and omitted their sound. These studies revealed enhanced activation of emotional compared to neutral video clips in brain regions well known for their involvement in emotional processing such as amygdala, thalamus and medial PFC, as well as dorsolateral PFC, inferior frontal gyrus (IFG) midbrain and lateral cerebellum. Adding musical compositions of different valences (fear or joy), to neutral movie clips resulted in increased activity in the amygdala, hippocampus, and lateral prefrontal regions, pointing to the enhanced emotional impact of multi-sensory stimuli (Eldar et al., 2007).

Materials and methods

Subjects

Sixteen healthy, right handed subjects (ages 23–30 years, 11 females), have participated in the experiment. Subjects gave written informed consent for their participation. All procedures were approved by the local ethics committee.

Task and stimuli

Scenes from 12 commercial films were chosen: ‘Champ’, ‘ET. The extra terrestrial’, ‘Forgetting Sara Marshall’, ‘Leon the professional’, ‘Love actually’, ‘Milk’, ‘Never ending story’, ‘Sophie’s choice’, ‘taxi driver’, ‘The good girl’, ‘There’s only one Jimmy Grindle’, and ‘When Harry met Sally’. An important consideration in choosing the scenes was including human characters in all the scenes while having a set of clips that varied in their emotional valence and arousal. The scenes were then edited by a professional editor into short, equalized in sound volumes, 14 sec clips, trying to condense the emotional essence of the scene into this short timeframe.

A day before the scan, subjects watched the complete scenes (3 min on average) from the commercial films. This was performed in order to equalize movie familiarity and to introduce subjects with the narrative and emotional context of the stimuli, as it has been shown previously that scene context has a meaningful effect on brain activity (Eldar et al., 2007; Hasson et al., 2008; J skel inen et al., 2008). In addition familiarity was quantified and compared statistically between emotional and neutral movie groups.

A one hour long fMRI scan was conducted, starting with audio–visual noise (random patterns and tones changing rapidly), to reduce scan novelty effects, followed by an initial rest period and a sequence of the short clips (14 s), in randomized order, separated by rest periods (12 s-fixation screen). Each movie clip was presented once or twice. In addition, three control experiments were conducted (Fig. 1). The subjects were instructed to watch the clips passively but attentively, and during the blank trials to focus on the fixation point, and not to think of anything specific (in particular not about the movie clips). To assess whether subjects were affected by the movie during the rest periods — the rest periods were categorized according to the content of the preceding movie clip. Thus, rest periods were defined as predictors in a separated GLM analysis (i.e. Rest following emotional vs. Rest following neutral movies).

Following the scan the subjects received a printed image of one frame from each movie as a reminder, and completed a questionnaire regarding their emotional experience while watching the movies during the scan (to avoid possible contextual artifacts as a result of editing and reducing the scenes to 14 s). Each movie was rated for valence and arousal level. Emotional arousal was rated on a 1 to 5 scale (reflecting low to high arousal respectively). Emotional valence was rated (on a 1–5 scale) both on a positive scale (“How happy was the movie?”), and on a negative scale (“How sad was the movie?”). In addition to the emotional arousal level, subjects were asked to identify the dominant distinct emotion experienced during the movie clips. Three out of the 16 subjects rated the movies for valence and arousal during the scan, following each movie. This sample group, which has participated in a more active version of the experiment, showed similar brain activity pattern as the main experimental group.

To control for low level perceptual effects, several control experiments were conducted:

Control for low level visual differences: the movies were rotated by 180° (inverted upside down), and presented without their...
associated sound tracks, to eliminate the semantic content without changing the basic visual features of the movies.

Control for audio–visual interaction: in order to isolate the audio and visual effects, two control experiments were conducted in order to examine each modality separately. In order to reduce potential imagery effects of the missing modality (sound or visual), a “surrogate” sound or video was added. In the visual–only control, a neutral audio sound-track (by St. Germain) was added. In the audio–only control, the original audio sound-track was played in conjunction with a neutral video (fish aquarium). Four segments of aquarium videos as well as four neutral music segments were randomly presented.

