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The iconography of mourning and its neural correlates: a functional neuroimaging study

Karin Labek,¹ Samantha Berger,¹ Anna Buchheim,¹ Julia Bosch,² Jennifer Spohrs,² Lisa Dommes,^{2,3} Petra Beschoner,³ Julia C. Stingl,^{4,5} and Roberto Viviani^{1,2}

¹Institute of Psychology, University of Innsbruck, Tyrol, Austria, ²Department of Psychiatry and Psychotherapy III, University of Ulm, Baden-Württemberg, Germany, ³Psychosomatic and Psychotherapy Clinic, University of Ulm, Baden-Württemberg, Germany, ⁴Federal Institute for Drugs and Medical Devices, Bonn, Germany, and ⁵Center for Translational Medicine, University of Bonn Medical School, Bonn, Germany

Correspondence should be addressed to Roberto Viviani, Institute of Psychology, University of Innsbruck, Innrain 52, A-6020 Innsbruck, Austria. E-mail: roberto.viviani@uibk.ac.at

Abstract

The present functional neuroimaging study focuses on the iconography of mourning. A culture-specific pattern of body postures of mourning individuals, mostly suggesting withdrawal, emerged from a survey of visual material. When used in different combinations in stylized drawings in our neuroimaging study, this material activated cortical areas commonly seen in studies of social cognition (temporo-parietal junction, superior temporal gyrus, and inferior temporal lobe), empathy for pain (somatosensory cortex), and loss (precuneus, middle/posterior cingular gyrus). This pattern of activation developed over time. While in the early phases of exposure lower association areas, such as the extrastriate body area, were active, in the late phases activation in parietal and temporal association areas and the prefrontal cortex was more prominent. These findings are consistent with the conventional and contextual character of iconographic material, and further differentiate it from emotionally negatively valenced and high-arousing stimuli. In future studies, this neuroimaging assay may be useful in characterizing interpretive appraisal of material of negative emotional valence.

Key words: mourning and bereavement; sadness; iconography; body posture perception; mirror system; empathy; empathy for pain; theory of mind

Introduction

Mourning is a process that follows the death of a loved one and during which grief is eventually replaced by acceptance. It has clinical relevance in the development and differential assessment of pathological affective states (Freed and Mann 2007; Zisook et al. 2007; Kendler et al. 2008; Karam et al. 2009; Wakefield and Schmitz 2012). Underscoring its possible importance, the Research Domain Criteria Initiative (NIMH RDoC Working Group 2011) includes mourning as a key endophenotype for the characterization of psychopathology. The question raised by this inclusion is the relevance of emotions and experiences of loss of a loved one for affective disorders more generally. However, it is difficult to assess processes associated with the mourning thematic using standardized procedures. In a pioneering functional neuroimaging study (fMRI), Gündel *et al.* (2003) exposed eight women to pictures of a deceased loved one and compared the ensuing brain activation with that obtained while viewing the picture of a stranger. While ecologically valid, this

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approach has the drawback that for obvious reasons it cannot be applied as part of a standardized fMRI battery for the assessment of endophenotypes of disordered affect.

In recent years, fMRI studies of empathy for physical and emotional pain have shown that the same neural substrates are active while personally experiencing and while viewing others experiencing pain (for recent reviews, see Keysers et al. 2010; Lamm et al. 2011; Bernhardt and Singer 2012; Decety and Svetlova 2012; Lamm and Majdandzic 2015; Betti and Aglioti 2016). This finding exemplifies a more general phenomenon in which neural activations are shared between direct first-person experience and appraising the experience of others and is consistent with observations from the study of cognition (Prinz 1997) and of animal behaviour (Preston and de Waal 2002). In a set of areas collectively referred to as the 'mirror system', previous neurophysiological recordings of motor and sensory neurons had provided evidence of shared activity when moving or observing others carry out the same movement, or being touched and observing others being touched (Rizzolatti and Craighero 2004; Keysers et al. 2010). Likewise, shared activations are present in experiencing as well as observing displays of emotion (Bastiaansen et al. 2009; Lamm and Singer 2010). Furthermore, there is evidence that the sharing of neural activations has a functional role. A recent study has shown that inducement of a placebo effect against pain affects the capacity of individuals to affectively empathize with others (Rütgen et al. 2015), simultaneously showing reduced recruitment of cortical areas associated with the affective component of pain (see also DeWall et al. 2010 for the effects of direct pharmacological manipulations).

These findings justify an interest in the neural correlates elicited by the passive exposure to drawings of mourning individuals. In the present study, we developed a set of drawings of individuals designed to convey mourning using selected iconographic features, and investigated their neural correlates using functional MRI. This differs from previous studies, in which participants were exposed to pictures of the object of their loss. Note that the different cortical networks in which shared activations are observed may correspond to different mechanisms through which appraisal of the experience of others may be attained and reflect its predominant domain (sensory-motor, affective, or cognitive: Lamm et al. 2009, 2011; Shamay-Tsoory 2011; Lamm and Majdandzic 2015). Cognitive forms appraisal are often referred to as theory of mind (Saxe and Kanwisher 2003; Frith and Frith 2005), a notion that includes models of latent motives and intentions in others. The issue we would like to address is what specific network associated with apprehending the mental state of others, if any, is recruited by passive exposure to these drawings.

