The neural basis of humour comprehension and humour appreciation: The roles of the temporoparietal junction and superior frontal gyrus

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ABSTRACT

Psychological well-being and social acumen benefit from the recognition of humourous intent and its enjoyment. The enjoyment of humour requires recognition, but humour recognition is not necessarily accompanied by humour enjoyment. Humour recognition is crucial during social interactions, while the associated enjoyment is less critical. Few neuroimaging studies have explicitly differentiated between the neural foundations of humour comprehension and humour appreciation. Among such studies, design limitations have obscured the specification of neural correlates to humour comprehension or appreciation. We implemented a trichotomous response option to address these design limitations. Twenty-four participants rated 120 comics (90 unaltered with humourous intent and 30 caption-altered without humourous intent) as either funny jokes (FJ), not funny jokes but intended to be funny (NFJ), or not intended to be funny or non-jokes (NJ). We defined humour comprehension by NFJ minus NJ and humour appreciation by FJ minus NFJ. We measured localized blood oxygen level dependent (BOLD) neural responses with a 3T MRI scanner. We tested for BOLD responses in humour comprehension brain regions of interest (ROIs), humour appreciation ROIs, and across the whole-brain. We found significant NFJ–NJ BOLD responses in our humour comprehension ROIs and significant FJ–NFJ BOLD responses in select humour appreciation ROIs. One key finding is that comprehension accuracy levels correlated with humour-comprehension responses in the left temporo-parietal junction (TPJ). This finding represents a novel and precise neural linkage to humour comprehension. A second key finding is that the superior frontal gyrus (SFG) was uniquely associated with humour-appreciation. The SFG response suggests that complex cognitive processing underlies humour appreciation and that current models of humour appreciation be revised. Finally, our research design provides an operational distinction between humour comprehension and appreciation and a sensitive measure of individual differences in humour comprehension accuracy.

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1. Introduction

Humour is a fundamental element of social interactions and communication (Chan et al., 2012; Martin, 2007; Osaka et al., 2014; Samson et al., 2009; Watson et al., 2007). It enriches social exchange and has both physical and psychological benefits (Martin, 2007; Vrticka et al., 2013). Its psychological benefits range from intellectual pleasure (Franklin and Adams, 2011) to enhancing one's social status or sexual appeal (Kane et al., 1977; Wanzer et al., 1996; Wilbur and Campbell, 2011), to serving as a socially effective way to provide social criticism (Vrticka et al., 2013; Watson et al., 2007). Interpersonal humour can be subtle. Among psychiatric populations, humour processing deficits exist (Frewen et al., 2008; Polimeni and Reiss, 2006; Polimeni et al., 2010; Samson et al., 2011; Samson et al., 2012, for a review see Vrticka et al. (2013)) and probably hinder social interactions.

Humour is a complex and multifaceted function involving a variety of specific cognitive and affective processes, content-related knowledge, and social-moral evaluations (Hempelmann and Ruch, 2005; Martin, 2007; Ruch, 2008; Vrticka et al., 2013). These complexities can be incorporated into a model based on two

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general outcomes: humour comprehension and humour appreciation (Chan et al., 2012; Vrticka et al., 2013; Wyer and Collins, 1992). Typically, humour comprehension (*getting the joke*) definitions have focused on understanding the context of the humour and recognizing expectation violations or incongruity (Coulson et al., 2006; Ruch, 1992; Uekermann et al., 2007; Vrticka et al., 2013). But, humour comprehension also requires affective processing. For example, humour comprehension requires the recognition of intended playfulness-a form of affective processing. Typically, humour appreciation (*enjoying the joke*) definitions have focused on both positive emotional responses and cognitively complex processes such as the formation of integrated mental representations not captured during humour comprehension (Coulson et al., 2006; Uekermann et al., 2007; Vrticka,et al., 2013; Wyer and Collins, 1992). However, within the neuroimaging literature there has been a tendency to adopt a relatively dichotomous interpretation of assigning affective or pleasure-related brain regions to humour appreciation and cognition-related brain regions to humour comprehension. We suggest that these simplified interpretations are likely attributable to past neuroimaging designs which have not been optimized to differentiate between humour comprehension and humour appreciation.

Not only do humour comprehension and humour appreciation represent distinctly different psychological phenomena, each concept has distinctly different implications. For example, in many interpersonal interactions, recognizing that an individual is intending to be humourous is crucial for basic communication (e.g., "Are they serious or joking?"), while enjoying the humour comment – seems to be less important. In other contexts, the experience or expression of joy during a humourous exchange has its own separate advantages, such as enhanced affability. Therefore, insight into each type of humour outcome-comprehension or appreciation-is relevant to a range of important interpersonal and mental health issues. In this project, we examine the neural basis of each type of humour outcome using a novel functional magnetic resonance imaging (fMRI) design.

1.1. Brain regions of interest

Before reviewing key design issues for discriminating between humour comprehension and humour appreciation neuroimaging findings, we first will identify the brain regions consistently proposed to underlie each of these humour outcomes (see Vrticka et al., (2013), Uekermann et al. (2007) and Wild et al. (2003) for broader reviews of the literature). The inferior frontal gyrus (IFG), overlapping with Brodmann Areas (BAs) 45, 46, and 47, is thought to reflect the incongruity detection (Samson et al., 2009) and language processing (Bekinschtein et al., 2011; Goel and Dolan, 2001; Mobbs et al., 2003; Moran et al., 2004; Watson et al., 2007) components of humour comprehension. The temporal poles (TP; BA38) are thought to reflect semantic knowledge processing crucial for understanding the content-dependent aspects of humour (Azim et al., 2005; Mobbs et al., 2003). The temporoparietal junction (TPJ; BA22, BA39, BA40), which sometimes extends ventrally to include the temporo-occipital-parietal junction (TOPJ; BA37, BA39, BA40), also is thought to reflect incongruity detection (Mobbs et al., 2003; Moran et al., 2004; Neely et al., 2012; Osaka et al., 2014) with a particular role in *theory of mind* relevant incongruity resolution (Kohn et al., 2011; Neely et al., 2012; Osaka et al., 2014; Samson et al., 2008, 2009) cognitive processes underlying humour comprehension.

In contrast, the neural basis of humour appreciation typically is attributed to reward-related mesolimbic brain regions (Vrticka et al., 2013) such as the substantia nigra (Neely et al., 2012; Vrticka et al., 2013; Watson et al., 2007), nucleus accumbens (Neely et al., 2012; Watson et al., 2007), ventral striatum (Franklin and Adams,

2011), and ventral medial prefrontal cortex (Chan et al., 2012; Goel and Dolan, 2001). The amygdala also is commonly associated with humour appreciation and is thought to reflect subjective amusement (Bartolo et al., 2006; Chan et al., 2012; Franklin and Adams, 2011; Watson et al., 2007) or emotional salience processing (Moran et al., 2004). Thus, the mesolimbic and amygdala brain regions will serve as regions of interest (ROIs) in our examination of the neural correlates of humour appreciation, while the IFG, TP, and TPJ will serve as ROIs for our humour comprehension examination.

Another brain ROI is the superior frontal gyrus (SFG). It has been associated with various types of humour processing tasks (Chan et al., 2013; Kohn et al., 2011; Marinkovic et al., 2011; Samson et al., 2008, 2009; Shibata et al., 2014). The SFG is more commonly attributed to humour comprehension (Chan et al., 2013; Samson et al., 2009; Shibata et al., 2014). For instance, Chan and colleagues (Chan et al., 2012, 2013) attributed their SFG activation to humour comprehension, and more specifically, to the incongruity resolution process. They suggest that the SFG response reflects a variety of higher cognitive processes including "organizing thoughts, developing insights, disambiguating information, schema-shifting, and developing bridging inferences to establish a new context" (Chan et al., 2013, p. 174). The SFG also has been attributed to pleasure-related processing typical of humour appreciation (Kohn et al., 2011). The SFG is capable of complex cognitive integration potentially reflective of either humour comprehension or humour appreciation (Marinkovic et al., 2011). The previous study designs do not allow us to differentiate between humour comprehension or appreciation.