Fifteen subjects participated in a dynamic visual localizer task, in order to map different components of the visual system. The localizer was composed of short (9 s) video clips of human faces, buildings, patterns and human actions performed on objects, separated by rest periods (9 second-fixation screen). Subjects were required to watch the clips attentively, and to imagine personally performing the observed action while watching the object clips. Previous research (Hasson et al., 2004) has demonstrated that these video categories effectively delineate both early visual cortex as well as high order category-selective visual areas.

Imaging setup

The scan was acquired on a 3 Tesla Trio Magnetom Siemens scanner, at the Weizmann Institute of Science, Rehovot, Israel. Functional images of blood oxygenation level dependent (BOLD) contrast comprising of 35 axial slices were obtained with a T2*-weighted gradient echo planar imaging (EPI) sequence (TR = 2000 ms, TE = 30, flip angle = 90°, FOV 240 mm, matrix size 80 × 80, no gap 3 × 3 × 4 mm voxel, ACPC) covering the whole brain. Anatomical images for each subject were acquired in order to incorporate the functional data into the 3D Talairach space (Talairach and Tournoux, 1988) using 3-D T1-weighted images with high resolution (1 × 1 × 1 mm voxel, MPRAGE sequence, TR = 2300 ms, TE = 2.98 ms).

Data analysis

Behavioral data. Both individual ratings used for parametric GLM analysis, and group ratings for non parametric GLM analysis, were obtained as follows: The rating for emotional arousal on a 1 to 5 scale (reflecting low to high arousal respectively) was averaged across all subjects, per movie clip. The valence rating consisted of two values (positive and negative scales), and was calculated for each subject as the difference between positive scale (1 to 5) and negative scale (−1 to −5). Finally the valence ratings were averaged across all subjects, per movie clip.

In addition, subjects specified the dominant distinct emotion experienced during the movie clips. In order to characterize better the type of emotional experiences elicited by the movie clips, and the dominance of specific emotions throughout the experiment, the frequency of distinct reported emotions was calculated per subject (for example – subject xx reported feeling sadness in 3 out of 12 movies), and the average frequency was calculated across subjects.

Brain imaging data. fMRI data was analyzed using Brain Voyager software package (Brain Innovation, Maastricht, The Netherlands), and Matlab software (MathWorks, Natick, MA). Behavioral data was analyzed using Microsoft Office Excel 2007.

Anatomic data. The cortical surface was reconstructed for each subject from the 3D-spoiled gradient echo scan, in a Talairach coordinate system (Talairach and Tournoux, 1988).

Functional data. The first 10 images of each functional scan were discarded. Functional scans preprocessing included 3D motion correction and filtering out of low frequencies up to 2 cycles per scan (slow drift), and spatial smoothing using a Gaussian filter of 6 mm. The functional images were superimposed on 2D anatomic images and incorporated into the 3D data sets through trilinear interpolation.

Statistical analysis was based on the general linear model (GLM) (Friston et al., 1995), in which all stimuli conditions were defined as positive predictors, and convolved with the hemodynamic response function (HRF). Since the hemodynamic response of movie clips was robust and sustained, and in order to avoid carry-over effects, the baseline was defined as the second half (6 last seconds) of the rest periods interspersed between the movie clips. A multi-subject, random effect, parametric model analysis was conducted, in which each movie clip presentation for each subject received a weight, according to each subject’s arousal rating. Thus the proportional arousal weight of each movie was considered in the model, and represented as differential amplitude of the BOLD signal.