Substantial knowledge already exists on the processes elicited by exposure to faces and their neural correlates in the activation of the amygdala (Botvinick *et al.* 2005; Lamm *et al.* 2007; Vuilleumier and Pourtois 2007), which constitutes an important neuroimaging marker of affective disorders, negative mood, and vulnerability to depression (Whalen *et al.* 2002; Hariri and Whalen 2011). In these and other related studies, activation of the amygdala is thought to be related to the arousal elicited by images that are generally rated not only as negative, but also as highly arousing by observers (Kapp *et al.* 1992; LeDoux 2000; Davis and Whalen 2001; Bradley and Lang 1994). In the drawings used in the present study, we avoided use of facial expression to minimize this direct effect of emotional display. Our intent was to differentiate the resulting fMRI probe from those already available in the study of affective disorder.

Apart from aspects related to the investigation of negative affect, the study of brain activity elicited by iconographic material is an issue of interest in its own right. In his classic work, Panofsky (1939) suggested that retrieval of the meaning of visual artefacts involved apprehension of pure forms (configurations of lines and colour), the perception of 'expressional qualities' such as facial expressions or gestures (see also Warburg 1932), the identification of concepts manifested in images by resorting a shared cultural tradition ('subject matter' as opposed to form), and the discovery of a latent symbolical value of images. Interpretation in the light of shared cultural notions and context becomes increasingly important in the later stages of this progression. Panofsky reserved the terms 'iconography' and 'iconology' to the later stages.

Interestingly, Panofsky compared this progression to levels of understanding in a social cognition task. Understanding the greeting of an acquaintance involved several strata of meaning that started with the recognition of form and body parts and sensing his mood by empathically registering nuances in his gesture, went through identifying the gesture as a greeting on the base of a culturally shared set of conventions, and ended with the appreciation of his personality by considering how all strata of meaning may contribute to his individual way of greeting. While Panofsky might have intended this example as a mere analogy, it is worth considering it with attention. It has been suggested that the shared neural activations when observing body postures or gestures may be the mechanism through which work of art attains its evocative force in the viewer (Freedberg and Gallese 2007; Freedberg 2011).

In the present study, we report not only on the selective activity elicited in the brain by these drawings, but also on its evolvement over time. The analysis of time trends is justified by the fact that the reaction to emotional stimuli is often modulated over time. For example, the activity of the amygdala to highly salient emotional stimuli is known to habituate over time (Breiter et al. 1996; Wright et al. 2001), but this process may be altered in pathological conditions (Siegle et al. 2002; Hazlett et al. 2012). However, little is known about the evolution of neural correlates of negatively valenced but not overly arousing material over time. Some studies have stressed the importance of complementing our knowledge concerning the automatic and immediate reactivity observed in highly arousing material by considering context (Lee and Siegle 2014) or the tendency to dwell on emotional content and its elaboration and semantic interpretation (O'Connor et al. 2008; Siegle et al. 2010). We will here show the existence of considerable changes in brain activity during exposure to iconographic renderings of mourning that is consistent with a progressive recruitment of interpretive processes in their appraisal. This suggests that the evocative force of this iconographic material, even if chosen to address a universal aspect of human experience, may be mediated by a complex process in which semantic interpretive traces are integrated with more elementary sensory processing.

Materials and methods

The present work reports on two studies. In the first, the visual material was surveyed to identify the postural elements of mourning. These elements were used to draw pictures that were subsequently characterized in term of valence and arousal values (Bradley and Lang 1994). Details on the methods on the collection of images and their valence and arousal ratings are given in the Supplementary Material available online. In the second study we sought to characterize the neural correlates elicited by viewing these drawings with fMRI.

Functional imaging paradigm

In each group (mourning-related and control), the 12 pictures were divided into three blocks of four pictures and presented in



Fig. 1. (A) Schematic illustration of the task in the scanner. Mourn: mourning block; ctl: control block. (B) Schematic illustration of the design matrix of the within blocks trend model. The interaction mourning × trend is given by the rightmost column (m × t). (C) Schematic illustration of the design matrix of the between blocks trend model, with the interaction in the rightmost column (in both cases, the design matrix also included realignment parameters and an intercept).

pseudorandomized order. In each block, the four pictures were presented sequentially for 3 s without interval, giving a block duration of 12 s. Blocks were separated by a baseline interval of 12 s in which scribbles were displayed using the same frequency and duration (i.e., four scribbles for 3 s each). These scribbles replaced the fixation point of an initial pilot (N = 6, not analyzed), in which participants reported thinking about the pictures in the interblock interval. In total, there were six picture blocks, six scribbles picture interblock intervals for an overall duration of about 2 min 30 s (Figure 1A). The pictures were displayed on a screen on the back of the scanner visible through mirrors mounted on the coil. The presentation of trials was programmed in standard software (Presentation 14, Neurobehavioral Systems Inc., Albany, CA).