1.2. Design considerations

There is a growing number of studies generating insight into the brain regions underlying humour processing and its components (Vrticka et al., 2013). However, the majority of these studies have focused on specific cognitive mechanisms that may underlie humour comprehension or humour appreciation. For instance, some of these studies have focused on incongruity detection or resolution (Chan et al., 2013; Samson et al., 2008, 2009), semantic or ambiguity processing (Bekinschtein et al., 2011; Goel and Dolan, 2001), humour-content specific effects (Feng et al., 2014; Goel and Dolan, 2007; Watson et al., 2007), or humour-related insight (Amir et al., 2013). Given their design focus, these studies cannot differentiate fully humour comprehension from humour appreciation.

1.2.1. Funniness Is not enough

Many of the past neuroimaging studies of humour processing have examined the neural correlates of funniness ratings (Azim et al., 2005; Feng et al., 2014; Franklin and Adams, 2011; Kohn et al., 2011; Marinkovic et al., 2011; Ozawa et al., 2000). Although informative for examining parametric effects or the intensity of neural responses, these ratings do not allow for a clear distinction between humour comprehension and humour appreciation. For example, two early studies assumed that neural responses to comics rated as funny represented humour appreciation while neural responses to non-funny comics represented humour comprehension (Bartolo et al., 2006; Mobbs et al., 2003). But, low (or non-) funny ratings may reflect either an absence of humour comprehension (not understanding the humourous intent) or a lack of humour-related appreciation (understanding the humourous intent, but not finding it funny). High funniness ratings also cannot distinguish between humour comprehension or appreciation interpretations. A high funniness rating typically reflects both humour comprehension and humour appreciation. Thus, contrasts based on funniness ratings alone are not sufficient to discriminate

between humour comprehension and humour appreciation neural responses.

1.2.2. Timing Is not everything

Another approach has been to discriminate between humour comprehension and humour appreciation neural responses based on temporal sequencing (Moran et al., 2004; Osaka et al., 2014). Under this approach, humour comprehension was defined by the neural responses which occurred during the presentation of pre-liminary humourous stimuli, which created comedic expectations and incongruities (Moran et al., 2004; Osaka et al., 2014). Humour appreciation was defined by the neural responses which occurred during the delivery of humourous stimuli which resolved the co-medic incongruity (Moran et al., 2004; Osaka et al., 2014). But, this design approach does not capture neural responses to understood, but unappreciated humourous stimuli. Moreover, the incomplete comedic presentations likely do not reflect the complete neural response associated with humour comprehension.

1.2.3. Humour-free parallel processes

A third design approach for differentiating between humour comprehension and humour appreciation has been to create a humour-free condition which matches the humour condition on a specific cognitive process (Amir et al., 2013; Bekinschtein et al., 2011; Chan et al., 2012, 2013; Shibata et al., 2014). The neural basis of humour comprehension per se was then defined by the neural response attributable to the cognitively parallel, but humour-free condition. In one such set of studies (Chan et al., 2012, 2013), humour comprehension neural responses were defined by re-solvable incongruity stories (e.g., garden-path stories) relative to unresolvable stories (e.g., non-sense stories, (Chan et al., 2012). This operational definition of humour comprehension, however, reflects only part of the humour comprehension process-the in-congruity-resolution part, and is missing other processes asso-ciated with the psychological perception of humourous intent. In summary, past neuroimaging designs have not distinguished be-tween humour comprehension and humour appreciation in a wholistic and direct manner.

1.3. Current study design

To address this research gap, we developed a trichotomous subjective humour-evaluation design. We had participants cate-gorize comics as either (1) funny (funny joke-FJ), (2) not funny, but intended to be funny (non-funny joke-NFJ), or (3) altered and not intended to be funny (non-joke-NJ). We then defined the neural basis of humour comprehension by NFJ trials relative to NJ (ac-curately recognized) trials. The NFJ trials represent humour com-prehension without humour appreciation. The NJ trials represent processing and comprehension of visual, language, and story-re-lated information conveyed in comics, but without a humourous component. Thus, the NFJ–NJ contrast avoids neural responses associated with humour appreciation, while capturing humour comprehension-specific processing. We defined the neural basis of humour appreciation by FJ trials relative to NFJ trials. The FJ trials represent humour appreciation and comprehension processing. Thus, the FJ–NFJ contrast removes NFJ-related humour compre-hension effects and reflects specific and unique neural responses of humour appreciation.

1.4. Hypotheses

Based on the extant literature, we hypothesized that humour comprehension would be associated with significant neural re-sponses in the inferior frontal gyri (IFG; BA45, BA46, BA47), the temporal poles (TP; BA38), and the temporoparietal junction (TPJ;

BA22, BA39, BA40). We hypothesized that humour appreciation would be associated with amygdala and mesolimbic centres of the brain, such as the substantia nigra, nucleus accumbens, and the ventral medial prefrontal cortex (Vrticka et al., 2013). We also expected that sub-regions of the superior frontal gyrus (SFG) would be associated with humour processing (Vrticka et al., 2013). Because the specific SFG location has varied from study-to-study (Amir et al., 2013; Bekinschtein et al., 2011; Chan et al., 2013; Kohn et al., 2011; Marinkovic et al., 2011; Samson et al., 2008, 2009), we adopted a whole-brain exploratory analysis approach for the SFG. We expected that our study design would clarify the role of the SFG in humour comprehension or humour appreciation proces-sing. In summary, we developed a novel test of humour processing to segregate neural responses to humour comprehension from those linked to humour-appreciation.

2. Materials and methods

2.1. Participants

We recruited 24 right-handed volunteers (14 females) through poster adver-tisements. A trained interviewer screened participants using the Mini International Neuropsychiatric Interview (MINI) screen (Sheehan et al., 1998) to exclude anyone with a major mental health disorder. Written informed consent was obtained from participants prior to participation, and procedures met the requirements of the local ethics board. The participants had a mean age of 30 years ($SD=13$); 17 par-ticipants had high-school or trade-school diplomas, and seven had university degrees.

2.2. Humour task

Participants were placed in a prone position within an MRI chamber. We pre-sented comic stimuli and recorded the participants' responses using EPrime soft-ware (version 2.0). Participants viewed images and text through a mirror-projec-tion screen system and responded via a five-button MRI compatible glove. To en-sure temporal synchrony between the comic presentations and the neuroimaging recordings, each experimental run initiation was synchronized with the onset of the functional MRI scans.

2.2.1. Comic selection criteria

With the goal of differentiating between the neural basis of humour compre-hension and humour appreciation, we had participants provide subjective comic ratings, via button-pressing, to indicate whether the comics were funny (FJ–third finger), not funny, but intended to be funny (NFJ–second finger), or not intended to be funny (NJ–first finger). We selected comics representing a diverse range of hu-mour topics and styles (described below) to appeal to a wide-range of humour preferences (Martin, 2007; Ruch, 2008). This diversity was designed to generate a reasonable number of both NFJ and FJ evaluations for each participant. Given the time restrictions inherent in fMRI experiments, we selected comics that partici-pants could view and evaluate quickly. For this purpose, we used single-panel comics with brief text-based captions or no caption.

2.2.2. Comic alteration method

The NJ comics served as a baseline control condition for the NFJ comics and, in one set of analyses, the FJ comics. We constructed our altered comics to induce basic visual, language, and semantic processing equivalent to the original comics (Samson et al., 2008, 2009). To achieve this equivalency, we replaced the original comic captions with captions that eliminated the humourous intent of the original comic. For example, one comic shows Santa Claus and his reindeer flying through the night sky with his whip in use. The original caption reads, "*For a kindly old man, he's mighty quick with the whip.*" The replacement caption reads, "*Merry Christmas to all! And to all a good night.*" In another comic, an image displays a crowd of people running in the same direction on a floor patterned in squares. The original caption reads, "*Back to square one*" presumably stated by the lead runner to a nearby bystander. The replacement caption reads, "*Where is everybody going?*" presumably asked by the bystander. Thus, the caption replacement represented a plausible and literally obvious description of the visual events or scene and re-moved the humourous intent of the original caption.