In addition to the parametric model, a binominal GLM analysis was conducted as well; three predictors were defined according to the averaged arousal rating: highly emotional (Emotional) clips, Slightly Emotional clips, and Neutral clips. Beta coefficients were calculated for the regressors, and a Student’s t test was performed. Multi-subject analysis was based on a random-effect GLM.
Multi-subject contrast maps (Emotional vs. Neutral — Fig. 7a, Emotional/Neutral > rest — Fig. 4) were projected on an unfolded or inflated Talairach-normalized brain. Significance levels were calculated, taking into account the minimum cluster size and the probability threshold of a false detection of any given cluster. This was accomplished by a Monte Carlo simulation (cluster-level statistical threshold estimator in “Brain Voyager” software), using the combination of individual voxel probability threshold and minimum cluster size; the probability of a false positive detection per image was determined from the frequency count of cluster sizes within the entire cortical surface.

An identical multi-subject, random effect, nonparametric GLM analysis was conducted for each control experiment. Multi-subject contrast maps of Emotional vs. Neutral movie clips are presented in Figs. 7a–d.

ROI definition and analysis

Four bilateral regions of interest (ROIs) were defined according to the visual localizer, in order to keep the measurements independent of the ROI definition. ROIs were defined as the activated voxels located within 30 mm of the multi subject activity center, \( p < 0.05 \) corrected.

Parahippocampal place area (PPA) was defined using the contrast buildings > faces, Fusiform face area (FFA) was defined using the contrast Faces > Buildings, Superior parietal lobule (SPL), and inferior parietal sulcus (IPS) were defined according to object (actions) > rest contrast.

ROI’s averaged beta weight (across voxels) was calculated per subject, for each predictor. Two-tailed paired t test (within subjects) was then conducted between Emotional and Neutral beta weights. FDR correction for multiple comparison was done according to Bonferroni method (\( \alpha = 0.01 \)).

Emotional index was calculated as follows: the difference between Emotional and Neutral activity (per ROI and individual subject), normalized by the group’s mean emotional activity, of that particular ROI [individual (E – N) / group (E)]. Index values for each subject were classified and averaged as Dorsal (SPL and IPS) or Ventral (FFA and PPA) emotional index. Finally a two-tailed paired t test (within subjects) was conducted, comparing emotional indexes of Dorsal vs. Ventral streams.

Laterality index was calculated in a similar fashion, only this time ROIs were grouped by hemisphere (right or left). A two-tailed paired t test was conducted, comparing emotional indexes of Left vs. Right hemispheres.

Percent signal change (normalization compared to baseline) of Emotional as well as Neutral movie clips was calculated for each ROI.

Finally, a right frontal eye field (FEF) ROI was defined according to previous work analyzing eye movements (Ramot et al., 2011). Paired t test was calculated between the Emotional and Neutral mean percent signal change during the movie clips.

Results

Behavioral reports

Following the fMRI scans, subjects were asked to report their emotional responses to each of the movie clips (see Methods for details). Subjects’ average ratings of emotional arousal across all movies on a 1–5 scale was 2.89 (n = 16, SEM = 0.33). For further analysis, movie clips were subdivided into 3 categories according to emotional arousal level, averaged across subjects; highly emotional (Emotional) clips, Slightly Emotional clips, and Neutral clips. These categories were defined as follows: The clips which were more than one SEM beneath the averaged emotional rating were considered as ‘Neutral’ (4 movies clips). In the same way, and in order to equalize group sizes, the four most highly rated movie clips (all exceeded one SEM above averaged rating), were considered as ‘Emotional’ (Fig. 2a). In addition to the emotional arousal level subjects reported the dominant emotions they experienced during each movie clip. The frequency of distinct emotional experiences (in percentages) was calculated per subject and averaged across subjects.

Analysis of reports of dominant emotions showed (Fig. 2b) that the most prevalent emotions (emotion frequency throughout the experiment, averaged across subjects) were sadness (18% of emotions reported, \( SEM = 0.02 \)), boredom (16%, \( SEM = 0.02 \)), and compassion (13%, \( SEM = 0.03 \)).

Familiarity (percentage of subjects that saw the full movies before the experiment) was not statistically different between ‘Emotional’ and ‘Neutral’ groups (t(6) = −0.645, p = 0.54).