Recruitment, data acquisition and statistical analysis

The fMRI study was conducted at the Psychiatry and Psychotherapy Clinic of the University of Ulm, Germany, after approval by the Ethical Review Board. This study was part of a larger research program to develop fMRI assays of positive valence/appetitive motivation and negative valence.

Healthy participants (N = 19) were recruited through local announcements and admitted to the study after providing written informed consent. The sample comprised 17 participants (three males, mean age 22.7, standard deviation 3.2). Data were collected in a Prisma 3T Siemens Scanner using a T2*-sensitive echo-planar imaging sequence (TR/TE: 2460/30 ms, flip angle 90°, 64×64 pixels, FOV 24 cm, 39 2.5 mm slices with a gap of 0.5 mm, giving an isotropic pixel size of 3mm). A 64-channels head coil was used with foam padding to minimize head motion.

Data were analyzed with the freely available software SPM12 (www.fil.ion.ucl.ac.uk/spm) running on MATLAB (The MathWorks, Natick, MA). After realignment, normalization, and smoothing (FWHM 8 mm), trials were modelled by a boxcar function convolved with a standard haemodynamic function. Realignment parameters were also included in the model as nuisance covariates. After estimating the model in each voxel separately, estimates of the contrast of interest were brought to the second level to account for the random effect of subjects.

We considered three main models in the analysis of the neuroimaging data. In the first, the mourning and control blocks were modelled as separate column of the design matrix to generate the contrasts of interest (mourning vs control, task as the effect of both blocks relative to the implicit baseline given by the scribble pictures). The second had the aim to elicit the effects of the time trend within the blocks, i.e. changes in activation from the beginning to the end of the block. Here, both block types (mourning and control) were included as a single predictor in a column of the design matrix, to which a 'parametric modulation' was added consisting of the weights of the linear trend (Figure 1B). Parametric modulations are weighted versions of the original predictor that capture variance not explained by the predictor alone. To test the interaction trend × mourning, a column of the mourning blocks and its respective parametric modulator was added in a separate model. The third model had the aim to elicit the effects of the trend between the individual blocks, i.e. changes in activation between the beginning and the end of the experiment. Here, both block types (mourning and control) were included as a single predictor in the same column of the design matrix. A parametric modulator was added consisting of the weights of the linear trend between blocks (Figure 1C). To test the interaction block trend \times mourning, a column of the mourning blocks and its respective parametric modulator was added in a separate model.

At the second level, we computed significance tests corrected at voxel and cluster level, with clusters defined *a priori* by the uncorrected threshold P = 0.001. Voxel-level correction was computed using both the random field theory-based correction available in SPM12 and permutation tests (2000 permutations) in software coded in MATLAB (The MathWorks, Natick, MA). The cluster-level corrections were computed with permutation tests. We reported effects at uncorrected significance levels in the text when looking for interactions or simple effects in clusters already detected as significant in previous analyses. Overlays were generated with the freely available software MriCron (Chris Rorden, http://people.cas.sc.edu/rorden/mricron/index.html).

Results

Iconographic survey and development of the picture set

The survey of the images of individuals depicted while mourning revealed that a small number of body and facial figural



Fig. 2. Body postures associated with grief in classic paintings. (A) Giotto's portrayal of the death of St. Francis of Assisi (detail) located in the church Santa Croce in Florence (around 1325). In the foreground, with their backs to the viewer, are monks in the crouched posture associated with inner withdrawal, a posture that here merges with a stance of devotion or prayer. On the far side of Francis' deathbed, facing the viewer on the upper right of the painting is a monk with arms thrown up in despair. (B) In Caravaggio's Deposition from the Cross (1603–1604), we see a similar posture of despair in the young women in the upper right corner. Just before her, another young woman is shown with bowed head and a hand covering her forehead. (C) The same posture of bowed head and hand to the face is visible in van der Weyden's deposition (The Descent from the Cross, 1435) in the woman with a white scarf on the left. Here, this posture is associated with a facial expression suggesting crying. Similar to the monks in Giotto's fresco, the woman on the furthest right bows her head and is bent forward in a gesture of inner withdrawal mingling pain and prayer. The body posture of the holy virgin (in a blue vest in the foreground) is characterized by a limp body, perhaps evoking a reaction at the view of her dead son.

elements recurred in the overwhelming majority of material (see Table 1). As a rule, these elements appeared in combination. Many of them can be traced back at least to the pictorial tradition of the humanism and renaissance (Figure 2), where they appear in portrayals of the deposition of Christ or the death of saints.