2.2.3. Pilot testing and item-level analyses

We conducted a pilot test of an initial set of 160 comics composed of 120 original comics and 40 caption-altered comics. Fifteen participants rated each of the 160 comics on a 1 (not at all) to 9 (extremely) funniness scale. We eliminated

the 30 least funny original comics and the 10 funniest caption-altered comics to provide a clear, subjective differentiation between the altered and original comics. An item-level analysis of the final set of 120 comics confirmed that the original comics ($M=4.88$, $SD=0.95$) were rated as significantly more funny, $t(98.2)=14.8$, $p<0.0001$, than the altered comics ($M=2.90$, $SD=0.49$). Among the 120 comics, original and altered comic sets did not differ significantly in the average number of characters (people and animals) within each comic set (Mdn=2, Mann-Whitney $U=1277$, $p=.64$, $z=-.47$). Similarly, the number of words in the 90 original un-altered comic captions (Mdn=7.5) did not differ significantly, ($U=1160$, $p=.25$, $z=-1.16$) from the 30 altered comic captions (Mdn=8.0). Finally, we also found that funniness ratings were not correlated with the number of characters within the comic nor the number of words within the caption, $r(118)=-0.06$, $p>0.50$ and $r(118)=-0.03$, $p>0.72$, respectively.

2.2.4. Comic sources

A detailed description of the full set of 120 Gray-scale, single-panel comics are presented in the Comic Appendix. Thirty of the comics came from a previous study of humour recognition (Polimeni and Reiss, 2006). Eight comics came from another humour processing study focused on perspective taking (Gallagher et al., 2000). The remaining 82 comics came from the internet and The New Yorker comic database ($n=53$; Mankoff et al., 2004, 2006, see Appendix). The comics include the work of more than 40 cartoonists, including those by Jim Unger (Herman), Gary Larson (Far Side), and Tom Wilson (Ziggy). Caption text was minimal (for quick responses useful in an fMRI study), and topics did not depend on awareness of particular current events or level of education. They did require a certain level of awareness of North American culture in that some comics showed sports such as boxing, basketball, or golf, or familiar characters such as Santa Claus, Martian space ships, cowboys, or prisoners (see Appendix for details). Our participants were Canadians familiar with North American culture.

2.2.5. Comic sequencing design

We presented the 120 comics in three experimental runs of 40 comics each, consisting of 30 original comics and 10 caption-altered comics. Previous event-related fMRI studies successfully used a similar number of items per condition (Bartolo et al., 2006; Watson et al., 2007). We counterbalanced the order of the three experimental runs across participants, and the sequence of comics within each run was pseudo-randomized and consistent across participants. This event-related design: (1) minimized confounding effects due to boredom and cognitive anticipation, (2) enabled a separate modelling of condition effects with closely spaced trials, and (3) allowed for optimal hemodynamic modelling of the neural response for trial timings based on participant-driven responses. The specific presentation sequence selected produced the least error variance for the contrasts of interest, based on a Monte Carlo simulation (Cox, 1996).

2.2.6. Comic timing

Each run lasted 7 min and 31.5 s. Within each run, each comic trial lasted 10.5 s; after every tenth comic, reminder task instructions were presented for 10.5 s to provide a short break for the participants. Within trials, the effective, user-driven inter-stimulus interval was 5.4 s ($SD=1.0$ s) for NJ, 5.0 s ($SD=1.0$ s) for NFJ, and 5.6 s ($SD=0.8$ s) for FJ.

2.3. MRI acquisition

Both structural and functional brain images were collected with a 3T Siemens TIM Trio MRI system with a standard transmit/receive head coil. The structural scan for each individual used a T1-weighted fast spin-echo sequence with 176 1-mm thick sagittal slices covering the whole brain with $TR=1900$ ms, **TE**$=2.2$ ms, flip angle=9, $FOV=25.6$ cm, $Matrix=256\times256$, and a resulting voxel size of 1 mm.[3] Functional scans for each individual were acquired using a single-shot gradient-echo, EPI sequence. T2 volumes were acquired using forty 3-mm thick oblique axial slices (30° from horizontal towards the dorsal surface of the brain) covering the whole brain with $TR=3000$ ms, $TE=30$ ms, flip angle=90, $FOV=230$ mm, $Matrix=64\times64$, and a resulting voxel size of 3.6 mm.[3] The TE of the functional scans is known to produce good quality images and reduce serious susceptibility artifacts in similar 3T systems (Deichmann et al., 2002).

2.4. Analyses

2.4.1. fMRI preprocessing and analyses

We conducted image processing and analyses with Analysis of Functional NeuroImages (AFNI) software (Cox, 1996). Functional data preprocessing steps included the following procedures (see afni_proc.py command for details): (1) excluding the first two volumes to allow for MRI saturation and equilibration, (2) correcting within-volume slice-time offsets, (3) conducting between-volume co-registration to the fifth volume of the first run, (4) warping and aligning structural and functional volumes into Talairach and Tournoux space (Saad et al., 2009), (5) spatial smoothing (isotropic 3.5-mm kernel) to reduce variability and generate group maps, (6) normalizing data to a mean of 100 to generate percent

signal change (Pose et al., 2011), and (7) creating time-series regression covariates of the six mean head-movement parameters (rotations and displacements). We also created temporally extended gamma-variate hemodynamic response function (HRF) convolutions (AFNI BLOCK 5.5 s) of the presentation time-series for each event type. These time-series convolutions were applied to the following statistical covariates: instructional reminders, inaccurately identified altered-comic trials, and inaccurately identified original comic trials. These HRF convolutions also were applied to the NFJ and FJ trials to create our time-series regression predictors of interest. The resulting humour-specific regression estimates of interest are relative to the accurately identified NJ trials and represent partial (residual) BOLD regression coefficients after controlling for all other predictors, covariates, the intercept, and polynomial trends in the model. The time-series analyses were based on an ordinary least squares (OLS) estimation method.

2.4.2. Hypothesized contrasts and supplementary contrasts

With the resulting NFJ and FJ regression coefficients, we tested our humour comprehension and humour appreciation hypotheses using a repeated-measures ANOVA to identify voxels and spatial clusters associated with NFJ trials, FJ trials, and an FJ versus NFJ contrast. For the humour-comprehension hypotheses, we contrasted NFJ trials relative to the NJ trials (the statistical baseline condition). For the humour-appreciation hypotheses, we also contrasted FJ trials relative to NJ trials. This common NJ control condition allowed us to compare FJ and NFJ responses at the cluster-level. To conduct the cluster-level FJ–NFJ contrasts, we used repeated measure ANOVAs based on the extracted cluster means for FJ and NFJ. We conducted a second set of humour-appreciation tests comparing FJ and NFJ neural responses directly at the voxel-level prior to clustering. This latter contrast provided a potentially more spatially precise neural test of humour appreciation. We used ordinary least squares software to analyse the extracted cluster-means using repeated measures ANOVAs and post hoc t-tests. We also conducted analysis of covariance (ANCOVA) or regression analyses to control for differences in participant-generated sampling density (trial counts) and response times among humour conditions. We also conducted exploratory correlational analyses between behavioural responses and neural responses.