Brain imaging

In order to reveal cortical regions that were preferentially associated with the emotional content of the stimuli, three methods were used based on the emotional arousal reports; the first was individual-parametric modeling, based on the reported emotional arousal (scale 1–5) (see Methods). The second approach was a more conventional group GLM analysis in which the fMRI activation to the Emotional and Neutral movies clips (see Fig. 2a for movie classification) was analyzed.
separately. Finally, we conducted a direct contrast of Emotional vs. Neutral movie clips. Figs. 4 and 5 depict the results of the first two approaches respectively, while Fig. 7a depicts the third.

When separately inspecting the maps of the Emotional and Neutral movies vs. rest baseline — two differences in the activity maps become apparent: First, in the Emotional vs. Rest map, there was positive activation of parietal cortex during the Emotional condition but not during the Neutral (see Fig. 4, marked dorsal ROIs: SPL and IPS). Second, in the Emotional > Rest contrast there was less deactivation of frontal regions compared to the Neutral > Rest contrast (Fig. 4).

The corresponding parametric analysis (see Methods), revealed cortical regions whose activity correlated with the emotional–arousal reports (Fig. 5). As can be seen, both the emotional–arousal parametric map (Fig. 5), as well as the direct contrast Emotional > Neutral (Fig. 7a), indicate that the most prominent regions manifesting preferential Emotional Activation Effect (EAE) were co-localized with intermediate and dorsal stream visual areas, while core regions of ventral stream representations such as the Fusiform face area (FFA) and Parahippocampal place areas (PPA), failed to show a significant EAE (Fig. 5). Brain regions showing positive parametric EAE included dorsal stream visual areas: superior parietal lobe (SPL), intra-parietal sulcus (IPS), and right temporoparietal junction (TPJ). Other cortical regions showing significant emotional enhancement included intermediate high order visual areas including the lateral occipital sulcus (LO), and the middle temporal cortex (MT).

Moreover, some cortical regions such as the cingulate cortex — the anterior (ACC) and posterior cingulate (PCC), and frontal regions such as middle frontal gyrus (MFG) and insular cortex, which were deactivated relative to fixation baseline during neutral clips (Fig. 4), also showed a reduced level of inactivation during the Emotional clips. The opposite effect — i.e. enhanced activation to Neutral clips was exhibited in the superior temporal sulcus (STS), the activity in this region was always above baseline level.

These results were robust and could be evident even at the single subject level (Sup. Fig. 1).

Valence analysis, i.e. comparison between negative and positive emotional activity, showed no significant difference between the two conditions.

In addition, no significant differences were found between rest categories (i.e. Rest following emotional vs. Rest following neutral movies).

In order to quantify the activation in specific high order visual regions, eight ROIs were defined based on the visual localizer (see Methods, Fig. 3). As can be seen (Fig. 5b), the ventral ROIs (bilateral FFA and PPA) did not show a significant difference between Emotional and Neutral activity. On the other hand dorsal ROIs (bilateral IPS and SPL)

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**Fig. 3.** ROI definition according to the dynamic visual localizer. Cortical activity maps of multi subjects (n = 15), random effect, GLM analysis (Monte Carlo corrected p < 0.05), are presented on inflated and unfolded cortex. Color scale indicates t values. (a) Objects (actions) vs. rest activity map presented on an inflated cortex. Yellow-orange scale represents regions which were more activated while watching clips containing manual object manipulations compared to fixation (blue-green scale). (b) Objects (actions) vs. rest activity map presented on an unfolded cortex. Superior parietal lobe (SPL), intra-parietal sulcus (IPS), Lateral occipital sulcus (LO), Fusiform face area (FFA), Parahippocampal place area (PPA), right hemisphere (RH), left hemisphere (LH). (c) Faces vs. buildings activity map presented on an unfolded cortex. Yellow-orange scale represents regions which were more activated while watching face containing clips compared to buildings (blue-green scale).
demonstrated a highly significant difference. To further quantify the EAE—an “emotional index” (per ROI)—was calculated as follows: The difference between mean Emotional and Neutral activity (per subject), divided (normalized) by the group’s mean emotional activity. Comparing the emotional index of Dorsal vs. Ventral stream areas revealed a significantly higher level in the Dorsal stream ($t(15) = 6.902, p < 5 \times 10^{-6}$), again confirming the stream-selectivity of the emotional effect (Fig. 6).

