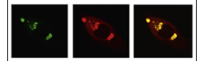


Available online at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

Brain Research



Research Report

The impact of egocentric vs. allocentric agency attributions on the neural bases of reasoning about social rules



Nicola Canessa^{a,b,c}, Giuseppe Pantaleo^a, Chiara Crespi^{a,b}, Alessandra Gorini^d, Stefano F. Cappa^{b,c,e,*}

^aUniversità Vita-Salute San Raffaele, Milan 20132, Italy

^bCenter for Cognitive Neuroscience, Università Vita-Salute San Raffaele, Milan 20132, Italy

^cDivision of Neuroscience, San Raffaele Scientific Institute, Milan 20132, Italy

^dUniversità degli Studi di Milano, Milan 20122, Italy

^eIUSS Pavia, Piazza della Vittoria 15, 27100 Pavia, Italy

ARTICLE INFO

Article history:

Accepted 1 June 2014

Available online 10 June 2014

Keywords:

Social reasoning

Wason Selection-task

Functional magnetic resonance imaging

Prefrontal cortex

Agency attribution

Parietal cortex

ABSTRACT

We used the “standard” and “switched” social contract versions of the Wason Selection-task to investigate the neural bases of human reasoning about social rules. Both these versions typically elicit the deontically correct answer, i.e. the proper identification of the violations of a conditional obligation. Only in the standard version of the task, however, this response corresponds to the logically correct one. We took advantage of this differential adherence to logical vs. deontical accuracy to test the different predictions of logic rule-based vs. visuospatial accounts of inferential abilities in 14 participants who solved the standard and switched versions of the Selection-task during functional-Magnetic-Resonance-Imaging. Both versions activated the well known left fronto-parietal network of deductive reasoning. The standard version additionally recruited the medial parietal and right inferior parietal cortex, previously associated with mental imagery and with the adoption of egocentric vs. allocentric spatial reference frames. These results suggest that visuospatial processes encoding one's own subjective experience in social interactions may support and shape the interpretation of deductive arguments and/or the resulting inferences, thus contributing to elicit content effects in human reasoning.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

The neural bases of deductive reasoning, i.e. the ability to reach secure conclusions from a set of given facts known to

be true, have been extensively investigated with functional neuroimaging. Despite complex and not always consistent results (Monti et al., 2007), the role of a common left frontolateral-frontomesial-parietal network across different

*Corresponding author at: IUSS Pavia, Piazza della Vittoria 15, 20700 Pavia, Italy. Fax: +39 03 8237 5899.

E-mail addresses: canessa.nicola@hsr.it, pantaleo.giuseppe@univr.it (G. Pantaleo), crespi.chiara@hsr.it (C. Crespi), alessandra.gorini@unimi.it (A. Gorini), stefano.cappa@iusspavia.it (S.F. Cappa).

deductive tasks was confirmed by qualitative (Goel, 2007) and quantitative (Prado et al., 2011) meta-analyses. Moreover, against the existence of a single – either rule-based (Rips, 1994) or visuospatial (Johnson-Laird, 1995) – neural system for deductive reasoning, different types of arguments flexibly recruit specific regions, namely right hemispheric visuospatial areas for relational reasoning and left inferior frontal ones for categorical reasoning (Prado et al., 2011). Other regions seem to underpin specific sub-processes, namely extraction and maintenance of the formal structure of arguments (fronto-parietal “support” areas; Rypma et al., 1999; Tanaka et al., 2005), as well as deductive operations (medial and rostrolateral prefrontal “core-logic” areas; Charron and Koechlin, 2010; Christoff et al., 2001; Volz et al., 2005) (Monti et al., 2007, 2009).