Among the elements shown in Figure 2, one may discern at least three basic posture types. The first, and the most predominant, may be viewed as expressing withdrawal: crouching or kneeling, bowing one's head or covering it with one's hands. A second quite different body posture portrays grieving subjects with their arms thrown up in an expression of despair, their bodies stretched outwards while looking out as if seeking help (see the individuals in the upper right corners in Figure 2A and B). A third body posture portrays limp bodies, as in individuals overwhelmed by the sight or the news of the loss (Figure 2C).

In the images retrieved from the Internet postural elements signalling withdrawal and crying facial expressions/ tears predominated. We did not consider crying facial

expressions or tears, since our intent was to differentiate the present stimulus set from those showing emotional facial expressions. We also found that expressive images of grief, depicting individuals throwing up their hands in despair, were uncommon in modern material, at least as long as the individuals depicted were of Western ethnic origin. In contrast, scenes of bereavement from other cultures would occasionally make use of this iconographic element. Because we intended to keep the arousal associated with the images low to avoid overlap with the typically high arousal scores of negatively valenced images, we did not include images of despair into the dataset. This left for the dataset the iconographic elements of crouching, bowing the body or the head, taking the hands to the head to cover it, or postures of prostration or limp bodies. In the Internet search it also emerged some of the most poignant images, especially when referring to body postures, were directly showing or replicating cemetery statues. For this reason, we used several cemetery statues as the source of the drawings (Figure 3).

Table 1. List of iconographic elements

| Iconographic element | Example |
|---|---|
| Crouching and/or bowed head Hands covering face or on head Prostrated or limp body, arms slung forward | Figures 2A and 3A Figures 2B-C and 3A Figures 2C and 3B and C |
| Kneeling | Figure 3A |
| Arms thrown up in despair | Figure 2A and B (not used in the battery) |
| Crying facial expression, tears | Figure 2C (not used in the battery) |

As one can see from the examples of the original image material and the drawings of Figure 3, the combinations of these iconographic elements often require subtle contextual hints to be interpreted as manifestations of mourning. In Figure 3A, for example, crouching and taking the hand to the head can also occur when taking something from the ground and examining it closely. In Figure 3C, the limp body of the Holy Virgin may be attributed to a loss of consciousness. For the same reasons, contextual details may be responsible for correctly interpreting the meaning of these drawings.

The mourning pictures were rated as strongly negative in valence but received average arousal scores (see Supplementary Material for details).

Functional neuroimaging

Main contrast: mourning vs Control. The contrast mourning vs control pictures revealed extensive bilateral activations in the posterior superior temporal gyrus that extended deeply in the Sylvian fissure to reach the parietal operculum (Figure 4 and Table 2, clusters n. 1 and 2). These activations were accompanied by more circumscribed activity in the supramarginal and postcentral gyri. On the medial wall of the cerebrum, this contrast was associated with larger activity in the middle/posterior cingulus and in the cuneus/precuneus (clusters n. 1 and 3). There was no significant effect in the contrast control vs mourning.

A specific question concerned the differential activation of the amygdala during the presentation of the mourning-related pictures. When applying a predefined anatomical region of interest correction in the mourning vs control contrast, no activation reached the cluster definition threshold. The amygdala, however, was moderately active when viewing the pictures than during the implicit baseline given by the scribble drawings (Montreal Neurological Institute coordinates x, y, z: -27, 1, -28, t = 3.98, peak-corrected for ROI P = 0.019; 29, 1, -27, t = 2.86, n.s.). Another similar question concerned the activation of the occipitotemporal cortex, which is the seat of the extrastriate body area (EBA), and of the fusiform gyrus (fusiform body area, FBA, Peelen and Downing 2007), areas that are specifically activated by the perception of bodies or body parts. These areas have also been shown to be more active when presenting bodies with emotional expressions (Hadjikani and de Gelder 2003; Peelen et al. 2007). Similarly to the amygdala, this area was not active in the contrast mourning vs control, but was active in the implicit contrast pictures vs scribbles (x, y, z: 56, -73, 7, t = 10.03, peaklevel corrected P < 0.001; x, y, z: 41, -48, -18, t = 11.24, P < 0.001; x, y, z: -47, -79, 8, t = 6.90, P = 0.011; x, y, z: -41, -52, -22, t = 7.55, P = 0.003).

Time trend within blocks. Another issue addressed in the present study is the evolution of the response over time. To investigate this issue, we first modelled changes in the signal within blocks (Figure 1B). Here, the strongest effects were in the direction of a relative reduction of response (activity higher at the beginning than at the end of the block), which affected the occipitotemporal area bilaterally that was active during the task (EBA, Figure 5A and Table 3, lower section). This effect extended into the fusiform gyrus, where the FBA is located (Peelen and Downing 2007). Finally, when testing the interaction of trend with block type, we found that the decrease over time of the response in these same areas was significantly different between the mourning and the control blocks (x, y, z:-41, -82, 1, t=4.92, k=880, P=0.005, cluster-level corrected; x, y, z: 32, -778, -12, t = 4.29, k = 213, P = 0.001, uncorrected), due to the fact that they were almost exclusively due to the decrease of response during the mourning blocks. During the mourning blocks there were also increases of response, which involved the cuneus and middle cingular cortex generally active in the contrast mourning vs control (x, y, z: -9, -70, 31, t = 4.42, P < 0.001, uncorrected; x, y, z: -3, -16, 31, t = 3.83, P < 0.001, uncorrected). There was no significant higher amygdala activity at the beginning of the mourning blocks. In summary, during the blocks there were progressive changes in the brain signal, predominantly due to changes in the mourning blocks where activation shifted from the body-selective regions in the occipitotemporal cortex to the cuneus and middle cingular cortex.