As the dorsal stream is a major player in attention processing (Corbetta et al., 2002), and given the arousing nature of the emotional clips, we examined whether general, bottom-up, stimulus-driven attentional effects (as opposed to emotionally-specific arousal) could account for the cortical activations that we observed. A prominent aspect of the bottom-up attention system is its lateralization to the right hemisphere (Corbetta et al., 2002). Hence, to examine the potential involvement of such generalized attentional effects we conducted a laterality $t$-test (between hemispheres) for each ROI. In addition, a laterality index was calculated (see Methods), comparing the preferential emotional activation between the right and left hemispheres. No significant bias to the right hemisphere in the dorsal stream was found (two tailed, paired $t$ test, $t(15) = 0.8358, p < 0.4164$).

The selective association of the EAE with dorsal stream visual areas raises the possibility that the differential activation was not driven by the emotional aspects of the stimuli per se—but rather by purely visual aspects of the stimuli that may have been differentially present in the Emotional vs. Neutral clips. For example, it could be the case that visual motion was more rapid, or of a larger amplitudes in the Emotional compared to the Neutral movie clips. To examine these potential confounds, we conducted several control experiments. First we compared brain activity of Emotional vs. Neutral movies when the movie clips were rotated upside down, and presented without their associated soundtracks. This control maintained all low level visual features—such as motion, contrast, and spatial frequency, while largely eliminating the emotional effects. This manipulation essentially removed all differences between Emotional and Neutral movies’ activations (Fig. 7b). In order to quantify this result, a two tailed, paired $t$-test (within subjects) between Emotional and Neutral beta values, was conducted for each visual ROI. In the rotated control clips the PPA was the only region to show a significant difference towards the Emotional movies (two tailed, paired $t$ test, $n=12, p < 0.01$, Bonferroni corrected for multiple comparison).

In order to study the impact of the visual and auditory modalities separately and ensure that subjects were not completing the missing modality through imagery processes, the Emotional vs. Neutral groups were compared in movies consisting of one original modality (sound or visual), while the other modality was kept neutral (see Methods). In the “Visual” control (Fig. 7c) the sound was neutral (unrelated music soundtrack, see methods). Similarly in the “Audio” control, the visual clips were neutral (video clips of fish swimming, see methods). The results are depicted in Fig. 7d, bottom panels. As can be seen, in these experiments the EAE was significantly reduced. Thus, in these two controls no significant difference was found in ROI activity between Emotional
Neutral control clips (two-tailed, paired t-test, n (Visual) = 16, n (Audio) = 15, p > 0.5 Bonferroni corrected), as opposed to the experimental clips which showed a clearly biased activity towards dorsal stream ROIs.

For further examination of involvement of attentional and eye-movement related activity (Corbetta and Shulman, 2002; Ramot et al., 2011), we examined differential activity in the frontal eye field (Corbetta and Shulman, 2002; Ramot et al., 2011) (see ROI definition in Methods). No significant difference in FEF activity was found between the Emotional and the Neutral clips (two-tailed paired t-test, p = 0.2392, t(15) = 1.2258).

Discussion

Our study revealed that emotional movie clips preferentially activated, in a robust and consistent manner, a broad range of brain areas, including the visual cortex, limbic cortex, prefrontal cortex, and inferior frontal cortex (Adolphs, 2002; Dalgleish, 2004; Dolan, 2002). In addition,
emotional movies activated the mirror neuron system (superior parietal lobe and opercular region in the inferior pre-central sulcus) more than the neutral movies (Carr et al., 2003; Dapretto et al., 2005; Gallese, 2001; Leslie et al., 2004). These results are in agreement with previous research on emotional processing (Bradley et al., 1988; Hendler et al., 2003; Lane et al., 1997; Murphy et al., 2003; Rauch et al., 1996).