Formal logic, i.e. the syntax of classical logic, has been traditionally considered a normative standard for deductive reasoning. Several studies, however, report systematic violations of formal logic in human reasoning, including so-called “content effects” on the Wason Selection task (Wason, 1983). In this task, subjects are asked to identify the violations of a conditional rule (“If P, then Q”), by testing the co-occurrence of its possible antecedents and consequents (P, not-P, Q, not-Q). The correct logical answer is to select P and not-Q, because they could reveal not-Q and P, respectively. However, subjects presented with so-called “descriptive” rules (i.e. describing states of the world, such as “If a person goes to X, then he does Y”) typically deviate from formal logic (below 20% accuracy, frequently selecting P and Q, or P alone; Manktelow and Evans, 1979). A significant improvement (65–80% accuracy) is observed with “deontic” conditional rules (i.e., describing situations in which, to obtain a benefit P, an individual must satisfy a requirement Q), such as social contracts of the form “If I give you X, then you must give me Y” (Manktelow and Over, 1991). The roots of this facilitation have been addressed from both cognitive (Cosmides, 1989; Fodor, 2000; Sperber and Girotto, 2002; Stenning and van Lambalgen, 2004) and social-psychological (Legrenzi, 2004; Pantaleo, 2004) viewpoints. Deontic reasoning competence is sensitive to both context and perspective (Gigerenzer and Hug, 1992), and the facilitation induced by social contracts, as well as by precautionary rules such as “If the hazard X exists, then you must take the precaution Y” (Fiddick et al., 2000), may reflect the engagement of domain-specific reasoning mechanisms (Fiddick, 2004). Several studies have highlighted brain regions differentially activated by social contracts vs. descriptive rules (Canessa et al., 2005), social contracts vs. precautionary rules (Fiddick et al., 2005), social contracts or precautionary rules vs. descriptive rules (Ermer et al., 2006), as well as reflecting selective impairments on social contract, relative to precautionary, reasoning (Stone et al., 2002).

The influence of extra-logical considerations on human reasoning is supported by a variant of the task, directly comparing logical vs. deontical accuracy despite an identical structure. In this variant, the “standard” version “If you take the benefit, then you must satisfy the requirement” is “switched” into the form “If you satisfy the requirement, then you (may) take the benefit” (Cosmides, 1989). In both cases, subjects testing a violation of the rule typically (e.g. 80%; Sugiyama et al., 2002) choose the “benefit accepted” and “requirement non

satisfied” cards. However, only in the “standard” version these cards incidentally correspond to the logically correct answer (P and not-Q), while in the “switched” version they correspond to the logically incorrect one (not-P and Q). Here we take advantage of this peculiar feature to test the hypothesis that the predominance of extra-logical considerations in reasoning on social contracts would reflect in neural activity exceeding “core-logic” brain regions. In particular, previous studies highlighted the perspective adopted to interpret the rule as a critical factor in social contract reasoning (Fiddick et al., 2000; Gigerenzer and Hug, 1992). Compared with descriptive rules, social contracts may be more easily encoded through visuospatial imagery processes rather than logic deductive operations. Their antecedents and consequents would thus be mapped onto a representational format other than that predicted by formal logic, e.g. in terms of spatial relationships between two interacting agents. This hypothesis would entail a differential involvement of neural mechanisms supporting one's own perspective and sense of agency across the standard and switched tasks, which engage opposite reference frames and corresponding social focal points with respect to the conditional obligation (“If I..., then you...” vs. “If you..., then I...”, respectively). Namely, it would entail an egocentric reference frame – or social focal point – in the standard task, in which the antecedent is encoded in a first-person perspective (“If I ...”), while the switched task (“If you ...”) can be expected to activate an allocentric reference frame.

We tested this hypothesis in 14 participants who solved the standard and switched versions of the Selection-task during functional-Magnetic-Resonance-Imaging. We predicted that the two tasks would involve differential activity in the regions associated with the adoption of egocentric vs. allocentric reference frames (medial parietal and inferior parietal cortex; Vogetley and Fink, 2003) rather than in the regions involved in logical processing (rostrolateral prefrontal cortex; Monti et al., 2007). We also performed regions-of-interest analyses to assess the consistency of our results with available data on the neural bases of deductive reasoning, reasoning on social contracts, logical inference and agency attribution in social interactions.

2. Results

2.1. Behavioral results

We considered as a correct answer in the standard (SSC) and switched (WSC) tasks the selection of both the “benefit accepted” and “requirement non satisfied” cards, regardless of their logical status (e.g. P and not-Q in the SSC task, not-P and Q in the WSC task). Under this convention, behavioral results during functional scanning showed no significant difference between the mean of correct answers in the SSC (mean=81.25%, SD=0.28) and WSC (mean=80.80%, SD=0.29) tasks, $F(2)=2.412$, $MSE=0.9$, $p>0.05$. Neither a significant main effect of the order of task presentation throughout the four scanning sequences, $F(3)=1.047$, $MSE=0.124$, $p>0.05$, nor a significant interaction between the task and the presentation order, $F(6)=0.529$, $MSE=0.46$, $p>0.05$, was observed, indicating that no learning occurred during the experiment.