Time trend between blocks. To complete the analysis of the evolution of the brain response over time, we then modelled the sequence of the blocks as a trend (Figure 1C). We first tested for a general trend over the whole experiment. Here, significant and extensive effects of time (increasing response) were found in the superior temporal and inferior frontal gyri bilaterally (Table 4). There was no significant effect in the other direction. We then tested the interaction of trend and block type, which revealed a progressive change in activity in the same part of the right inferior frontal gyrus (Figure 5B and Table 5, clusters n. 3 and 5), due to an incremental response during the mourning blocks. This interaction was accompanied by a similar effect on the controlateral side, which however failed to reach significance (x, y, z: -42, 5, 31, t = 3.02, n.s.). In summary, during the experiment the superior temporal lobe and inferior frontal gyrus increased in activity. Additionally, the increase in the inferior frontal gyrus was larger in the mourning than in the control blocks.

Considering these two analyses of the changes of the signal over time, we can see that they have important elements in common. First, even when they involved both type of pictures, they were more pronounced for the mourning pictures. Second, they shifted activation from visual association areas such as the occipital cortex and the fusiform gyrus to more dorsal networks, located predominantly in the posterior part of the brain, but also involving the inferior frontal gyrus.

Discussion

Mourning and the loss of a loved one are universal aspects of human experience. Nevertheless, the existence of variations in the representation of mourning individuals, even if limited, suggests the existence of a cultural component in its overt manifestations. In the present picture set, contextual elements may have been essential to interpret the body posture correctly. Another aspect characterizing the picture set at hand comprises



Fig. 3. On the left, examples of visual material used for the drawings; in the centre-left, examples of mourning-related drawings; in the centre-right, the respective control drawings; on the right, scribble drawings. (A) This statue, widely available on the internet on sites dealing with grief, exemplarily combines crouching with the act of bringing the hands to the face. (B) The angel of grief (left), originally a sculpture by William Wetmore Story in Rome's protestant cemetery, was the starting point of many replicas. It shows a prototypical body posture with prostration and arms slung forward. (C) Limp body of the Holy Virgin (detail from Figure 1, right). In the battery drawing in the centre, we combined the loss of muscular tone in the upper part of the body (and especially in the right arm) with the postural element of the hand to the head.



Fig. 4. Effects of the contrast mourning vs control, overlaid on a template brain. Data thresholded for illustration purposes at P < 0.001, uncorrected (see Table 2 for inference).

the average arousal ratings of the mourning pictures. These two characteristics are consistent with the finding of an activation of cortical substrates located in association areas during the exposure to drawings of mourning. In contrast, brain structures typically associated with expressive faces and high arousal pictures, such as the amygdala, where not preferentially active.



Fig. 5. (A) Effects of the within-blocks time trend and (B) of the between blocks trend. Data thresholded for illustration purposes at P < 0.001, uncorrected (see Tables 3 and 4 for inference).

In visual representations of facial expressions, faces are of special interest because the emotions they express may be universally recognizable (Tomkins and McCarter 1964; Ekman and Friesen 1971), thus epitomizing expressional qualities (Freedberg 2014). However, the emotion underlying facial expression may be conveyed also through less expressive mechanisms, as for example in stylised drawings Freedberg

| Cluster # | Location | MNI coord. | k | p clust.(perm) | t | p peak (RFT) | p peak (perm) |
|-----------|--------------------------------|-------------|------|----------------|------|--------------|---------------|
| 1 | Sup. Temporal (BA22) | 56 –182 | 8122 | <0.001 | 8.20 | 0.001 | < 0.001 |
| | Mid./Sup. Temporal (BA21) | 45 - 40 5 | | | 7.36 | 0.005 | 0.003 |
| | | 54 - 24 - 6 | | | 6.36 | 0.036 | 0.014 |
| | Mid./Post. Cingulus (BA23) | 8 - 25 22 | | | 6.25 | 0.045 | 0.018 |
| 2 | Mid. Temporal (BA20-21) | -48 -25 -12 | 4705 | 0.001 | 7.43 | 0.004 | 0.003 |
| | Sup. Temporal (BA48) | -42 - 284 | | | 5.78 | 0.117 | 0.054 |
| | | -50 -25 7 | | | 5.58 | 0.172 | 0.079 |
| | Supramarg./Postcentral (BA48) | -57 -28 17 | | | 5.44 | 0.221 | 0.103 |
| 3 | Precuneus (BA7) | -5 - 7343 | 4317 | 0.001 | 5.68 | 0.142 | 0.066 |
| | Cuneus (BA23) | -15 -61 22 | | | 5.61 | 0.161 | 0.076 |
| | | -12 -72 28 | | | 5.23 | 0.325 | 0.153 |
| 4 | Supramarg./Postcentral (BA2-3) | 53 - 21 37 | 363 | 0.086 | 5.00 | 0.468 | 0.220 |
| 5 | Inf. Frontal gyrus (BA6/44) | 63 14 14 | 159 | 0.241 | 4.60 | 0.755 | 0.394 |
| 6 | Ant. Hippocampus | 35 -7 -21 | 294 | 0.110 | 4.49 | 0.825 | 0.452 |

