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Emotional and cognitive stimuli differentially engage the default network during inductive reasoning

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The brain's default network (DN) is comprised of several cortical regions demonstrating robust intrinsic connectivity at rest. The authors sought to examine the differential effects of emotional reasoning and reasoning under certainty upon the DN through the employment of an event-related fMRI design in healthy participants. Participants were presented with syllogistic arguments which were organized into a 2 $\times$ 2 factorial design in which the first factor was emotional salience and the second factor was certainty/uncertainty. We demonstrate that regions of the DN were activated both during reasoning that is emotionally salient and during reasoning which is more certain, suggesting that these processes are neurally instantiated on a network level. In addition, we present evidence that emotional reasoning preferentially activates the dorsomedial (dMPFC) subsystem of the DN, whereas reasoning in the context of certainty activates areas specific to the DN's medial temporal (MTL) subsystem. We postulate that emotional reasoning mobilizes the dMPFC subsystem of the DN because this type of reasoning relies upon the recruitment of introspective and self-relevant data such as personal bias and temperament. In contrast, activation of the MTL subsystem during certainty argues that this form of reasoning involves the recruitment of mnemonic and semantic associations to derive conclusions.

Keywords: default network; emotional reasoning; certainty; uncertainty; fMRI

INTRODUCTION

Reasoning is undoubtedly a heteromodal process that involves the recruitment of several cognitive domains. These include, but are not limited to: working memory, episodic retrieval, analogy and abstraction. Still, some authors have pointed to supramodal neural networks responsible for reasoning (Rodriguez-Moreno and Hirsch, 2009), and there is evidence to suggest that the type of network being recruited is dependent on the 'content' of the logical problem to be solved (Goel, 2007a). Two types of content-the emotionality of the logical argument, and the extent to which the reasoner is certain or uncertain about the conclusion-seem to have particularly strong influences upon the reasoning process. This is possibly due to the fact that in both of these types of reasoning, the reasoner must draw upon some form of personal or introspective data in order to derive a conclusion. With respect to the effects of emotion upon reasoning, there is mounting evidence to suggest that reasoning can be biased by an emotional investment in the conclusion being drawn. For instance, behavioral studies (Blanchette and Richards, 2004; Blanchette, 2006; Oaksford and Chater, 2001) have found that subjects were more likely to make invalid deductions while reasoning about emotional material in comparison to neutral materials. Still, emotional reasoning should not be conceptualized as simply being reasoning in presence of emotional (or semantically rich) materials. Instead, we define 'emotional reasoning' as being a form of logical reasoning in which a conclusion is drawn that is implicitly influenced by the affective state induced in the reasoner. In a related manner, reasoning also appears to heavily depend upon the reasoner's prior knowledge of, and thus certainty of, the material contained within a logical argument. For example, one study involving patients with prefrontal lesions found a hemispheric specialization for reasoning in certain and uncertain contexts (Goel *et al.*, 2007b). Although it is tempting to define 'certainty reasoning' as reasoning which is less cognitively taxing, we here define it as being a form of logical reasoning in which the conclusion is influenced by mnemonic and semantic associations employed by the reasoner.

Still, the neural instantiation of emotional and certainty reasoning, as here defined, remain poorly understood. One

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of the few studies to examine emotional reasoning was performed by Goel and Dolan (2003). These authors demonstrated reciprocal activations between the dorsolateral prefrontal cortex (DLPFC) and the ventromedial prefrontal cortex (vMPFC), based upon whether subjects reasoned about neutral material or emotional material, respectively. The authors went on to argue that the association of vMPFC with emotional reasoning resonated with several other studies of emotional decision-making. For example, vMPFC is critical to reward-based learning (Hansel and Van Kanel, 2008; Knutson *et al.*, 2005; McClure *et al.*, 2004). In addition, Damasio and colleagues' showed that the orbitofrontal cortex coordinates somatic markers which convey emotional and motivational relevance during decision-making (Bechara *et al.*, 1997; Damasio, 1996). Such a role for the vMPFC in emotional decision-making is also supported by lesion data, and on the basis of rich anatomical interconnections between vMPFC and areas which accumulate emotionally salient information from visceral structures and the outside world (Fellows, 2007).

However, Goel and Dolan used a 'deductive' and not an 'inductive' reasoning task. This distinction is critical, as inductive reasoning more closely parallels real-world judgments, where the reasoner can only assess the probability of a given conclusion, and not its inherent validity (Goel and Dolan, 2000). That is, deduction relies upon the application of premises contained within a logical argument, and thus is often predicated on syntactic and linguistic features of said argument (Goel, 2007). Induction, on the other hand, involves the extrapolation of given premises in order to formulate new rules and hypotheses. In this way, during induction the reasoner is more prone to draw upon his/her own 'personal' knowledge and experience, than in deduction, where one is more likely to depend upon 'external' and universally established rules (Goel *et al.*, 1997). Therefore, induction is far more likely to be biased by content such as emotional valence and level of certainty.

We thus set out to employ an inductive task to examine the neural instantiation of the effects of both emotion and certainty upon reasoning. We hypothesized that each of these factors would result in activation of a network of areas, (rather than one circumscribed region such as vMPFC) and that these areas would anatomically overlap with those of the brain's Default Network (DN). We based this hypothesis on two general properties about the DN: (i) that the use of an inductive task would be more likely to activate the DN than a deductive one and (ii) that emotional content and certainty during induction would both cause preferential recruitment of the network. First, prior evidence suggests that the DN might be involved in the inductive process. The network is thought to mediate the computation of probabilities (Raichle and Gusnard, 2005), a process central to inductive reasoning (Goel and Dolan, 2004). Also, the DN relies upon mnemonic associations to compute such probabilities (Bar, 2009; Bar *et al.*, 2007), and Corcoran (2010) has argued that this process parallels the hypothesis generation characteristic of inductive reasoning. Also, when directly contrasting deduction and induction, inductive reasoning activated key anterior components of the DN, specifically Brodmann areas 9, 24 and 32 (Goel *et al.*, 1997). Second, extant data supports a potential role for the DN in emotional reasoning and for reasoning with certainty. The DN has repeatedly been shown to activate during decision-making which relies upon implicit social knowledge and self-reflection (Schneider *et al.*, 2008; Gusnard *et al.*, 2001), thus making the case for it to be so activated during emotional reasoning. There is also evidence to suggest that reasoning which relies on well established semantic associations and prior knowledge (and thus greater certainty) activates components of the network-specifically the medial temporal lobe (Bar, 2009).