Surprisingly, the regions that showed the highest level of preferential emotional activation were not among the areas well known to be specialized for emotional processing but rather the set of cortical visual areas known as the dorsal stream (Fig. 5). As discussed in the Introduction — the source of this new observation may be attributed to the complex and more naturalistic nature of our stimuli.

The functional specialization in the primate visual system into a dorsal–parietal and a ventral–temporal “stream” (Felleman and Van Essen, 1991; Maunsell and Van Essen, 1983; Ungerleider et al., 1998; Van Essen and Maunsell, 1983) has been a fundamental principle of visual cortex organization. In contrast to the ventral stream, showing specialization for recognition processes (Grill-Spector and Malach, 2004; Ungerleider and Haxby, 1994), extensive research implicated the dorsal stream in spatial aspects of the stimuli and rapid top-down object processing including emotional evaluation (Barrett and Bar, 2009). Importantly, an action-related functional specialization has been suggested to be one of the dorsal stream's core functions (Chao and Martin, 2000; Corbetta and Shulman, 2002; Goodale and Milner, 1992; Goodale et al., 1991; Grill-Spector and Malach, 2004; Mishkin et al., 1983; Shmuelof and Zohary, 2005; Shulman et al., 1997; Ungerleider and Haxby, 1994). Thus, our findings extend previous studies by revealing emotionally-related functional specialization within the visual system — with a preferential link to the dorsal-action related stream.

It could be argued that the enhanced emotional activation of the dorsal stream is due to confounds in the visual stimuli — for example if emotional clips on average contained different low-level visual features — such as faster visual motion, higher contrast, different spatial frequency contents or any of a number of visual dimensions that have been previously shown to preferentially activate the dorsal stream (Corbetta and Shulman, 2002; Corbetta et al., 2002; Culham et al., 2001; Fias et al., 2002; Hesselmann and Malach, 2011; Ungerleider and Haxby, 1994). However, our control experiments, specifically designed to examine these potential confounds, strongly argue against such interpretation.

In our first control, where movie clips were rotated upside down, the content of all low level visual features remained similar to the original clips, specifically image size, magnitude and speed of visual motion, contrast, spatial frequency content, distribution of oriented lines etc. — all remained the same under the rotation manipulation. In this control experiment the preferential activation of the emotional stimuli was eliminated (Fig. 7a compared to 7b), demonstrating that the effect was not a result of low-level visual confounds, but rather the emotional aspects, which were eliminated by rotating the clips.

A second issue that we examined is whether our results could be attributed to differences in high order visual aspects of the stimuli — for example; there may have been a gesture speed and amplitude effect that could be detected in the upright clips but not the inverted ones. However, the significant modulation in brain activation when the auditory stimuli were incongruent with the emotional effect — while the visual stimuli remained identical (see “Visual” 7c), argues against a purely visual source of the preferential dorsal stream activation. These results are compatible with a previous study showing similar emotional audio–visual synergistic effect in the amygdala, PFC, and hippocampus (Eldar et al., 2007).

A third concern was that eye movements may have been different between the emotional and neutral movies. Although we did not track the eye movements during the scan, our results show no difference in frontal eye field (FEF) activity — that has been shown previously to be differentially modulated by eye movements (Birin, 1968; Bruce and Goldberg, 1985; Corbetta et al., 1998; Ramot et al., 2011). Furthermore, different eye movements during the emotional and neutral clips, would have affected retinal motion with direct impact on retinotopic visual cortex activations (Mohler and Wurtz, 1977; Snodderly et al., 2001; Wurtz, 1969). Such retinotopic activations were not found in the present experiments (Fig. 5).