Table 2. Effects of the contrast mourning vs control

Reported peaks are at least 4 mm apart. Peaks located in the same brain area within the same cluster are indicated by blanks in the Locations

column. MNI coord: Montral Neurological Institute coordinates (in mm.); k: cluster extent (in voxel of isotropic size 2 mm); p clust. (perm): significance level, clusterlevel correction computed by permutation; t: Student's t; p peak (RFT): significance level, random field theory peak-level correction; p peak (perm): significance level, peak-level correction computed by permutation; BA: Brodmann Area; Inf., Mid., Sup.: inferior, middle, superior; Ant., Post: anterior, posterior; Supramarg; supramarginal.

Table 3. Time trend within blocks

| Cluster # | Location | MNI coord. | k | p clust.(perm) | t | p peak (RFT) | p peak (perm) |
|-----------|-----------------------|--------------|------|----------------|-------|--------------|---------------|
| 1 | Lingual (BA37) | -33 -46 -1 | 762 | 0.038 | 6.30 | 0.039 | 0.021 |
| 2 | Calcarine (BA17) | -8 -85 -3 | 568 | 0.044 | 6.23 | 0.045 | 0.023 |
| 1 | Mid. Temporal (BA37) | -50 -64 7 | 2517 | 0.002 | -6.78 | 0.015 | 0.008 |
| | Fusiform (BA37) | -36 -45 -19 | | | -5.25 | 0.296 | 0.139 |
| | Inf. Occipital (BA19) | -39 -66 -10 | | | -4.80 | 0.591 | 0.276 |
| 2 | Fusiform (BA19) | 33 - 64 - 13 | 1346 | 0.009 | -5.83 | 0.099 | 0.050 |
| | Inf. Temporal (BA20) | 45 - 43 - 19 | | | -4.69 | 0.672 | 0.326 |
| | Fusiform (BA37) | 36 - 40 - 19 | | | -4.61 | 0.728 | 0.352 |
| 3 | Mid. Temporal (BA37) | 50 - 57 13 | 743 | 0.027 | -4.90 | 0.517 | 0.234 |

Reported peaks are at least 4mm apart.

MNI coord: Montral Neurological Institute coordinates (in mm.); k: cluster extent (in voxel of isotropic size 2mm); p clust. (perm): significance level, cluster-level correction computed by permutation; t: Student's t; p peak (RFT): significance level, random field theory peak-level correction; p peak (perm): significance level, peak-level correction computed by permutation; BA: Brodmann Area; Inf., Mid.: inferior, middle.

(2014). In this respect, note that while some body postures (such as those implying fear or aggression, Tamietto *et al.* 2009) may be universally recognized, this may not always be the case (Ekman 1965). Furthermore, the capacity of visual art to bring about a process of understanding beyond the immediate reaction to expressive drawings, including those expressing grief (Gombrich 1960), suggests the availability of diverse mechanisms in the appraisal of emotion, including cognitive forms of appraisal.

Neuroimaging studies of the perception and encoding of body postures and motion have generally shown that emotional postures tend to increase activation in the occipitotemporal areas involved with the analysis and identification of bodies or of body parts (de Gelder and Hadjikhani 2006; Hadjikani and de Gelder 2003; de Gelder et al. 2004; Grosbras and Paus 2006; Peelen et al. 2007). These areas constitute a perceptual analysis channel that runs and is located parallel to the substrates for the analysis of faces (extrastriate body area, EBA, and fusiform body area, FBA, Peelen and Downing 2007; de Gelder 2009). In the present study no increased activation of these areas was observed when contrasting mourning and control pictures, although these areas were active in the contrast pictures (showing bodies) vs scribbles, as they should. We did observe, however, strong effects in areas further up in the perceptual analysis and encoding stream that are traditionally referred to as associative, such as the posterior superior temporal sulcus (STS) and the anterior parietal cortex. The discrepancy between the present and previous findings is consistent with the contextual nature of the emotional information conveyed by the mourning pictures. As reported for example by Downing *et al* (2006), the level of analysis of the input images determines the level of activation of cortical areas in a hierarchy of progressively higher semantic encoding (Petersen *et al.* 1988). These associative and motor areas belong to the shared activation system (Peelen *et al.* 2010). The posterior STS and the adjacent parietal cortex, in particular, have been found to host supramodal representation of affect (Peelen *et al.* 2010).