We went on to formulate more specific hypothesis with respect to the ways in which the DN would be activated by emotional and certainty reasoning. That is, we theorized that two different network subsystems would be engaged during each of these conditions. Andrews-Hanna and colleagues (2010) recently differentiated two subsystems of the DN: a dorsomedial (dMPFC) subsystem [comprised of the dMPFC, the temporoparietal junction (TPJ), the lateral temporal cortex (LTC) and the temporal pole (TP)], which is activated when affective information is referenced to the self, and during the reflection of one's mental state (and the mental state of others); and a medial temporal (MTL) subsystem. The latter subsystem, comprised of the hippocampal formation (HF), vMPFC, the retrosplenial cortex (RsP), the parahippocampus (PHC) and the posterior lateral inferior parietal cortex (pIPL), appears to be involved in using mnemonic information to simulate future contexts. This raises the possibility that in the context of high levels of mnemonic association to, or semantic knowledge about, an inductive argument, the MTL subsystem might be mobilized. The authors therefore hypothesized that emotional reasoning, relative to neutral reasoning, would increase activity in the dorsomedial subsystem of the DN; whereas reasoning in the context of high levels of certainty, relative to reasoning in the context of uncertainty, would increase activity in the medial temporal subsystem of the DN. To test these hypotheses, we employed a 2×2 factorial design in which inductive arguments varied based on emotional salience and on the basis of certainty level. The former was accomplished by dividing arguments into emotional and neutral categories. The latter was accomplished by partitioning arguments into 'certain' and 'uncertain' categories.

METHODS

Subject participants

Twenty right-handed (confirmed by the Edinburgh handedness inventory) healthy adults (10 females; ages 21–32 mean = 24.25, s.d = 3.04) participated in the experiment. All subjects were native English speakers. Participants were recruited through the Division of Psychiatric Neuroscience Research and Neurotherapeutics at the Massachusetts General Hospital via bulletin board notices within the hospital. All participants provided written informed consent prior to participation in accordance with the guidelines of the Subcommittee on Human Studies of the Massachusetts General Hospital. Participants were screened to ensure the absence of any neurological or psychiatric condition via the use of clinical interviews performed by a physician as well as via the use of the following diagnostic assessment batteries: the Structured Clinical Interview for DSM-IV (SCID) (First *et al.*, 1995), the Beck depression Inventory (Beck *et al.*, 1996) and the Hamilton Depression Rating Scale (Hamilton, 1960).

Task

We patterned the experimental task from that used by Goel and Dolan (2003). Subjects were presented with logical arguments in the form of a syllogism, which is a three sentence logical argument in which the first two sentences constitute premises of the argument and the third sentence represents the conclusion (Goel, 2007a). As an example, subjects were presented with the following two premises: 'Molly plays a rare sport' and 'Molly is rather tall' and this was followed by the conclusion: 'Most women who play this sport are tall'. Upon presentation of the third sentence subjects were asked to make a button press based on whether the third sentence was thought to be 'probably true' or 'probably false', given that the first two sentences (i.e. premises) were true. A total of 256 syllogistic arguments were presented in a 2×2 factorial design (Tables 1 and 2). The first factor was emotional salience. That is, half of all arguments (128) contained emotionally valenced material whereas the other half contained material that was expected to be emotionally neutral. Of note, all of the emotional arguments involved negative, and not positive, emotions (e.g. horror, grief, disgust). The second factor was level of certainty, such that half of all arguments (128) were created in a way that the correct answer was ambiguous and the other half were devised in such a manner that the correct answer would be obvious and rapidly forthcoming. The former was accomplished by providing less clueing in the first two premises and/or by discussing themes with which subjects were not expected to have *a priori* knowledge. Certainty, in contrast, was achieved by manufacturing arguments in which subjects could draw a rapid conclusion based on common semantic knowledge, or by providing information in the initial premises that heavily primed a subject to arrive at a given conclusion. Certain arguments were also counterbalanced so that half of the arguments were anticipated to draw a conclusion of 'probably yes' and the other half were expected to draw the conclusion of 'probably no'. To summarize, all arguments were divided into four overall conditions: emotional uncertain (EU), neutral uncertain (NU), emotional certain (EC) and neutral certain (NC).

Table 1 Sample uncertain inductive arguments used as stimuli

Emotional Uncertain (EU) arguments	Neutral Uncertain (NU) arguments
Amy has a fatal form of breast cancer	Molly plays a rare sport
Amy has blood seeping out of her nipple	Molly is rather tall
This is always a bad sign in breast cancer	Most women who play this sport are tall
Ted lost fifty pounds in one month	Tony has a B negative blood type
Ted did not try to lose this weight	Tony can donate blood to other B negatives
Ted is probably dying	He can donate blood to B positive people
Adults can go missing	An average adult has a certain heart rate
Adults missing for a month are often dead	An average child has a faster rate
Kids missing for a week are often dead	An average baby has an even faster rate
A mother and father died at the same time	Max has a certain occupation
Their son was with them at that moment	Max is constantly writing at work
Their son probably died with them	Most people who have this job write a lot
Premature babies weigh very little	Babies tend to sleep more than adults
They can get a massive brain bleed and die	Dreams occur in a stage of sleep
Most low weight babies are prone to this	Babies tend to dream more than adults
Liz had three miscarriages	A woman cannot see the color green
Liz then gave birth to a stillborn baby	She lacks the gene needed for this
Liz will not have a normal pregnancy	The woman is unable to see other colors
The World Trade Center was destroyed	Some stars shine brighter than others
A big smoke cloud was visible miles away	Light from stars has to travel very far
The smoke could be seen from space	The brighter stars are closer to Earth
A lethal injection contains potassium	A chemical keeps produce fresh
Injecting a big dose of potassium is fatal	A second chemical is structurally similar
Swallowing a big dose is also fatal	This chemical also keeps produce fresh
The bible condemns homosexuality	Several cave paintings were found
A rare religion is similar to Christianity	Many of the paintings depicted the sun
Its holy book condemns homosexuality	They were made by a sun worshipping culture
The AIDS virus is hard to kill	A type of bird eats only nuts
This is because the virus mutates a lot	The bird type has a specialized beak
Most deadly viruses can mutate a lot	All birds with this beak eat only nuts
Monkeys can feel intense pain	Some fish live on the ocean floor
The rat nervous system is much simpler	There is virtually no light there
Rats feel pain less than monkeys do	These fish are blind
Many unwanted cats are put in shelters	Flowers are important to bumblebees
Even more dogs are put in shelters	Bees can discriminate many flower colors
More dogs are killed in shelters each year	Bees must have good vision in general

Sample uncertain inductive arguments (EU and NU). Numbers of arguments dealing with other people were counterbalanced across conditions (32 trials per each of the four conditions). Note that for uncertain trials no correct conclusion was anticipated.