It is well established that activity in visual areas, including the dorsal stream, can be modulated by attentional demands (Corbetta and Shulman, 2002; Corbetta et al., 2002; Culham et al., 2001; Kastner and Ungerleider, 2000; Shulman et al., 1997). Thus, it could be argued that the preferential activations are in fact a general effect of heightened attention. However it has been previously documented that both early visual cortex (Andersen, 1989; Somers et al., 1999) as well as ventral stream areas (Desimone and Duncan, 1995; Hinrichs et al., 1994; Itti and Koch, 2001), and frontal eye field (Corbetta et al., 2002) show attentional modulation of their fMRI activation — yet, in our results these
areas showed only marginal modulation by the emotional stimuli. In addition, laterality index analysis showed that the emotional activity was not biased to the right hemisphere as in bottom-up attention system (Corbetta et al., 2002), but was rather symmetrical. We can thus conclude that attentional effects were unlikely to be the major factor in producing the observed effect.

An additional concern could be a global increase in arousal associated with the emotional stimuli. However, such interpretation is incompatible with the selective nature of the effect-targeting specifically dorsal stream visual areas while early retinotopic areas and ventral stream recognition areas such as the FFA and PPA remained unaffected.

According to the behavioral results the dominant emotions reported in our experiment were sadness and compassion, rather than fear and anxiety, which are more common in emotion research, and known to activate the amygdala (Adolphs et al., 1999; Murphy et al., 2003). This specific mix of movie clips may thus explain the fact that we have not found a significant emotional effect in well-known subcortical structures such as the amygdala.

While most brain regions showed a tendency for higher activation in response to the emotional stimuli, the superior temporal sulcus (STS) showed the opposite effect. This reduced activation in STS during emotional movies was not observed in previous studies of emotional stimuli or movies. However, since the STS deactivation occurred only when the original movie sound was present (in the main experiment and in the "Audio" control) and was eliminated when the original sound was missing (in the 'inverted — no sound' and in the 'Visual' controls, Fig. 7), it is likely that this effect was related to auditory rather than emotional aspects of the stimuli.

Finally, we did not find a differential brain activity between positive and negative emotional experience. Being complex and longer than the...
typical static emotional stimuli, the clips are probably less valence-specific, as multiple emotions could be induced within a single short clip. Fig. 2b uncovers this complexity by depicting the variety of distinct emotions elicited, and the complex emotional experience while watching the clips. Each movie elicited a mixture of emotions, and perhaps there was a trade-off between naturalistic complex stimuli and valence specificity. Furthermore, it should be noted that the clips used in the experiment were prepared by editing the movie scenes to achieve a 14 sec clip involving the relevant emotions. Such editing added discontinuities in the movie, potentially resulting in additional effects beyond the emotional content of the clips. It has been shown before that using complex emotional stimuli such as a movie clip, requires several analytic approaches in order to reveal the full complexity of neuronal processing (Raz et al., 2012). Further research including different experimental designs may be needed to unravel potential valence effects.

Conclusion

An emotion–action link? The use of narrated, dynamic, audio–visual clips as emotional stimuli highlighted the dorsal stream visual areas as major players in the emotional brain response. This chain of areas has been also termed the "action stream", and is activated during preparation for action, particularly towards an object (Culham and Valyear, 2006; Goodale and Milner, 1992; Shmuelof and Zohary, 2005). Our results thus support the hypothesis that emotional processing is naturally linked to action preparation. However, it is important to note that the present study does not present a direct behavioral demonstration of such action-preparatory activity. Nevertheless, given the established behavioral link between dorsal stream and action preparation, a parsimonious interpretation of our findings is that the realistic emotional content itself created a mental preparation for action reflected in dorsal stream activation. This emotion–action link has been fundamental for the 'motivation theory' defining emotions as action dispositions, organized on a "defensive–appetitive" scale (Cacioppo et al., 1986; Davidson et al., 2000; Frijda, 1986; Lang et al., 1990, 1997b). Our results are thus compatible with this long standing proposal of a link between emotion and action.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.08.032.

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