Table 1 – The brain regions activated by “standard” (SSC) conditional rules compared with the baseline condition ($p < 0.05$ corrected for multiple comparisons). IFG = Inferior Frontal Gyrus, SMA = Supplementary Motor Area.

Cluster-size	Hemisphere	Anatomical region	MNI			t-value
			x	y	z	
3050	Left	Middle Frontal Gyrus	−34	12	34	7.38
	Left	IFG (pars Triangularis)	−38	34	18	7.07
	Left	Superior Medial Gyrus	−10	34	52	6.64
	Left	Superior Frontal Gyrus	−10	38	48	6.49
	Left	Superior Medial Gyrus	−8	32	32	5.57
	Left	SMA	−10	18	62	5.54
	Left	Middle Frontal Gyrus	−20	44	26	5.5
604	Left	IFG (pars Opercularis)	−42	16	10	6.57
	Left	IFG (pars Orbitalis)	−42	22	−10	5.97
	Left	IFG (pars Triangularis)	−32	24	14	4.21
	Left	Insula Lobe	−28	24	0	4.05
1384	Right	Insula Lobe	44	18	−6	7.63
	Right	Middle Cingulate Cortex	16	18	36	6.41
	Right	Middle Frontal Gyrus	42	30	30	5.19
	Right	IFG (pars Opercularis)	50	20	10	5.13
	Right	SMA	14	24	56	4.45
	Right	Superior Medial Gyrus	12	30	44	4.15
1909	Left	Angular Gyrus (PGa)	−42	−62	36	9.72
	Left	Inferior Parietal Lobule (PFm)	−46	−56	44	9.23
	Left	Middle Temporal Gyrus	−52	−60	14	7.16
	Left	Inferior Parietal Lobule (PFm)	−52	−48	38	5.91
	Left	SupraMarginal Gyrus (PFcm)	−46	−46	30	5.45
321	Right	Middle Occipital Gyrus (PGp)	40	−70	32	5.23
	Right	Inferior Parietal Lobule (PFm)	48	−48	38	4.43
576	Left	Precuneus	−4	−62	36	6.24
	Right	Precuneus	2	−60	36	5.96

Table 2 – The brain regions activated by “switched” (WSC) conditional rules compared with the baseline condition ($p < 0.05$ corrected for multiple comparisons). IFG = Inferior Frontal Gyrus, SMA = Supplementary Motor Area.

Cluster-size	Hemisphere	Anatomical region	MNI			t-value
			x	y	z	
3634	Left	Superior Medial Gyrus	−8	34	52	7.53
	Left	IFG (pars Triangularis)	−40	28	24	5.92
	Left	Middle Frontal Gyrus	−42	16	44	5.76
	Left	SMA	−12	16	60	5.1
	Left	IFG (pars Orbitalis)	−38	20	−10	4.47
2380	Left	Angular Gyrus (PGa)	−40	−62	36	8.65
	Left	SupraMarginal Gyrus (PF)	−46	−48	30	5.65
	Left	Middle Temporal Gyrus	−52	−58	14	5.2
347	Right	Angular gyrus	36	−56	28	4.26
	Right	Middle Occipital Gyrus (PGp)	40	−70	30	3.53
481	Left	Precuneus	−4	−64	36	5.33
	Right	Precuneus	14	−60	32	3.01

Also the analysis of response times showed no significant difference between the SSC (mean 14.54 s, SD=1.37) and WSC (mean=14.65 s, SD=1.34) tasks, $F(2)=0.162$, $MSE=0.313$, $p>0.05$. Moreover, no significant main effect of the order of task presentation on response times, $F(3)=1.01$, $MSE=1.673$, $p>0.05$, nor a significant interaction between the task and the presentation order, $F(6)=1.301$, $MSE=2.99$, $p>0.05$, was observed.