Every attempt was made to create arguments in which neither Theory of Mind nor moral reasoning would be recruited to arrive at the conclusion. For example, when the arguments involved other people, subjects were asked to reason about non-mentalizing aspects of them (i.e. physical/material traits about the individual, or the likelihood of said individual surviving a disease or an accident). Critically, each of the four conditions contained an equal number of arguments in which people were involved (32 arguments per condition). This was done because certain investigations have found that reasoning about others, even when not reasoning about another's mental state, can involve the medial prefrontal cortex (Saxe and Powell, 2006), an *a priori* region of interest in this experiment. The remaining arguments (32 per condition) did not contain themes about people, rather, these centered on various themes such as animals, abstract historical events, or physical objects

Table 2 Sample certain inductive arguments used as stimuli

Emotional Certain (EC) arguments	Neutral Certain (NC) arguments
'Certain' arguments in which a conclusion of 'yes' was expected	
A young couple is extremely poor	An athlete broke a world record
They sometimes have to eat dog food	The record was broken in a certain sport
They probably do not live in a nice house	The athlete is probably good at that sport
A man got stabbed many times in the face	Jeremiah has a red colored beard
He also got stabbed many times in the heart	Jeremiah also has red colored eyebrows
The man probably died	Jeremiah might have red hair
A very thin girl with anorexia died	Alexander has Russian parents
She looked like a concentration camp victim	Alexander also has Russian siblings
She may have died from starvation	Alexander might also be Russian
A baby was kidnapped and then abandoned	A boy is in elementary school
She was left alone for an entire week	The boy wears a certain shirt size
She might have died as a result	He likely wears smaller shirts than his dad
A rope was used to commit suicide	Airplanes are designed a certain way
The rope was tied into a noose	They all have the same shape
The rope was used in a hanging	This shape probably facilitates flying
A gas was synthesized	An animal lives in the north pole
It was made for use in a gas chamber	This animal has a very thick fur coat
The gas is probably poisonous	The animal can tolerate cold weather
'Certain' arguments in which a conclusion of 'no' was expected	
Jeff was murdered during a hate crime	A woman was born and raised in America
Jeff was not Jewish	The woman now drives a Japanese car
Thus Jews are never victims of hate crimes	Therefore she must now live in Japan
Kim snapped her neck in a diving accident	Spanish is a common language in America
Kim is still able to move her hands	Elizabeth is an American citizen
Broken necks never cause total paralysis	Thus Elizabeth must speak Spanish
Retarded people are never smart	Wrinkles are a sign of aging
Smart people can contribute to society	Amanda just got her first wrinkle
Retarded people never contribute to society	Thus Amanda must be over ninety years old
A restaurant kitchen is filled with roaches	A dog from a certain breed was observed
This roach species is not poisonous	The dog was noted to be a male
Roaches can safely crawl on the food	Females must not exist in this breed
Anthrax is a biological weapon	A battery held its charge for one week
It usually causes death via inhalation	Another battery still works after two weeks
Thus it is probably safe to ingest	The second battery will work forever
Terrorism occurs in the name of Islam	An average coin was flipped three times
The Muslim religion is based on a holy book	Each time the coin came up heads
This book only preaches violence	This means it will always come up heads

Sample certain inductive arguments (EC and NC). Certain arguments were counterbalanced so that half of these were expected to elicit a conclusion of 'probably yes' and half were expected to elicit a conclusion of 'probably no'.

(each of which was also equal in number across conditions). Finally, all words in the syllogistic arguments were compared across conditions using a psycholinguistic database (www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). The arguments did not differ statistically across the four conditions with respect to the following: amount of letters ($F = 0.824$, $df = 3, 77$, $P = 0.485$), amount of words ($F = 0.09$, $df = 3, 77$, $P = 0.965$), frequency of the words in the English language ($F = 0.008$, $df = 3, 77$, $P = 0.999$) and the concreteness/abstract quality of the words used ($F = 0.095$, $df = 3, 77$, $P = 0.963$).

Stimuli presentation

Each syllogism was presented for a total of 12 s (12000 ms). The first sentence was presented for 3000 ms, after which the second sentence appeared and was presented for an additional 3000 ms. The third sentence then appeared at time $t = 6000$ ms and remained on the screen for an additional 6000 ms, during which time subjects were instructed to respond with a button press. The first two sentences remained on the screen for the duration of the trial (Figure 1). The 256 syllogisms were presented over the course of four functional runs (64 trials per run). In each functional run, the same number of syllogisms (16) was presented for each of the four conditions. Trial (syllogism) presentation was done in a pseudo-random fashion using an optimization sequence program. The inter-trial interval (ITI) ranged from 0 ms to 12 000 ms.

Post-scan ratings

Immediately following the scanning procedure subjects completed a questionnaire in which they re-read each of the 256 syllogistic arguments. For each of these, subjects were again asked to rate the argument as 'probably true' or 'probably false'. Next, for each argument subjects were asked to rate the percent certainty of their answer (on a scale of 0–100, 0% being completely unsure and 100% being completely certain). In addition, subjects rated the valence and arousal of each syllogism read in the scanner via the use of the Self-Manikin Assessment Scale (Lang, 1980). This is a 9-point scale in which a score of 1 corresponds to extremely negative valence and a score of 9 corresponds to extremely positive valence. In a similar fashion, with respect to arousal ratings, a score of 1 indicated very low arousal and a score of 9 indicated extremely high arousal. Lastly, behavioral measures also included reaction times (computed as mean reaction times across the four functional runs).

fMRI acquisition

MRI data were acquired using a 3.0-T whole-body scanner (Allegra; Siemens Medical Solutions), equipped for echo planar imaging (Siemens Medical Systems, Iselin, NJ, USA) with a 12 channel 3-axis gradient head coil. Head movements were restricted using foam cushions. Images were projected using a rear projection system. Following automated scout and shimming procedures, two high-resolution 3D MPRAGE sequences (TR = 2.53 ms, TE = 3.45 ms, flip angle = 7°, voxel size = $1.3 \times 1.0 \times 1.3$ mm) were collected for positioning of subsequent scans. fMRI images (i.e. blood oxygenation level dependent signal or BOLD) were acquired using T2*-weighted sequences (TR = 3000 ms, TE = 30 ms, flip angle = 90°, voxel size = $3.1 \times 3.1 \times 5.0$ mm, slice thickness = 5.0 mm, FoV = 200 mm, number of slices = 27). The paradigm included four functional runs, each lasting 960 s (with each containing 320 image volumes).

fMRI Data analysis

Functional Data were processed using SPM5 software (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm). fMRI images were motion

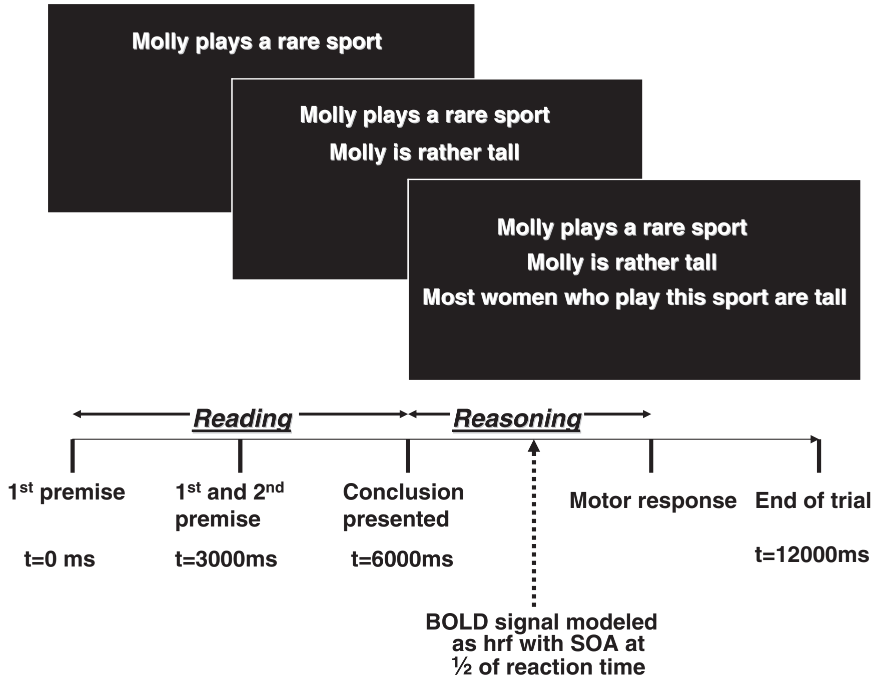

Fig. 1 Stimuli presentation. Each syllogism was presented for a total of 12 s (12000 ms). The first premise was presented for 3000 ms, after which the second premise appeared and was presented for an additional 3000 ms. The third premise (the conclusion) then appeared at time $t = 6000$ ms and remained on the screen for an additional 6000 ms, during which time subjects were instructed to respond with a button press. The BOLD signal was modeled as a hemodynamic response function with SOAs assigned at the temporal midpoint between the presentation of the third sentence and the motor response (i.e. the button press).