A related perspective is provided by the neuroimaging studies of the empathy for pain (Lamm et al. 2011; Keysers et al. 2010; Betti and Aglioti 2016). This literature has highlighted a distinction between several shared activation networks involved in the appraisal of pain, reflecting different possible mechanisms through which it may be attained (Lamm et al. 2011; Lamm and Majdandzic 2015). An anterior network, consisting prevalently of the anterior insula and the dorsal anterior cingulate cortex, may be associated with the subjective vicarious experiencing of

| Cluster # | Location | MNI coord. | k | p clust.(perm) | t | p peak (RFT) | p peak (perm) |
|-----------|----------------------------------|--------------|------|----------------|------|--------------|---------------|
| 1 | Inf. Frontal Gyrus (BA44-45) | 56 20 28 | 1776 | 0.008 | 6.91 | 0.011 | 0.003 |
| | | 57 31 29 | | | 6.59 | 0.021 | 0.006 |
| | | 54 17 37 | | | 6.47 | 0.027 | 0.009 |
| 2 | Rol. Operc./Sup. Temporal (BA48) | -45 - 28 10 | 1896 | 0.004 | 6.56 | 0.023 | 0.006 |
| | | -35 -34 19 | | | 5.15 | 0.351 | 0.156 |
| | | -44 -13 -10 | | | 3.79 | 0.998 | 0.812 |
| 3 | Inf. Parietal (BA40) | 41 - 45 43 | 671 | 0.038 | 6.37 | 0.033 | 0.010 |
| 4 | Mid./Sup. Temporal (BA22/48) | 57-185 | 1317 | 0.008 | 5.75 | 0.116 | 0.047 |
| | | 50 - 12 2 | | | 5.26 | 0.292 | 0.126 |
| | | 42 - 19 - 10 | | | 3.89 | 0.995 | 0.764 |

Table 4. Time trend between blocks

Reported peaks are at least 4 mm apart. Peaks located in the same brain area within the same cluster are indicated by blanks in the Location column. MNI coord: Montral Neurological Institute coordinates (in mm.); k: cluster extent (in voxel of isotropic size 2 mm); p clust. (perm): significance level, cluster-level correction computed by permutation; t: Student's t; p peak (RFT): significance level, random field theory peak-level correction; p peak (perm): significance level, peak-level correction computed by permutation; BA: Brodmann Area; Inf., Mid., Sup.: inferior, middle, superior; Rol. Operc: Rolandic operculum.

Table 5. Interaction time trend \times block type

| Cluster # | Location | MNI coord. | k | p clust (perm) | t | p peak (RFT) | p peak (perm) |
|-----------|--|--------------|------|----------------|------|--------------|---------------|
| 1 | Mid. Occipital/Angular Gyrus (BA19/39) | -38 -76 29 | 1385 | 0.009 | 5.91 | 0.087 | 0.04 |
| | | -36 -85 11 | | | 5.86 | 0.095 | 0.05 |
| | | -35 - 73 14 | | | 4.12 | 0.970 | 0.66 |
| 2 | Inf. Occipital (BA18) | 26 -91 -6 | 1761 | 0.007 | 5.87 | 0.094 | 0.04 |
| | Mid. Occipital/Angular Gyrus (BA19/39) | 38 - 76 28 | | | 5.11 | 0.381 | 0.19 |
| | | 38 – 78 7 | | | 3.78 | 0.999 | 0.84 |
| 3 | Inf. Frontal Gyrus (BA45) | 48 28 10 | 549 | 0.048 | 5.33 | 0.262 | 0.13 |
| | | 59 32 5 | | | 4.67 | 0.696 | 0.37 |
| 4 | Inf. Occipital (BA18-19) | -27 -90 -4 | 669 | 0.032 | 4.87 | 0.546 | 0.28 |
| | | -36 -81 -9 | | | 4.17 | 0.960 | 0.64 |
| | | -17 - 1001 | | | 3.94 | 0.993 | 0.78 |
| 5 | Inf. Frontal Gyrus (BA44) | 45726 | 220 | 0.176 | 3.95 | 0.992 | 0.77 |

Reported peaks are at least 4 mm apart. Peaks located in the same brain area within the same cluster are indicated by blanks in the Location column.