2.4.3. Humour-comprehension ROIs

Based on the literature, we defined three bilateral humour-comprehension ROIs. Given the variability in reported activation foci in the literature, we used relatively large search regions for the inferior frontal gyrus (IFG), temporal pole (TP), and temporoparietal junction (TPJ). We defined our ROI search regions using the Talairach coordinate system with positive numbers indicating a right, anterior, or superior placement within the Talairach system. The IFG search region was defined by the AFNI Talairach Atlas (i.e., IFG map) and then further constrained within an x-axis range of 32–64 (or -32 to -64), a y-axis range of -20 to 20, and a z-axis range of 0–50. Each lateral IFG search volume was 20,580 µL. The TP search region was defined by the AFNI Middle and Superior Temporal gyri maps and further restricted to an anterior position of $y\geq-6$. Each lateral TP search volume encompassed BA38 and was 25,254 µL. For the TPJ, AFNI maps of the superior temporal, supramarginal, and angular gyri were selected and then constrained within a y-axis range of -32 to -64 and a z-axis range of 0–34. Each lateral TPJ search volume was 22,295 µL. These ROI masks encompassed the previous humour-related findings in the IFG (Mobbs et al., 2003; Samson et al., 2008; Watson et al., 2007), TP (Bekinschtein et al., 2011; Franklin and Adams, 2011; Mobbs et al., 2003; Moran et al., 2004; Samson et al., 2008, 2009) and TPJ (Franklin and Adams, 2011; Neely et al., 2012; Samson et al., 2008, 2009; Watson et al., 2007).

2.4.4. Humour-appreciation ROIs

Based on the literature, we defined four humour-appreciation ROIs. The ventromedial (vm) PFC was defined by the left and right AFNI DKD Desai Atlas map of the medial orbitofrontal cortex (search volume=18,136 µL). This vmPFC search region encompassed the previously identified humour-appreciation-related vmPFC areas (Chan et al., 2012; Goel and Dolan, 2007; Goel and Dolan, 2001). The bilateral nucleus accumbens, substantia nigra, and amygdala ROIs were defined using 8 mm spheres (3.5 mm[3] blocky volumes=2144 µL). Consistent with previous findings, the nucleus accumbens was centred on $x=\pm11$, $y=-10$, and $z=-8$ (Azim et al., 2005; Chan et al., 2012; Goel and Dolan, 2007, 2001; Mobbs et al., 2003; Watson et al., 2007), the substantia nigra was centred on $x=\pm10$, $y=-18$, and $z=-8$ (Neely et al., 2012; Watson et al., 2007), and the amygdala was centred on $x=\pm24$, $y=2$, and $z=-16$ (Bartolo et al., 2006; Chan et al., 2012; Moran et al., 2004). If, for any of these ROI maps, voxels were not present in at least 80% of the participants' anatomical images (due to variability in brain volume and structure), they were removed.

2.4.5. Superior frontal gyrus

The specific location of the SFG associated with humour processing has varied across studies (Chan et al., 2012, 2013; Kohn et al., 2011; Marinkovic et al., 2011; Samson et al., 2008, 2009; Watson et al., 2007). So, we did not create a specific search region for the SFG. Instead, we conducted a whole-brain exploratory search for humour-related SFG responses. Moreover, based on the literature, we considered SFG responses as potentially important in either humour comprehension, humour appreciation, or both.

2.4.6. Statistical criteria

To maintain an overall corrected family-wise alpha of $p=0.05$ for each set of ROIs, we applied a Monte Carlo simulation procedure to estimate the voxel-wise p-value and minimum cluster size needed (via the AFNI alphasim procedure), based on non-directional tests and the empirically estimated latent spatial correlation (via AFNI 3dFWHMx procedure). For the whole-brain search region, a minimum cluster of 1204 μL (28 voxels) and a voxel-wise $p=0.005$ maintained the overall $p=0.05$. Across the set of humour-comprehension ROIs (bilateral IFG, TP, and TPJ), an overall p-value$=0.05$ was maintained with a voxel-wise p-value$=0.005$ (height threshold) and a minimum cluster size of 558 μL (13 voxels extent threshold). Across the set of humour-appreciation ROIs (medial vmPFC, bilateral substantia nigra, bilateral nucleus accumbens, and bilateral amygdala), an overall p-value$=0.05$ was maintained with a voxel-wise p-value$=0.005$ (height threshold) and a minimum cluster size of 472 μL (11 voxels extent threshold).

3. Results

Humour-task performance results, fMRI BOLD responses, and exploratory tests of the association between task-performance results and neural responses are presented below.

3.1. Behavioural results

Participants' ratings of comics generated a mean of 43 FJ trials ($SD=12$), 34 NFJ trials ($SD=12$), and 18 accurately classified NJ trials ($SD=5$). The mean number of FJ trials was borderline significantly higher than the mean number of NFJ trials among the 90 originals comics, $t(23)=1.93$, $p<.07$. As well, the participants who identified more comics as FJ trials identified fewer trials as NFJ among the 90 comics, $r=-0.91$, $p<0.001$.

Across all trials, recognition of humourous intent was high with a mean accuracy score of 80% ($SD=5.5\%$). However, the mean accuracy rate for the original comics (90 comics, $M=86\%$, $SD=5.6\%$) was significantly higher, $t(23)=7.3$, $p<0.0001$, than for altered comics (30 comics, $M=61\%$, $SD=15.5\%$). Classification errors of the *original* comics represented falsely identifying an original comic as an altered comic without humourous intent. Thus, classification errors of original comics are humour-comprehension errors by operational definition. However, the classification errors of *altered* comics (NJ errors) may reflect either humour-comprehension errors or humour-appreciation responses. Across participants, a median of 8 of the 30 altered comics were misclassified as NFJ comics ($M=29\%$ of the 30 comics, $SD=14\%$) while a median of 2 of the 30 comics were classified as FJ comics ($M=10\%$, $SD=9\%$). Thus, the NJ classification errors primarily reflect humour-comprehension errors rather than humour-appreciation responses.

We estimated mean response times (RTs) excluding outliers (i.e., $RT>2.5\ SD$ from the mean). There was an overall RT difference by comic type, $F(2, 46)=15.7$, $p<.00001$. Post hoc comparisons revealed that NFJ responses were significantly slower ($M=5.5$, $SD=1.0$) than both FJ responses ($M=4.9\ SD=0.8$,
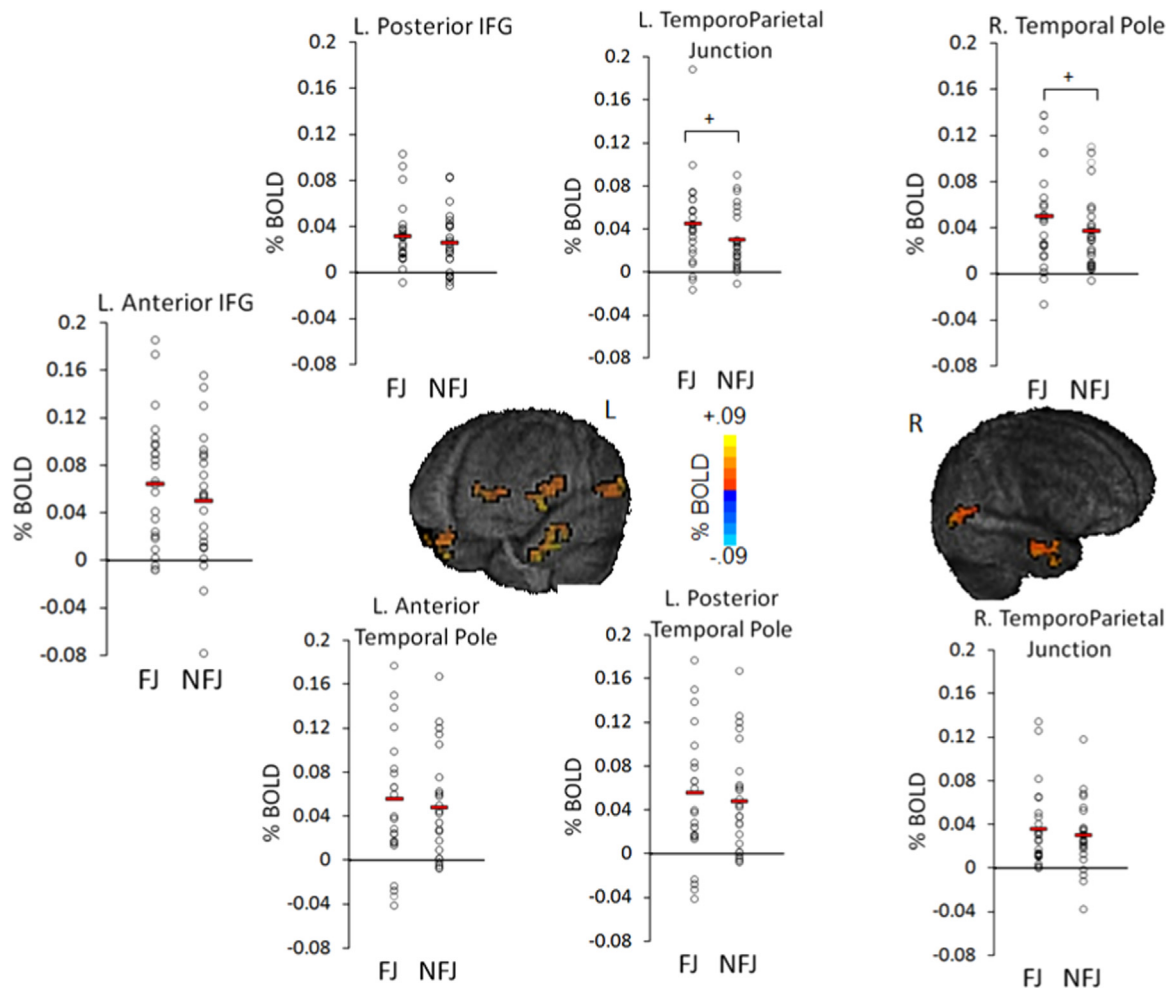