corrected, spatially normalized to the standardized space established by the Montreal Neurologic Institute (MNI; www.bic.mni.mcgill.ca), re-sampled to $2\,\text{mm}^3$ voxels, and smoothed with a three-dimensional Gaussian kernel of 6 mm width (FWHM). All collected data had minimal head motion (<3 mm linear movement in the orthogonal planes; <0.5° radians of angular movement). The general linear model was applied to the time series, convolved with the canonical hemodynamic response function and a 128 s high-pass filter.

Following the analysis performed by Goel and Dolan (2003), the temporal midpoint between the presentation of the third sentence and the motor response was modeled and included in the design matrix. In other words, the BOLD signal was modeled as a hemodynamic response function with SOAs assigned at this temporal midpoint (e.g. if a response time for a certain trial for a certain subject was 4000 ms, the SOA was assigned at 2000 ms; Figure 1). This was done on a subject by subject, and trial by trial basis. This yielded four conditions of interest: EU, NU, EC and NC, with each of these modeled on the basis of the temporal midpoint between the presentation of the conclusion and the motor response. The following conditions were also modeled and included in the design matrix: fixation trials, the initial visual presentation of the third sentence (i.e. the onset of the conclusion) and the motor response to the conclusion (as assessed by a button press), however, all of these were treated as effects of no interest. In sum, separate regressors were created for: the onsets of (i) the temporal midpoint between the presentation of the stimulus and the motor response (for each of the four conditions of interest: EU, NU, EC and NC) (ii) the visual presentation of the third sentence (iii) the motor response and (iv) the fixation trials. Because the first three of these regressors exist in such close temporal proximity to one another, we directly tested the possibility of multicolinearity between them. Correlations between these regressors were in the range of 0.2–0.39, thus suggesting that the regressors were correlated with one another to a small extent, but that they can still be considered to be orthogonal. We also examined the effects of removing the visual presentation and motor response regressors from the first level analysis. When this was done, the resultant BOLD activation was qualitatively very similar to that which was observed when the regressors were included.

For each subject, condition effects were estimated at each voxel, and statistical parametric maps (SPMs) were produced for the contrast of interest [e.g. $(\text{EU} + \text{EC}) > (\text{NU} + \text{NC})$]. For group analysis, each subject's contrast image (SPMs) was entered into a second-level random-effects analysis. In the random-effects analysis, a flexible factorial analysis was employed via a 'subject by condition' model. Because the role of the DN during emotional reasoning was being investigated, cortical regions of the DN were considered *a priori* regions of interest. Nonetheless, cortical activations (with the exception of PHC) are reported on the basis of a whole brain analysis. In addition, only activations surviving a stringent statistical threshold of $P < 0.05$ family-wise error (FWE) corrected, with the added requirement that at least 75 contiguous voxels exceeded this statistical level (i.e. $k_E \geq 75$), are reported. Certain medial temporal structures were also considered *a priori* regions of interest: the amygdala (owing to its association with emotional stimuli), and the PHC and hippocampus proper [owing to their known functional connectivity with the DN (Andrews-Hanna *et al.*, 2010, Buckner *et al.*, 2008)]. For these structures a separate region of interest analysis was performed using the following masks provided by Anatomical Automatic Labeling tool implemented in the WFU Pickatlas [http://www.ansir.wfubmc.edu: Amygdala (left and right) for amygdala, Hippocampus (left and right) for hippocampus, and Parahippocampal Gyrus (left and right) for the PHC. In addition, because of the size of these structures, a requirement of a minimum of only 10 contiguous voxels exceeding a statistical threshold of $P < 0.05$ FWE corrected was employed.

RESULTS

Behavioral data

Behavioral results are provided in Tables 3 and 4. Subjects rated emotional reasoning trials (EU and EC) as having significantly greater emotional valence and arousal than their neutral counterparts (NU and NC). Specifically, an ANOVA indicated a main condition effect of emotion upon valence ratings ($F = 4432.787$, $P < 0.0001$) and arousal ratings ($F = 2014.896$, $P < 0.0001$). However, there was no main effect of the condition of uncertainty on valence ($F = 2.590$, $P = 0.108$) or arousal ($F = 0.668$, $P = 0.414$), nor was there an effect of the interaction between emotion and uncertainty on valence ($F = 0.634$, $P = 0.426$) or arousal ($F = 2.175$, $P = 0.141$).

Support that uncertain trials were appreciated as more uncertain than certain trials came in subjects' ratings. Subjects reported a significantly lower amount of certainty on uncertain trials (EU and NU) than on certain trials (EC and NC) on the post-scanning questionnaire (Table 3). The mean rating for the uncertainty trials across all subjects was 59.35% and for certain trials was 84.57%. Also, an ANOVA indicated a main condition effect of uncertainty upon these ratings ($F = 100.566$, $P < 0.0001$). Moreover, there was no condition effect of emotion on certainty ratings ($F = 1.038$, $P = 0.308$), nor was there an effect of the interaction between emotion and uncertainty on them ($F = 1.475$, $P = 0.225$). Of note, the authors did not assess the 'correctness' of subjects' true/false responses because by definition inductive arguments cannot be assessed as 'correct' or 'incorrect', but can only be graded on the basis of the strength of the argument.

With respect to reaction times (RT), mean RTs were significantly slower for uncertain trials (3230.16 ms) as compared to certain trials (2407.30 ms), but there was not a significant difference in mean RTs between emotional (2847.84 ms) and neutral trials (2789.62). Further, an ANOVA indicated a main condition effect of uncertainty on RT ($F = 194.845$, $P < 0.0001$), but not the interaction of emotion and uncertainty ($F = 1.697$, $P = 0.207$). The main effect of emotion on RT was also not significant. However, this did trend towards significance ($F = 3.082$, $P = 0.065$). Therefore, we cannot fully exclude the possibility that BOLD activation in emotional > neutral trials was partly due to the fact these arguments were generally easier to resolve.