MNI coord: Montral Neurological Institute coordinates (in mm.); k: cluster extent (in voxel of isotropic size 2 mm); p clust. (perm): significance level, cluster-level correction computed by permutation; t: Student's t; p peak (RFT): significance level, random field theory peak-level correction; p peak (perm): significance level, peak-level correction computed by permutation; BA: Brodmann Area; Inf., Mid.: inferior, middle.

pain, i.e. with the affective component of empathy (Lamm et al. 2011; Lamm and Singer 2010; see also Lee and Siegle 2012; Gu et al. 2013). A posterior network, mainly consisting of somatosensory regions centred on the parietal operculum and the superior temporal gyrus (Gazzola et al. 2006; Gazzola and Keysers 2009; Keysers et al. 2010), may be concerned with the appraisal of the representations of the sensory experience of pain (Lamm et al. 2011; see also Adolphs et al. 2000). In the present study, the activation in the contrast mourning vs control was consistent with the activation of the posterior network. We also observed an extension of the parietal opercular activation into the adjacent and abutting medial face of the superior temporal gyrus, extending into the cortex surrounding Heschl's gyrus. The auditory associative cortex has also been reported to be part of the mirror system (Gazzola et al. 2006). In contrast, there was little trace of activation of the anterior insula and the anterior cingulus, two core components of the network identified by the empathy for pain studies. This may be due to the fact that viewing these drawings does not necessarily elicit an affect in participants corresponding to the vicarious affective component of pain of those studies. We did observe, however, relative activation of areas that have been

reported by previous neuroimaging studies as specifically involved in grief from bereavement (Gündel *et al.* 2003; Kersting *et al.* 2009; Freed *et al.* 2009; Arizmendi *et al.* 2016). This concordance concerned, in particular, the recruitment of the precuneus (Gündel *et al.* 2003; Freed *et al.* 2009; Arizmendi *et al.* 2016) and of the middle/posterior cingular cortex (Gündel *et al.* 2003; Kersting *et al.* 2009; Arizmendi *et al.* 2016). The posterior cingular cortex in particular has been proposed as a key neural correlate of the mourning process (O'Connor 2012).

Also the activation of the superior temporal gyrus has been reported in neuroimaging studies investigating the attentional bias to grief-related content in bereaved individuals (Freed *et al.* 2009; Arizmendi *et al.* 2016). In the literature, however, the temporoparietal junction and the superior temporal gyrus have been prevalently associated with cognitive forms of appraisal of the feelings or intentions of others, or 'theory of mind' (Frith and Frith 2003; Van Overvalle 2009; Saxe 2010). Recruitment of these areas is consistent with a previous study in which participants were exposed to drawings that are relevant to probe the activation of attachment patterns (Labek *et al.* 2016).

Another result of the present study, and one which sets it apart from previous investigations with similar scope, was to demonstrate that significant changes in brain activity were present when one looked at the evolution of the signal over time. Importantly, these analyses revealed activation of areas associated with emotional body appraisal or the shared activations system that were missing in the original mourning vs control contrast. As mentioned, the comparison mourning vs control pictures failed to activate areas corresponding to the EBA and FBA as in previous literature. However, these areas were involved in the interaction with the time trend, showing that the lack of effect in the main contrast ensued from a decrease of activation by the mourning pictures during the individual blocks. This decrease was accompanied by increased activation of the middle/posterior cingulate and precuneus. Similarly, the inferior frontal gyrus, an important part of the mirror system, was weakly but non-significantly active in the contrast mourning vs control. However, there was a significant interaction between picture type and the time trend indexing the progression of the blocks, due to a preferential late recruitment of this area while looking at the mourning pictures.

All these changes reflected a shift of activation from lower to higher associative areas that was more pronounced when viewing mourning pictures. Hence, the adaptations that took place over the course of the experiment may have reflected the progressive use of contextual information to appraise the negative meaning of drawings, suggesting progressive involvement of semantic analysis. A group of related models of the significance of shared activations seems particularly relevant in this respect (Wolpert et al. 2003; Wilson and Knoblich 2005; Kilner et al. 2007; Koster-Hale and Saxe 2013). These models propose that the recruitment of sensory and motor areas to identify bodies and actions can be explained by the predictive coding implemented in hierarchical cortical structures. This allows information to flow both ways between sensory and semantic representations. According to this model, representations active in areas higher in the hierarchy provide priors for inference on the appropriate representations at lower levels. In return, these latter provide further information to the higher areas to update the priors. Thus, the shift of activation to higher areas observed in the present study would in this model correspond to the evolution of the interaction between low and high levels in the perceptual hierarchy. The increased weight of semantic priors in the later phases of the experiment would reflect the increasing reliance on context to encode stimuli that are ambiguous at the level of visual form.

It is interesting to note the parallels between notions of modelling of motives and intentions implicit in the most sophisticated forms of cognitive appraisal and the existence in Panofsky's account of interpretive stages in the retrieval of meaning of visual artefacts that included 'insights into essential tendencies of the human mind' (Panofsky 1939, p. 15). Common to both is that meaning is retrieved through a construct that is never explicitly observable. Our participants may have not carried out an iconographic analysis as an art historian would have, but may have still retrieved the common thematic element of the mourning drawings, progressively appreciating different aspects of experience reflected in the individual pictures as variations of a latent common theme.

Supplementary data

Supplementary data are available at SCAN online.

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