Fig. 1. The regions of interest humour-comprehension results are based on the within-voxel contrast of not-funny-as-intended comics (non-funny jokes; NFJ) relative to not-intended-to-be-funny comics (non-jokes; NJ) followed by clustering, based on voxel-wise $p<0.005$ and minimum cluster volume of 558 μL. The brain images show the clusters of significant blood oxygen level dependent (BOLD) responses in the left inferior frontal gyri (IFG), bilateral temporal poles (TP), and bilateral temporoparietal junctions (TPJ). In the scatterplots, a mean cluster-level BOLD response for each participant is represented by an open circle for the FJ and NFJ conditions. The group mean of these BOLD responses is represented by the solid rectangle in the scatterplots.

Table 1
Humour comprehension: ROI BOLD responses (NFJ trials relative to NJ trials).

Region	BA	Volume (µL)	Peak coordinates	Cluster t (23)		
				NFJ	FJ	FJ–NFJ
Left IFG	44,45,46,6	1415	− 54 22 13	4.8	5.7	6.3
–	47,45	686	− 54 26 − 2	4.4	5.8	6.3
Left TP	21,38	1458	− 44 2 − 30	4.8	4.0	5.6
Right TP	21,38	1244	47 12 − 32	3.6*	3.6*	4.5
Left TPJ	19,21,22,39	1500	− 61 − 58 16	5.4	5.3	6.1
Right TPJ	21,22,39	943	61 − 58 9	4.6	4.8	5.1

Note. ROI=Region of Interest. BOLD=Blood Oxygen Level Dependent. BA= Brodmann Area; IFG=Inferior Frontal Gyrus included the pars triangularis and pars opercularis; TP=Temporal Pole gyrus; TPJ=Temporo-Parietal Junction. Talairach coordinates reflect a positive right, anterior, and superior (RAS) orientation. Cluster t-values represent one-sample t-tests of the cluster means relative to zero.

  * t-value is significant at $p < 0.002$ while all other t-values are significant at $p < 0.001$ or less.

$p < .001$) and NJ responses ($M=5.1$, $SD=1.0$, $p=.001$). The FJ and NJ trials did not differ from one another in RT ($p > .05$). In summary, participants found a mean of 48% (43/90) of the original comics funny and 38% (34/90) non-funny. Misclassification errors of altered comics predominantly reflected humour comprehension errors. The mean evaluation RT was 5.1 s ($SD=0.9$ s) across all comic trials.

3.2. Imaging results

3.2.1. Humour-comprehension ROIs results

As hypothesized, significant humour-comprehension BOLD responses were found in the IFG (left), bilateral TPs, and bilateral TPJs (Fig. 1) within the ROIs. We presented the cluster volume and peak voxel locations for each of these ROIs in Table 1. Each participant's mean BOLD response for each of these clusters is displayed in the NFJ plots in Fig. 1. Given that funny trials also require humour-comprehension processing, we extracted and examined the FJ mean BOLD responses (relative to NJ trials) in the identified NFJ humour-comprehension ROIs. As expected, these FJ responses also were significant (see Table 1 and Fig. 1 FJ plots). Repeated-measures ANOVA contrasts of these FJ and NFJ cluster means confirmed that the FJ and NFJ BOLD responses did not differ from each other ($p > 0.05$, see Fig. 1 for two borderline differences). These results support the hypothesized role of the IFG (left), TP, and TPJ in humour comprehension for subjectively non-funny comics as well as subjectively funny comics.

3.2.2. Humour-comprehension whole-brain results

The unconstrained exploratory, whole-brain analyses replicated and extended the ROI findings. Although a right IFG cluster was not found within the pre-defined IFG ROI, a right IFG cluster that extended outside of the ROI search region was identified (see Table 2 and Supplementary Fig. 1). The whole-brain analysis also identified larger temporo-occipito-parietal junction (TOPJ) clusters which subsumed the TPJ findings in the pre-defined ROIs. The whole-brain analyses identified additional significant humour-comprehension-related BOLD responses in the supplementary motor area-cingulate cortex, post-central gyrus, and bilateral posterior ventral regions, including the fusiform gyrus and the cerebellum (see Table 2). Taken together, these results indicate that a broad set of brain regions are engaged reflecting the diverse set of tasks necessary for humour-comprehension.

Table 2
Humour comprehension: BOLD responses to NFJ comics relative to NJ comics.

Region	BA	Volume (µL)	Peak coordinates	t^*
Right fusiform gyrus	20,37,36	27,311	40 − 24 − 22	3.6
Parahippocampus	36	–	32 − 30 − 14	4.5
Cerebellum		–	18 − 48 − 18	7.4
Temporal and occipital gyri	18,19	–	50 − 74 − 6	5.1
Right TPJ	21,22,37,39	–	54 − 62 6	6.3
Left postcentral gyrus	2,3,4, 40	16,039	− 40 − 27 62	3.5
Precentral gyrus	4,6	–	− 34 − 18 58	6.0
Inferior parietal lobule	40	–	− 38 − 42 46	4.3
Left medial frontal gyrus	6,8,24,31	7546	0 − 12 56	4.3
Left cingulate gyrus	32	–	− 2 19 41	3.3
Right cingulate gyrus	24	–	7 4 39	3.3
Left inferior occipital gyrus	18,19,21,22,37,39	7417	− 50 − 76 − 2	3.7
Middle temporal gyrus	21	–	− 62 − 48 8	4.1
Left TPJ	37	–	− 54 − 62 8	6.3
Left fusiform gyrus	20	2230	− 37 − 37 − 19	4.1
Left cerebellum		–	− 28 − 39 − 21	3.7
Left IFG	44,45	1629	− 54 22 13	3.9
Left temporal pole	21,38	1586	− 44 2 − 30	3.7
Right middle frontal gyrus	6,9,44	1290	56 8 34	3.9
Right IFG	44	–	56 6 18	3.5

Note. BOLD=Blood Oxygen Level Dependent. BOLD responses are based on the non-funny comics intended to be funny (NFJ) relative to comics recognized as not intended to be funny (NJ). Talairach coordinates reflect a positive right, anterior, and superior (RAS) orientation reflecting either the peak voxel or a representative centre of mass voxel location for the identified sub-region. BA=Brodmann's Area; IFG=Inferior Frontal Gyrus; TPJ=Temporo-Parietal Junction.