Table 3 Behavioral data

	Percent certainty (s.d.)		Reaction times (s.d.)	
	Emotional (%)	Neutral (%)	Emotional (ms)	Neutral (ms)
Uncertain trials	58.9 (13.0)	59.7 (12.5)	3275 (492)	3186 (450)
Certain trials	84.7 (7.5)	84.5 (8.3)	2421 (400)	2394 (426)

Percent certainty rated by subjects for each logical argument on a post-scan questionnaire and reaction times measured in milliseconds across the four reasoning conditions.

Table 4 Behavioral data

	Emotional valence rating (s.d.)		Emotional arousal rating (s.d.)	
	Uncertain	Certain	Uncertain	Certain
Emotional trials	2.91 (0.7)	2.98 (0.6)	3.87 (1.8)	3.89 (1.7)
Neutral trials	5.18 (0.4)	5.26 (0.4)	1.41 (0.7)	1.29 (0.5)

Ratings of valence and arousal for each of the reasoning conditions. Ratings were made on a 9-point scale. For valence 1 coded for most negative, 5 was completely neutral and 9 was most positive. For arousal 1 coded for least arousing and 9 corresponded to most arousing.

fMRI data

Main effect of reasoning

The main effect of reasoning *vs* baseline [(EU + EC + NU + NC) − Fixation] resulted in activation of posterior medial cortex, inferior frontal cortex, lingual gyrus and subcortical structures such as the caudate nucleus (Table 5). These areas are concordant to those found as a main effect of reasoning by Goel and Dolan (2003) in the study upon which the current study was based, as well as in other investigations by these authors (Goel and Dolan, 2000).

Main effect of emotion

Based on a whole brain analysis, the main effect of emotion (EU + EC) > (NU + NC) revealed robust activation in established regions of the DN, including the PCC (BA 31) (−12, −50, 34; $T = 11.20$, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$). In addition, there appeared to be more specific activation of the dorsomedial subsystem of the network, namely: the dorsomedial prefrontal cortex (BA 9) (−4, 54, 28) (T = 12.60, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$), the left TPJ (BA 40) (−54, −52, 32; T = 9.24, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$), and the right lateral temporal cortex [(BA 21) (52,−18,−14; T = 7.50, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$)] (Tables 6 and 7 and Figure 2). Notably, there was no activation of 'ventral' MPFC, even at much lower cluster thresholds. Given the emotional nature of the stimuli employed, a separate ROI analysis revealed that bilateral amygdala [(22, −8, −12, $z = 4.17$, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} = 0.002$) (−26, 0, −16, T = 4.53 $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} = 0.003$)] were also activated by the main effect of emotion. However, using a ROI analysis with the same threshold level [$k_E \geq 10$ exceeding a statistical threshold of $P < 0.05$ (FWE corrected)] there was no activation in other medial temporal structures (e.g. the PHC and hippocampus). The contrast of neutral trials minus emotional trials (NU + NC) > (EU + EC) resulted in far less activation at the aforementioned threshold, with activation of only the Right superior parietal lobule (BA 7) (30, −68, 50) (T = 5.96, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$).

Main effects of uncertainty and certainty on reasoning

The main effect of uncertainty during reasoning [i.e. Uncertainty (EU + NU) > Certainty (EC + NC)], irrespective of emotional valence, was activation of established executive and attentional control areas. For example, this contrast revealed activation in a rather posterior portion of the medial prefrontal cortex: (BA 8) (−4, 24, 48; T = 10.12, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$). There was also marked activation in left dorsolateral PFC (lateral portions of BA 9 and BA 10) [(−50, 18, 28; T = 8.23, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$) and (−42, 48, 0; T = 8.33, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$)] (Table 8 and Figure 3). Of note, a similar trend of activating executive control centers was observed when uncertainty level was increased 'within' emotional arguments (e.g. EU > EC).

The main effect of certainty, [i.e. Certainty (EC + NC) > Uncertainty (EU + NU)], resulted in significant activation of key hubs of the DN, specifically: right supramarginal gyrus (BA 40) (58, −46, 32; T = 11.58, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$), precuneus (BA 31) (−14, −64, 28; T = 10.66, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$), retrosplenial cortex (BA 23) (4, −42, 22; T = 9.10, $\mathbf{P}_{\mathbf{FWE}\text{-corrected}} < 0.001$), anterior medial prefrontal cortex (aMPFC) (BA 10) (12, 48,−2; T = 7.10,

Table 5 Brain regions activated in conjunction with all four conditions *vs* fixation

Region	Brodmann area	Cluster size K_E	MNI-coordinates[a] *x*	*y*	*z*	Max voxel T-score[b]
Posterior dorsomedial PFC	8	597	2	26	46	7.11
Right inferior frontal gyrus	47	221	34	24	−8	5.82
Right inferior frontal gyrus	45	52	48	14	16	5.76
Right caudate nucleus	N/A	34	16	4	12	5.95
Left inferior frontal gyrus	47	25	−52	22	−2	4.72
Left lingual gyrus	18	24	−4	−80	−4	6.44
Right anterior thalamus	N/A	23	10	−6	4	6.04
Left insular cortex	13	21	−48	−18	22	5.71

Whole brain analysis of regions activated by the contrast of all four conditions (EU, EC, NU and NC) *vs* fixation.
[a]*x* indicates right (+) or left (−); *y* indicates anterior (+) or posterior (−); *z* indicates superior (+) or inferior (−) to the anterior commissure.
[b]T-scores ≥ are shown reflecting an uncorrected statistical threshold of $P \leq 0.05$; K_E = number of voxels in a cluster (we only report activations of ≥20 contiguous voxels).

Table 7 Brain regions showing activation as a result of the main effect of emotion

Region	Cluster size K_E	MNI-coordinates[a] *x*	*y*	*z*	Max voxel T-score[b]
Right and left amygdala	10	22	−8	12	4.53
	37	−26	0	−16	4.38

[a]ROI analysis showing activation of bilateral amygdala as a result of the Main Effect of Emotion.
[b]T-scores ≥ are shown reflecting a FWE-corrected statistical threshold of $P \leq 0.05$ with activations of a minimum of 10 contiguous voxels.

Table 6 Brain regions showing activation as a result of the main effect of emotion

Region	Brodmann area	Network affiliation	Cluster size K_E	MNI-coordinates[a] *x*	*y*	*z*	Max voxel T-score[b]
Dorsomedial PFC	9	dMPFC subsystem	1647	−4	54	28	12.60
Precuneus	31	DN core hub	738	−12	−50	34	11.20
Left TPJ (Supramarginal gyrus)	40	dMPFC subsystem	475	−54	−52	32	9.24
Left middle temporal cortex	21	dMPFC subsystem	358	−52	−18	−14	6.23
Left inferior frontal gyrus	47	None	248	−44	26	−10	7.81
Right TPJ (Sup temp gyrus)	39	dMPFC subsystem	126	50	−58	24	7.06

Whole brain analysis of the main effect of emotion. The second column indicates whether the region in question corresponds to an established region of the core DN system, the dMPFC subsystem, the MTL subsystem or none of the above.
[a]*x* indicates right (+) or left (−); *y* indicates anterior (+) or posterior (−); *z* indicates superior (+) or inferior (−) to the anterior commissure.
[b]T-scores ≥ are shown reflecting a FWE-corrected statistical threshold of $P \leq 0.05$; K_E = number of voxels in a cluster (we only report activations of ≥75 contiguous voxels).

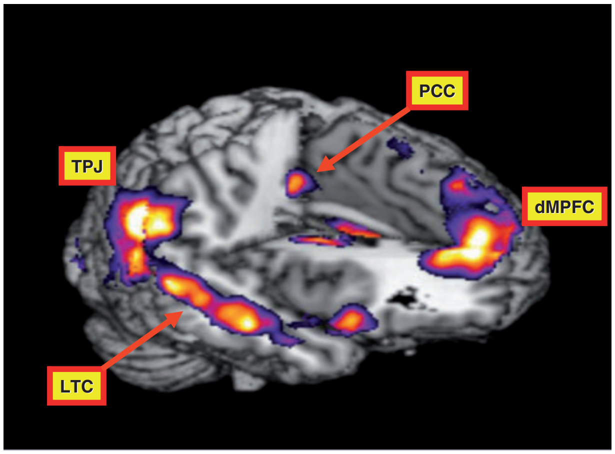

Fig. 2 Main effect of emotion. SPMs of voxel-wise T-scores at a minimum significance of $P < 0.05$ FWE corrected, and with a minimum cluster size of 75 contiguous voxels. SPM maps were 3D rendered onto a standardized template. Main effect of emotional salience on reasoning (EU + EC) > (NU + NC) shows activation in the dMPFC subsystem of the DN including: dMPFC (BA 9), Right TPJ (BA 39) and lateral temporal cortex LTC (BA 21). There was no activation in the MTL subsystem as a result of this contrast. Figures generated with MRIcron (http://www.cabiatl.com/mricro/mricron/index.html).

Table 8 Brain regions showing activation as a result of the main effect of uncertainty

Region	Brodmann area	Cluster size K_E	MNI-coordinates[a]			Max voxel T-score[b]
			x	*y*	*z*	
Posterior dorsomedial PFC	8	438	−4	24	48	10.12
Left DLPFC	9	897	−50	18	28	8.23
Left inferior frontal gyrus	10	235	−42	48	0	8.33

Main effect of uncertainty.
[a] *x* indicates right (+) or left (−); *y* indicates anterior (+) or posterior (−); *z* indicates superior (+) or inferior (−) to the anterior commissure.
[b] T-scores ≥ are shown reflecting a FWE-corrected statistical threshold of $P \leq 0.05$; K_E = number of voxels in a cluster (we only report activations of ≥75 contiguous voxels).

$P_{FWE\text{-corrected}} < 0.001$) and vMPFC (BA 24) (−6, 8, 38; $T = 6.75$, $P_{FWE\text{-corrected}} = 0.001$) (Tables 9 and 10 and Figure 3). Because of the *a priori* hypothesis that reasoning with certainty might recruit medial temporal structures, we performed a ROI analysis of HF and PHC. This revealed activation in the Right hippocampus (28, −28, −10; $T = 6.05$, $P_{FWE\text{-corrected}} < 0.001$, $k_E = 55$) and bilateral parahippocampal gyri (BA 34) [(22, 2, 16; $T = 6.26$, $P_{FWE\text{-corrected}} < 0.001$, $k_E = 47$) and (−24, 2,−14; $T = 3.99$, $P_{FWE\text{-corrected}} < 0.001$, $k_E = 11$)]. We also noted activation of areas of the DN when certainty was increased within emotional arguments (e.g. EC > EU). This contrast revealed robust activation in both PCC [BA 31 (6, −66, 28; $T = 9.57$, $k_E = 1017$, $P_{FWE\text{-corrected}} < 0.001$)] and in vMPFC [BA 10 (0, 58, 10; $T = 7.63$, $k_E = 752$, $P_{FWE\text{-corrected}} < 0.001$)].

DISCUSSION

Emotional reasoning relative to neutral reasoning drives activation in the DN

The DN is characterized by several cortical regions, including the medial wall of the prefrontal cortex, the precuneus, the posterior cingulate (PCC) and retrosplenial cortex (RsP), the lateral temporal cortex (LTC) and the bilateral inferior parietal cortices; all of which were initially highlighted on the basis of common deactivations occurring during the execution of active cognitive tasks and reciprocal activations during rest (Gusnard and Raichle, 2001; Raichle *et al.*, 2001; Raichle, 2006; Buckner *et al.*, 2008). The current investigation substantiates a role for this network in certain forms of content-specific reasoning. Specifically, the authors observed activation in areas of the DN both when participants reasoned about emotional (relative to neutral) themes, and when they reasoned in the context of certainty (relative to uncertainty). Of note, the authors do not posit that the DN has a privileged role in resolving logical arguments-only that it is mobilized for certain forms of logical arguments-specifically, those that invoke the hypothesized cognitive functions of the network. To illustrate this, previous investigators have demonstrated activation in the DN for tasks of moral reasoning and Theory of Mind reasoning (ToM) relative to control tasks (Amodio and Firth, 2006; Saxe *et al.*, 2004; Greene *et al.*, 2001; Greene *et al.*, 2004).

In order to interpret the observed BOLD activations in the DN during the emotional conditions it is necessary to elaborate upon the potential effects of emotional content upon the reasoning process. For example, the case could be made that the DN activation we report was reflective of a ‘cognitive’ reappraisal of an induced affective state. In other words, perhaps the emotional nature of the syllogisms served as a source of distraction or load, and, as a result, the observed activation in the DN reflected some form of conscious emotional regulation to modulate or suppress this. We argue that this was not the case. Unlike other studies that have been designed to induce ‘explicit’ emotional regulation (Ochsner and Gross, 2005; Hariri *et al.*, 2003), our study involved ‘implicit’ emotional regulation. That is, participants were not asked to regulate their emotional reaction to the arguments, but were rather instructed to integrate all of the presented information (whether emotional or neutral) into deriving their conclusion. The distinction between explicit and implicit affect regulation was eloquently described in a study of motivated political reasoning by Westen and colleagues (2006). These authors explained that in reasoning underwritten by implicit affect regulation, there is a tendency for the brain to derive conclusions which achieve a maximally positive (and minimally negative) affective state, while still attempting to satisfy ‘cognitive’ constraints of the argument. Similar to existing integrative models of cognition and emotion (Pessoa, 2008; Gray *et al.*, 2002), we posit that the DN was not activated simply as a byproduct of the stimuli being emotional, or as a