  * t-value is significant at $p < 0.005$ or less.

3.2.3. Humour-appreciation ROIs results

Based on the FJ versus NJ humour-appreciation contrast, we found significant FJ responses in the bilateral substantia nigra (SN) and bilateral amygdala ROIs (see Fig. 2 FJ scatter plots and Table 3). Post hoc analyses on the cluster means revealed that the FJ BOLD responses were significantly greater than the NFJ BOLD responses in the right SN and right amygdala clusters (along with a borderline greater FJ response in the left SN). These FJ–NFJ cluster-extracted contrasts are displayed in the Fig. 2 bar charts with 95% confidence intervals. Unexpectedly, the voxel-level FJ versus NFJ humour-appreciation contrast did not identify any significant BOLD responses within our humour-appreciation ROIs.

3.2.4. Humour-appreciation whole-brain results

For the whole-brain exploratory assessment, the FJ versus NJ contrast identified a wide-range of significant FJ BOLD responses which subsumed all of the regions identified previously in the humour comprehension whole-brain analysis (Table 2) and the humour appreciation ROI analysis (Table 3). For the sake of brevity, we displayed these findings visually in Supplementary Fig. 2. The more specific voxel-wise contrast of FJ versus NFJ identified one significant cluster, the left superior frontal gyrus (SFG, Fig. 3a). In this SFG cluster, the mean BOLD response was significantly greater during FJ trials compared to the NFJ trials. This SFG region had a total volume of 2487 µL, overlapped with Brodmann Area (BA) 8, 9 and 10 maps, and had a peak voxel located at the Talairach coordinates of $x = − 16$, $y = 54$, and $z = 38$. The cluster mean BOLD responses for each participant for each condition (the circles) are displayed in the Fig. 3b scatterplots along with the group mean (the rectangles). The cluster mean BOLD response is significantly greater than zero for the FJ trials, $t(23)=4.1$, $p < 0.0005$, but non-
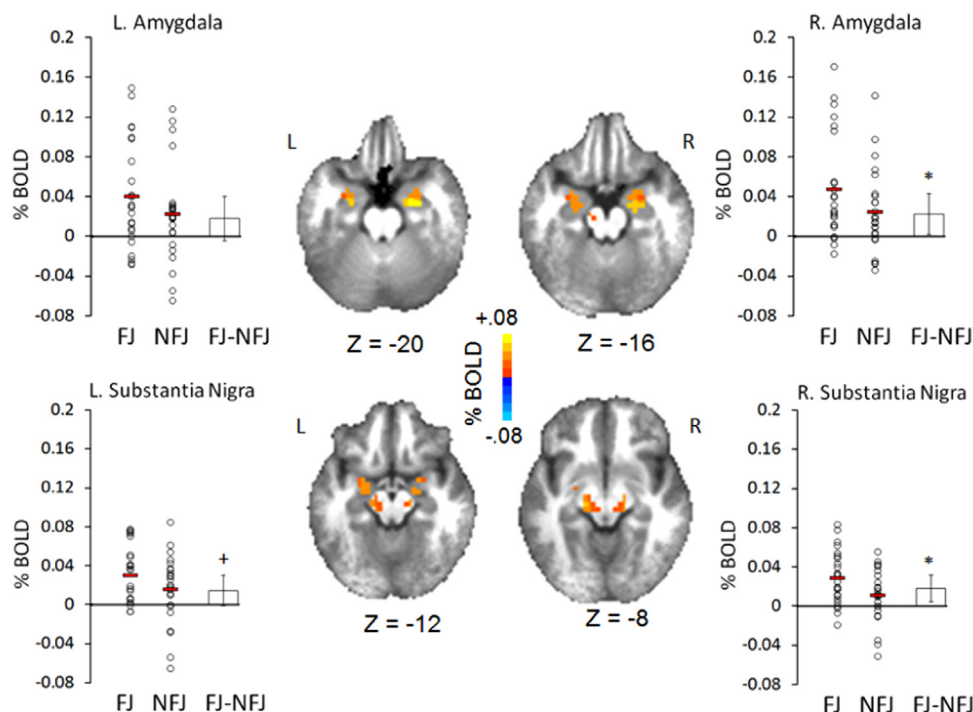
Fig. 2. The regions of interest humour-appreciation results are based on the within-voxel contrast of funny-as-intended comics (funny jokes; FJ) relative to not-intended-to-be-funny comics (non-jokes; NJ) followed by clustering, based on voxel-wise $p < 0.005$ and minimum cluster volume of 472 μL. The axial brain images show the clusters of significant blood oxygen level dependent (BOLD) responses in the bilateral amygdala and bilateral substantia nigra (SN). In the scatterplots, a mean cluster-level BOLD response for each participant is represented by an open circle for the FJ and NFJ conditions. The group mean of these BOLD responses is represented by the solid rectangle in the scatterplots. The bar graphs represent the mean of participants' cluster-level FJ minus NFJ difference scores and the error bars represent 95% confidence interval (CI) for this group-mean difference score. The 95% CIs illustrate that the right amygdala and right SN are significant, and that the left SN is trend-level significant. L=left, R=right, and negative z values indicate an inferior Talairach coordinate position.

Table 3
Humour appreciation: ROI BOLD responses based on the preliminary voxel-based contrasts of FJ trials relative to NJ trials.

Region	Volume (μL)	Peak coordinates	Cluster t (23)		
			FJ	NFJ	FJ–NFJ
Left Substantia Nigra	1500	−12 −20 −8	5.2[*]	2.2[†]	3.3[~]
Right Substantia Nigra	557	12 −20 −8	5.2[*]	1.9	7.2[†]
Left Amygdala	1243	−24 4 −20	3.7[†]	2.2[†]	2.5
Right Amygdala	1372	22 6 −18	4.3[*]	2.8[‡]	4.6[†]

Note. ROI=Region of Interest. BOLD = Blood Oxygen Level Dependent. Talairach coordinates reflect a positive right, anterior, and superior (RAS) orientation. Cluster t-values represent one-sample t-tests of the cluster means relative to zero.

[*] $p < 0.005$.
[†] $p < 0.05$.
[~] $p < 0.10$.
[‡] $p < 0.01$.

significant for the NFJ trials, $t(23)=0.6$, $p > 0.5$. The bar chart in Fig. 3b displays the significant mean difference score and 95% confidence interval for the FJ minus NFJ contrast, $F(1,23)=21.2$, $p < 0.0002$. The SFG finding represents a unique neural response associated with humour-appreciation processing separate from humour comprehension.

3.2.5. Examination of behavioural–neural associations

Under the behavioural results section, we reported on differences in the number of comic trials underlying funny (FJ) and non-funny (NFJ) neural response estimates, differences in the accuracy rates between altered and original comics, and differences in RT between NFJ trials relative to FJ and NJ trials. These behavioural differences could influence neural response estimates. NFJ, FJ, and FJ minus NFJ mean BOLD responses identified in the *a priori* ROIs

and the whole-brain SFG finding remained significant and were equivalent to the unadjusted analyses after controlling for individual differences in the number of NFJ or FJ trials relative to the number of NJ trials and the RT differences.