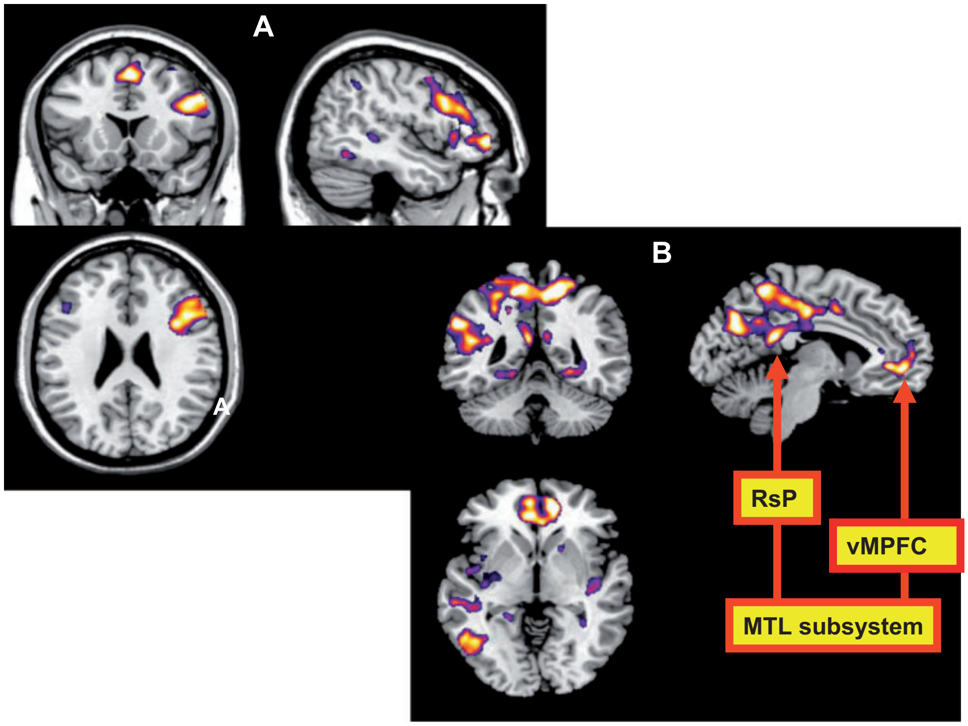

Fig. 3 Main effects of uncertainty (**A**) and certainty (**B**). SPMs of voxel-wise T-scores at a minimum significance of $P < 0.05$ FWE corrected and with a minimum cluster size of 75 contiguous voxels are rendered onto standardized coronal, sagittal and axial sections (clockwise from top left). (A) Main effect of uncertainty revealed activation in posterior medial prefrontal cortex (BA 8) and Left DLPFC (lateral BA 9). (B) Main effect of certainty activated DN regions including the precuneus and aMPFC. It also activated some areas specific to the MTL subsystem of the DN, including the RsP and vMPFC, as well as hippocampus and parahippocampal gyrus [based upon an ROI analysis (not shown)]. Figures generated with MRIcron (http://www.cabiatl.com/mricro/mricron/index.html).

Table 9 Brain regions showing activation as a result of the main effect of certainty

Region	Brodmann area	Network affiliation	Cluster size	MNI-coordinates[a]			Max voxel T-score[b]
			K_E	x	y	z	
Rsp	23	MTL Subsystem	2729	4	−42	22	9.10
Precuneus	31	DN core hub	1726	−14	−64	28	10.66
Right TPJ (Supramarginal gyrus)	40	dMPFC Subsystem	989	58	−46	32	11.58
aMPFC	32	DN core hub	408	−12	48	−2	7.10
vMPFC	24	MTL Subsystem	93	−6	8	38	6.75

Whole brain analysis of the main effect of certainty. The second column indicates whether the region in question corresponds to an established region of the core DN system, the dMPFC subsystem, the MTL subsystem or none of the above.
[a]x indicates right (+) or left (−); y indicates anterior (+) or posterior (−); z indicates superior (+) or inferior (−) to the anterior commissure.
[b]T-scores ≥ are shown reflecting a FWE-corrected statistical threshold of $P \leq 0.05$; K_E = number of voxels in a cluster (we only report activations of ≥75 contiguous voxels.)

Table 10 Brain regions showing activation as a result of the main effect of certainty

Region	Brodmann area	Network affiliation	Cluster size	MNI-coordinates[a]			Max voxel T-score[b]
			K_E	x	y	z	
Right hippocampus	NA	MTL Subsystem	55	28	−28	−10	6.05
Right PHC	34	MTL Subsystem	47	22	2	16	6.26
Left PHC	34		11	−24	2	−14	3.99

[a]ROI analysis showing activation of bilateral PHC and Right hippocampus as a result of the Main Effect of Certainty.
[b]T-scores ≥ are shown reflecting a FWE-corrected statistical threshold of $P \leq 0.05$ with activations of a minimum of 10 contiguous voxels.

way of down-regulating the induced affective state, but instead was recruited to implicitly 'integrate' the emotional data contained in the premises into the process of deriving a logical induction.

There is extant evidence to support a role for the DN in emotional reasoning. First, the DN is anatomically composed of, or highly interconnected to, regions which are critical for processing emotional and motivational data (Gusnard *et al.*, 2001), and Raichle (Raichle and Gusnard, 2005) has opined that, 'it is highly likely that [intrinsic functional activity in the brain] will be increasingly recognized as playing an important role in the ultimate shaping and expression of basic appetites and drives'. Second, a role for the network in emotional processing in general has been experimentally substantiated. For instance, one investigation found that DN activity is modulated on the basis of whether musical sounds are neutral or unpleasant (Pallesen *et al.*, 2008), and another study found alterations in resting state functional connectivity with sad mood induction (Harrison *et al.*, 2008). Also, depressed patients and those suffering from chronic pain are less capable of suppressing their DN (Sheline *et al.*, 2009, Grimm *et al.*, 2009 and Baliki *et al.*, 2008), and such patients appear to have altered functional connectivity between DN regions (Greicius *et al.*, 2007, Anand *et al.*, 2005).

Emotional reasoning specifically activates the dorsomedial subsystem of the DN

Our results also demonstrate that the dorsomedial subsystem of the DN was preferentially recruited by emotional reasoning, as the Main Effect of Emotion activated dMPFC, TPJ and LTC, while failing to activate any of the components specific to the MTL subsystem. A myriad of investigations have linked the dMPFC to self-referential processing (Lane *et al.*, 1997; Johnson *et al.*, 2002; Gusnard *et al.*, 2001; Vanderwal *et al.*, 2008), and to the metacognitive appraisal of one's emotional state (Seeley and Sturm, 2007; Ochsner and Gross, 2005). In their meta-analysis, Kober *et al.* (2008) found that dMPFC was most likely among medial prefrontal regions to co-activate with the hypothalamus and the periaqueductal gray, which themselves serve critical roles in the physiological mediation of emotional states. Moreover, Andrews-Hanna *et al.* have provided evidence that tasks which accentuate 'self-other' distinctions specifically activate the entire dorsomedial subsystem (not just the dMPFC). In the current paradigm, we posit that the dMPFC subsystem was activated during emotional trials in order to mobilize introspective/self-relevant data to arrive at a conclusion. By this argument, the emotional syllogisms employed were inherently more 'personal' or 'self-relevant' than the neutral ones, as they often involved people being ill, injured or dying (Tables 1 and 2). This is not to say, however, that the activations observed in the dMPFC subsystem were solely based upon a personal/impersonal distinction, as the emotional stimuli used did not have direct relevance to the participants on an individual level (as is the case with other studies which probe self/non-self distinctions).

Interestingly, at the statistical thresholds employed, vMPFC was not highlighted by the main effect of emotion. This is in contrast to the findings of vMPFC activation during emotionally valenced deductive reasoning in the Goel and Dolan (2003) experiment. However, when using a different intensity threshold (FDR correction), we did detect activation in vMPFC as a function of the Main Effect of Emotion [BA 11 (0, 46, −16; $T = 4.57$, $k_E = 45$, $\mathbf{P}_{\mathbf{FDR}\text{-corrected}} = 0.003$)]. Our results also differ from those of Goel and Dolan in that these authors did not observe activations in other DN areas, such as TPJ, LTC, PCC and dMPFC. We argue that this discrepancy can be explained by two considerations. First, as noted in the Introduction, there is evidence to link dMPFC to inductive, and not deductive reasoning. Second, it is quite possible that our emotional stimuli were more empathetic than those employed by Goel and Dolan, as they often involved graphic depictions of specific individuals or animals suffering. Meta-analyses have linked empathic processing to nodes of the dMPFC subsystem, such as dMPFC itself and TPJ (Lamm *et al.*, 2011; Amodio and Firth, 2006). Also, Decety and Chaminade (2003) found that sympathy is associated with activation in dMPFC. Finally, our study is not alone in finding activation in DN areas during emotional reasoning. The above referenced study of motivated reasoning by Westen *et al.* (2006) found robust activation in PCC and in dMPFC, in addition to vMPFC.

Certainty and uncertainty differentially engage and disengage the DN, respectively

Increases in uncertainty during reasoning were associated with increased activity in a posterior region of the MPFC (BA 8), as well as with activation of left DLPFC (a lateral portion of BA 9) (Figure 3). Notably, this was true even within emotional trials (e.g. in the contrast of EU-EC). These regions are quite similar to those found in a study on the neural basis of uncertainty during decision-making by Volz *et al.* (2004). Specifically, those authors demonstrated activation in posterior medial frontal cortex (BA 8) during uncertainty and additional activation in DLPFC when said uncertainty was internally attributed. Moreover, in a meta-analysis, Ridderinkhof and colleagues (2004) implicated the posterior medial frontal cortex (BA 8) in the reconciliation of uncertainty and the detection of response conflict. The DLPFC has often been associated with executive control tasks during which information must be continually updated and/or manipulated (e.g. via the utilization of working memory or set shifting) (Mansouri *et al.*, 2009; Stuss and Alexander, 2000). Therefore, activation of posterior MPFC and DLPFC during the resolution of uncertainty seems concordant with established theories about these regions.

Certainty (when contrasted with uncertainty) during reasoning also yielded activations in the DN. Specifically, we observed activations in aMPFC and in PCC. One possible interpretation of this trend is that certain trials were less difficult than uncertain trials. Several prior observations have shown that deactivations in the DN become more pronounced as the level of task difficulty is increased (Pallesen *et al.*, 2009; Greicius and Menon, 2004), and these deactivations have been shown to be proportional to the degree of task difficulty in a parametric fashion (McKiernan *et al.*, 2003). This phenomenon is often explained via a resource allocation model as proposed by McKiernan *et al.*

However, we put forth an alternative explanation: that areas of the DN were recruited during certain trials because of the nature of this type of reasoning. Certain trials were designed to elicit the use of prior knowledge and/or well established semantic/mnemonic associations. Interestingly, the Main Effect of Certainty also activated areas selective to the MTL subsystem of the DN, including HF, PHC, RsP and vMPFC. This finding resonates with prior studies. As mentioned in the introduction, Bar and colleagues (2007) have shown that reasoning which relies upon established semantic associations specifically activates the medial temporal portions of the network. Further, there is extant evidence linking medial temporal structures (e.g. HF and PHC) to reasoning based which is based on episodic memory (Girelli *et al.*, 2004; Suzuki *et al.*, 2009).

To disentangle the contributions of task difficulty and certainty to DN (and MTL subsystem) activation, we parametrically weighted the four conditions of interest (EU, NU, EC and NC) by both the subject's trial-by-trial certainty ratings, and by their trial-by-trial reaction times (with the assumption that reaction time is a proxy of task difficulty). Parametric weighting by certainty scores revealed activation in the MTL subsystem of the DN as a result of the Main Effect of Certainty in: left PHC (−32, −30, −14; $k_E = 23$, $T = 4.12$, uncorrected $P < 0.001$), right HF (30, −6, −28; $k_E = 3$, $T = 3.51$, uncorrected $P < 0.001$) and right pIPL (44, −30, −14; $k_E = 15$, $T = 4.12$, uncorrected $P < 0.005$) on a whole brain analysis. In contrast, parametric weighting by reaction time did not reveal activation in the MTL subsystem or in the DN, but rather resulted in activation in the left caudate nucleus (−8, 6, 18; $k_E = 30$, $T = 4.63$, uncorrected $P < 0.001$) and the right premotor area (12, 26, 50; $k_E = 32$, $T = 3.23$, uncorrected $P < 0.005$). These findings suggest that DN/MTL subsystem activation occurring during certainty reasoning was the result of the certainty of the subject's conclusions, above and beyond the effect of difficulty level. Nonetheless, these two factors are inherently interrelated, and as such, a limitation of our study is that our design did not allow for them to be directly compared.

CONCLUSION

The DN is characterized by of a nexus of brain regions with remarkably strong functional inter-connectedness

Fig. 4 Anatomical overlap of the main effects of emotion and certainty upon reasoning. Both the Main Effects of certainty (shown in green/blue) and emotion (shown in red/yellow) activated components of the DN. However, the main effect of emotion activated a more dorsal portion of the medial prefrontal cortex (in addition to other components of the dorsomedial subsystem), whereas the main effect of certainty activated a more ventral portion. SPMs of voxel-wise T-scores at a minimum significance of $P < 0.05$ FWE corrected and with a minimum cluster size of 75 contiguous voxels are rendered onto standardized coronal, sagittal and axial sections (clockwise from top left). Figures generated with MRIcron (http://www.cabiatl.com/mricro/mricron/index.html).

consuming a large amount of the brain's energy budget (Raichle, 2006). Investigations have linked reasoning in certain contexts to activation in the DN, and the DN has often been linked to probability assessment. Our findings suggest that the DN is mobilized during probability assessments (as reflected by inductive conclusions) when emotional salience is involved, and when there is certainty about the conclusion being drawn. We also show that these two types of reasoning specifically mobilize different subsystems of the DN (Figure 4), with the dMPFC subsystem being activated during emotional reasoning and the MTL subsystem being activated during certainty reasoning. Activation of the dMPFC subsystem of the DN during emotional reasoning suggests that participants arrived at emotional conclusions based in part upon self-relevant or introspective cues. One caveat to these findings is that the emotional stimuli used were all negative (and not positive) in content. As such, another potential limitation of this study is that the observed activations in the dMPFC subsystem were the result of the effects of negative valence upon reasoning and not emotionality in general. Reasoning under certainty, in contrast, activated components of the MTL subsystem, raising the possibility that this subsystem might assist in making judgments rooted in well learned information or in episodic memory. We argue that future investigations of the neural basis of human reasoning should focus on network models. We also posit that the DN may play an important role in the integration of cognitive and implicit affective processing.

Conflict of Interest

None declared.

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