As an exploratory analysis, we conducted correlations between each of the NFJ, FJ, and NJ trial counts and RT responses with each identified ROI cluster and the SFG cluster. With one exception, all tested correlations were non-significant with $rs < \pm 0.35$, $ps > 0.05$. One interesting correlation was identified between the number of accurate trials identified for altered comics (out of 30) and the intensity of the BOLD response in the left TPJ cluster, $r=0.63$, $p < 0.002$. This indicates that higher levels of accuracy were associated with larger BOLD responses in this region. To verify that this correlation is robust and evident at the voxel level, we conducted a group-level, regression-based, AFNI analysis testing for the association between altered-comic accuracy levels and voxel-by-voxel BOLD responses. We identified a spatially equivalent left TPJ cluster (volume=1887 μL) with a minimum voxel-wise p of 0.005, and a peak voxel located at the Talairach coordinates of $x=−61$, $y=−51$, and $z=20$.

4. Discussion

This study differentiates the neural responses of humour comprehension from humour appreciation in a unique and direct manner. Our results suggest a revision to current neural models of humour processing (Chan et al., 2013; Vrticka et al., 2013). Specifically, we established neural involvement of the SFG during humour appreciation, not only during humour comprehension as typically proposed (Chan et al., 2013; Vrticka et al., 2013). Our design also enabled us to test for individual differences in humour comprehension accuracy leading to a second novel finding.
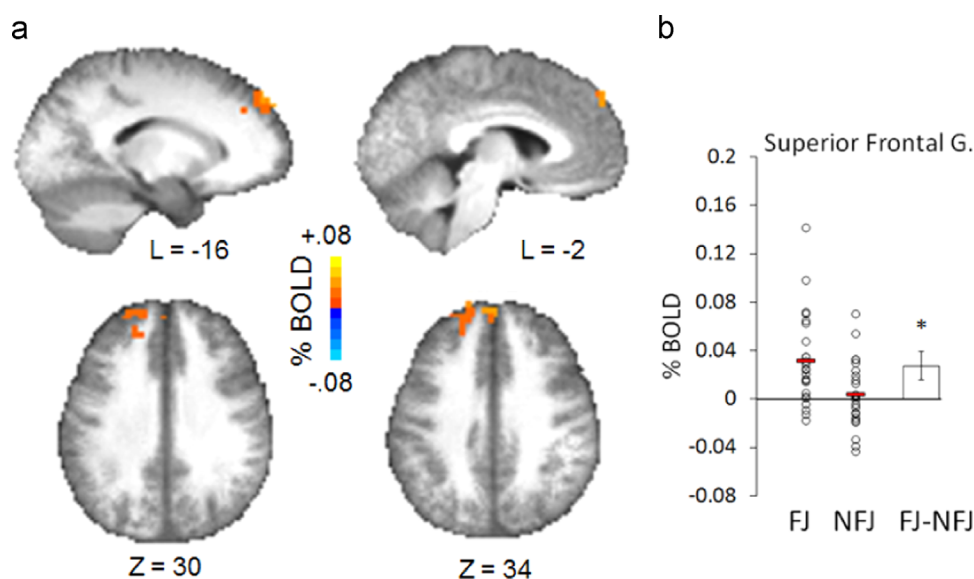
Fig. 3. The whole-brain exploratory humour-appreciation results are based on the within-voxel contrast of funny-as-intended comics (funny jokes; FJ) relative to not-funny-as-intended comics (non-funny jokes; NFJ) followed by clustering, based on $p < 0.005$ and a minimum cluster value of 1204 μL. a. The sagittal and axial brain images show the significant blood oxygen level dependent (BOLD) response in the dorsomedial superior frontal gyrus (SFG). $L=$ left, and Z refers to superior Talairach coordinate positions. b. In the scatterplots, a mean cluster-level BOLD response for each participant is represented by an open circle for the FJ and NFJ conditions. The group mean of these BOLD responses is represented by the solid rectangle in the scatterplots. The bar graph represents the mean of participants' cluster-level FJ minus NFJ difference scores, and the error bar represents the 95% confidence interval (CI) for this significant group-mean difference score.

Individual differences in humour comprehension accuracy are positively associated with left TPJ responses – a key humour comprehension processing brain region. We also replicated previous evidence of IFG, TP, and TPJ responses during humour comprehension and the right amygdala and right substantia nigra during humour appreciation. Below we discuss in greater detail the interpretations of these findings and explore future directions for building upon these results.

4.1. Humour comprehension

Our neural correlates of humour comprehension reflect non-funny evaluations of original comics recognized as having humourous intent (NFJ) relative to altered comics recognized to be without humourous intent (NJ).

4.1.1. Inferior frontal gyrus

We found significant BOLD responses in the left IFG, and to a lesser extent, the right IFG. Functional MRI studies suggest that the IFG (BA45, BA46, BA47), especially the left, is thought to play a central role in humour comprehension based on three key processes: language processing (Bekinschtein et al., 2011; Goel and Dolan, 2001; Mobbs et al., 2003; Moran et al., 2004; Watson et al., 2007), activation of semantic knowledge (Ferstl et al., 2005; Vrticka et al., 2013), and incongruity detection (Samson et al., 2009). Studies with neurological patients (Bihrle et al., 1986; Farrant et al., 2005; Heath and Blonder, 2005) and electrophysiological brain responses (Coulson and Williams, 2005; Marinkovic et al., 2011) also point to the role of the right IFG in humour-related incongruity resolution (Uekermann et al., 2007). Our results indicate that humour intent alone, without the experience of humour appreciation, is sufficient to induce humour-related IFG responses.

4.1.2. Temporal parietal junction

We found significant BOLD responses in the bilateral TPJ as well as the ventrally extended TOPJ during humour comprehension (NFJ) trials. We also identified a novel correlation between humour comprehension accuracy levels and degree of left TPJ response

intensity. This is a unique empirical finding and represents strong evidence of the link between humour comprehension and TPJ functioning. The TPJ (Mobbs et al., 2003; Moran et al., 2004; Neely et al., 2012; Osaka et al., 2014) and TOPJ (Kohn et al., 2011; Neely et al., 2012; Osaka et al., 2014; Samson et al., 2008, 2009) are thought to serve incongruity detection and incongruity resolution functions.

The interpretation of these IFG and TPJ findings may be informed by a language processing model, reporting parallel, but inter-related processing functions (Ferstl et al., 2005; Tesink et al., 2009). In this model, the bilateral IFG and left TPJ work together to unify contextual, linguistic, and extralinguistic knowledge (Ferstl et al., 2005; Tesink et al., 2009). Furthermore, the IFG is proposed to exert top-down control over the left TPJ to incorporate semantic information into a mental model to achieve unification. We propose that the IFG and TPJ play a central role in the *unification* of information activated by humourous stimuli.

4.1.3. Temporal Poles

Humour comprehension also requires accessing relevant world knowledge or semantic associations implied by the humourous stimulus (Vrticka et al., 2013). The temporal poles (TP, BA38) are thought to play an important role in semantic retrieval during humour processing (Azim et al., 2005; Mobbs et al., 2003), and we found significant BOLD responses in the bilateral TP, as hypothesized. As well, in our whole-brain exploratory analyses, we found BOLD responses in bilateral posterior ventral regions, including the fusiform gyrus, consistent with previous studies (Vrticka et al., 2013). These ventral posterior regions are thought to support visual-semantic knowledge retrieval and integration (Vandenberghe et al., 2013)-an essential requirement of processing visual humour. Our participants' recognition of humourous intent implies semantic association retrieval consistent with the engagement of the TP.

The whole-brain humour comprehension analysis identified a posterior section of the dorsal anterior cingulate cortex (dACC) and supplementary motor area (SMA). The dACC response is potentially reflective of incongruity detection-related processing (Vrticka et al., 2013). The SMA finding appears to reflect a

cognitive, humour-comprehension function rather than an expressive smiling response as previously suggested (Mobbs et al., 2003; Wild et al., 2003).

The current study reveals a diverse set of brain regions associated with humour-comprehension processing. Each region likely serves a specific, but inter-related processing function. Our design and neural findings demonstrate that humour comprehension can be differentiated from humour appreciation. However, humour comprehension is a necessary condition to humour appreciation. Consistent with this logical implication, we found humour appreciation-related neural responses in each humour comprehension brain region. An interesting next step will be to manipulate comic complexity to induce different levels of semantic associations (Samson et al., 2008) or ambiguity (Bekinschtein et al., 2011) under both non-funny and funny conditions, while ensuring humourous intent is understood. Such a study would generate a deeper understanding of the neural basis of humour processing.

4.2. Humour appreciation

We hypothesized significant BOLD responses in a number of reward-related and emotional salience centres within the brain (Bartolo et al., 2006; Chan et al., 2012; Franklin and Adams, 2011; Neely et al., 2012; Vrticka et al., 2013; Watson et al., 2007). We found partial support for these hypotheses with SN, amygdala, and SFG responses to humour appreciation. We did not find NA and vmPFC responses to humour-appreciation-related BOLD responses. Below we discuss the likely function each of these findings and suggest future investigations.

4.3. Substantia nigra: less predictable, but more funny

Previous studies report bilateral SN involvement in humour-appreciation-related neural responses (Neely et al., 2012; Vrticka et al., 2013; Watson et al., 2007). We identified a significant humour appreciation response in the right SN and a trend-level response in the left SN based on the cluster-extracted BOLD responses. These results reinforce the importance of the SN to the humour-appreciation process (Neely et al., 2012; Vrticka et al., 2013; Watson et al., 2007). As a core region of the brain's dopaminergic reward network (Ljungberg et al., 1992), the SN likely plays a central role in the experience of pleasure during humour appreciation.

Experiments in both primates and humans have shown that dopaminergic neurons are activated more intensely by unpredictable rewards and less intensely by fully predictable rewards (Ljungberg et al., 1992; Mirenowicz and Schultz, 1994). This unpredictability may parallel the incongruity detection and incongruity resolution elements of humour processing (Vrticka et al., 2013). For example, initially comics engender a certain interpretation of a scene, and thus create a subjective expectation or prediction. With continued evaluation, however, the comic captions (text) or visual detail violate the initial expectation. Further integration of the semantic associations resolves the violated expectation and leads to the reward and pleasure of the unpredicted experience. If the predictability of reward underlies the SN engagement in the humour-appreciation process, future studies could manipulate the predictability of humourous rewards to test further the role of the SN in humour appreciation.

4.4. Amygdala: a rewarding evaluation or salient?

Within the right amygdala, we found a significant humour appreciation response based on the cluster-extracted BOLD responses. This finding provides direct support for the hypothesized amygdala-humour appreciation association (Bartolo et al., 2006; Chan et al., 2012; Franklin and Adams, 2011; Watson et al., 2007).

Some researchers suggest that humour-related amygdala activation reflects the experience of positive emotions (Bekinschtein et al., 2011; Chan et al., 2012). Others suggest the amygdala serves to associate a new rewarding value to objects previously linked to an unrewarding value (Waracynski, 2006), consistent with the incongruity-resolution component of humour appreciation. A third interpretation is that the interpersonal relevance of humour engages the amygdala in its role as a salience detector (Vrticka et al., 2013). Our amygdala results indicate a clear link between the right amygdala response and the subjective experience of funniness, consistent with both the positive emotional experience and salience interpretations. Future studies will be needed to test among these alternative amygdala interpretations.

4.5. Voxel-level FJ–NFJ contrasts

We conducted a second set of humour-appreciation contrasts to differentiate between the enjoyment of humour and the understanding of humourous intent at the voxel-level. This analysis required a significant FJ minus NFJ difference within each voxel prior to clustering. These voxel-level analyses did not replicate the SN and right amygdala ROIs differences identified based on the cluster-level FJ–NFJ contrasts. We suspect that voxel-level FJ–NFJ contrasts lack the sensitivity of the cluster-level FJ–NFJ contrasts. As well, our humour appreciation control condition (NFJ trials) is highly similar in content and processing demands to funny (FJ) experimental condition representing a precise, but stringent control condition. Previous findings of voxel-level reward-centre funny responses (Bartolo et al., 2006; Bekinschtein et al., 2011; Chan et al., 2012; Franklin and Adams, 2011; Moran et al., 2004; Watson et al., 2007) may reflect less stringent control conditions or more effective humour-appreciation manipulations (i.e., funnier materials) resulting in relatively larger neural responses in the brain's reward circuits.

4.6. Superior frontal gyrus: humour appreciation is more than simple pleasure

Despite the stringent nature of our voxel-level *FJ minus NFJ* contrast, we find a significant SFG response to humour appreciation in the whole-brain analysis. Our SFG BOLD responses reflect humour-appreciation processing separate from humour-comprehension processing. Although other research groups have reported similar SFG cluster locations during humour processing (Bekinschtein et al., 2011; Chan et al., 2012, 2013; Samson et al., 2008, 2009), these previous studies have tended to attribute these SFG cortical regions to the humour comprehension process. A recent neural model (Chan et al., 2012) proposed that SFG responses reflect the humour comprehension process, not the humour elaboration process associated with amusement (funniness). The current results suggest that this model may need to be revised.

In general, the neuroimaging humour literature has tended to attribute responses in cortical regions-typically associated with complex cognitive processing-to humour comprehension, while responses in reward- and emotion-related brain regions are attributed to humour appreciation. This interpretation is likely overly simplistic. In a recent meta-analytic review, Vritcka and colleagues speculated that "… humour appreciation differs from a more generalized response to reward. This difference is probably related to the satisfaction of detecting and resolving incompatible elements of humour" (Vrticka et al., 2013, p. 4). Our empirical SFG finding provides evidence for this perspective. Our SFG finding emphasizes that the neural basis of humour appreciation is more than a simple pleasure response. It likely plays a crucial role in the development of an integrated and cohesive evaluation of humourous experience.

4.7. Limitations and future directions

Although select areas of the brain's reward circuit were engaged during humour appreciation, other reward regions were not engaged. One potential explanation is that the humour stimuli are not sufficiently funny. The behavioural response data show that participants reported a substantial number of the comics as funny. However, we did not measure funniness intensity with continuous post-scan humour ratings (Bekinschtein et al., 2011; Chan et al., 2013; Franklin and Adams, 2011; Goel and Dolan, 2001; Mobbs et al., 2003; Watson et al., 2007). Humour content also may have limited the sensitivity to vmPFC engagement, which appears to be moderated by the social appropriateness of the content (Goel and Dolan, 2007). Socially inappropriate content, for example, was minimal in the current study's set of comics and may have reduced our vmPFC engagement. Future studies should utilize a broader set of comics in terms of humourous intensity, complexity, and morality to offer a more sensitive assessment of humour appreciation and a stronger differentiation from humour comprehension.

5. Conclusions and implications

We developed a trichotomous humour assessment procedure to separate the neural correlates of humour comprehension from humour appreciation. This design reveals that the dorsomedial superior frontal cortex shows unique neural responses to humour appreciation, implying that complex cognitive processing underlies humour appreciation. This finding suggests that neural models of humour appreciation need to include the SFG, not only mesolimbic and other affect-related brain regions. Our trichotomous research design also allowed us to capture individual differences in humour comprehension accuracy. With this information, we show that individual differences in humour accuracy levels correlate with the intensity of participants' left TPJ responses – a strong indication of its role in humour comprehension. This simple and sensitive measure of individual differences in humour comprehension opens up new investigation avenues. Taken together, our findings suggest that, with careful design, humour investigations can provide insight into complex cognitive and emotional functioning in future studies of both healthy and clinical populations known to show humour processing deficits (Frewen et al., 2008; Polimeni et al., 2010; Samson et al., 2012, 2013).

Acknowledgements

The neural basis of humour comprehension and humour appreciation: The roles of the temporoparietal junction and superior frontal gyrus

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2015.10.013.

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