2.2. fMRI results

The statistical parametric maps for the SSC and WSC tasks (Tables 1 and 2), as well as a conjunction-analysis between them (Table 3; Fig. 1), showed that both tasks recruited a common set of areas involving the left frontolateral cortex (from precentral gyrus to inferior frontal and rostrolateral prefrontal cortex), medial superior frontal gyrus and middle temporal gyrus, as well as the angular gyrus (encompassing posterior parietal cortex and parieto-occipital junction) in both hemispheres. Regions-of-interest (ROIs) analyses confirmed a priori hypotheses on the engagement of the key regions of deductive reasoning highlighted by the meta-analysis of Prado et al. (2011), e.g. left inferior frontal cortex (−46, 15, 23), middle frontal gyrus (−42, 10, 42) and angular gyrus (−37, −59, 38) (Supplementary Table 5-a). Additional ROIs analyses confirmed that both SSC and WSC tasks activated the regions previously reported by Canessa et al. (2005), with the only exception being the lack of activation of the right middle and superior frontal gyri which did not survive a corrected threshold in the WSC task (Supplementary Table 5-b). Moreover, both tasks activated the critical regions reported by Fiddick et al. (2005), including the dorso-medial prefrontal cortex and bilateral inferior parietal cortex (Supplementary Table 5-c). These regions encompassed both the core (e.g. left rostrolateral prefrontal cortex, Brodmann area (BA) 10p: −36, 56, 8) and support (e.g. left

inferior frontal gyrus, BA 47: −32, 20, −8; left middle frontal gyrus, BA 6: −46, 10, 50, BA 9: −56 22, 32) regions of Monti et al. (2007) (Supplementary Table 5-d).

Whole-brain direct comparisons showed that the SSC task, compared with the WSC one, elicited stronger activity in two right-hemispheric medial parietal and inferior parietal clusters (Table 4, Fig. 2-top). The first one was located in the dorso-medial parietal cortex, and involved the middle/posterior cingulate cortex, postcentral gyrus and sensorimotor cortex (BA 2,3,4), extending into the right superior parietal lobule. The second cluster involved several structures encompassing the inferior parietal cortex, namely the right post-central gyrus (BA 3b), parietal operculum (OP1) and supramarginal gyrus. No region survived a correction for multiple comparisons in the reverse contrast. All whole-brain results (i.e. both simple effects and direct comparisons) were confirmed by a control analysis in which we specified an equal duration of 10 s for all reasoning and baseline trials (see Supplementary Tables 1–4).

Subsequent ROIs analyses showed that none of the core-logic or support brain regions reported by Monti et al. (2007) were differentially activated by the SSC vs. WSC tasks. A re-analysis of our previous data (Canessa et al., 2005) rather showed that the “support” right inferior frontal cortex (BA 47; 32, 28, −2) was more strongly activated in the DES task than in both the SSC ($t(26)=3.74$; $p<0.001$) and WSC ($t(26)=4.92$; $p<0.001$) tasks. This result is also consistent with our previous data, showing stronger activation of the right anterior lateral frontal cortex (Brodmann area 46) when reasoning on descriptive rules vs. social contracts (see Fig. 2 of Canessa et al. (2005)). In line with our hypothesis, instead, a significant difference between standard and switched rules emerged in brain regions which a recent meta-analysis (Sperduti et al., 2011) associated with internal vs. external agency (Supplementary Table 5-e). Namely, the SSC task, compared with the WSC one, was associated with higher activity in a region of the postcentral gyrus associated with self-agency (BA 3; 34,

Table 3 – The brain regions commonly activated by “standard” and “switched” conditional rules, after baseline subtraction ($p<0.05$ corrected for multiple comparisons). IFG=Inferior Frontal Gyrus, SMA=Supplementary Motor Area.

Cluster-size	Hemisphere	Anatomical region	MNI			t-value
			x	y	z	
4979	Left	Superior Medial Gyrus	−10	34	52	6.64
	Left	IFG (pars Triangularis)	−40	28	24	5.79
	Left	Middle Frontal Gyrus	−42	16	44	5.65
	Left	SMA	−12	16	60	5
	Left	IFG (pars Orbitalis)	−38	20	−10	4.37
	Left	IFG (pars Opercularis)	−42	16	10	3.89
2642	Left	Angular Gyrus (PGa)	−40	−62	36	8.47
	Left	SupraMarginal Gyrus (PFcm)	−46	−46	30	5.14
	Left	Middle Temporal Gyrus	−52	−58	14	5.07
464	Right	Middle Occipital Gyrus (PGp)	40	−70	30	3.45
	Right	Angular Gyrus (PGp)	50	−62	32	2.3
726	Left	Precuneus	−4	−64	36	5.21

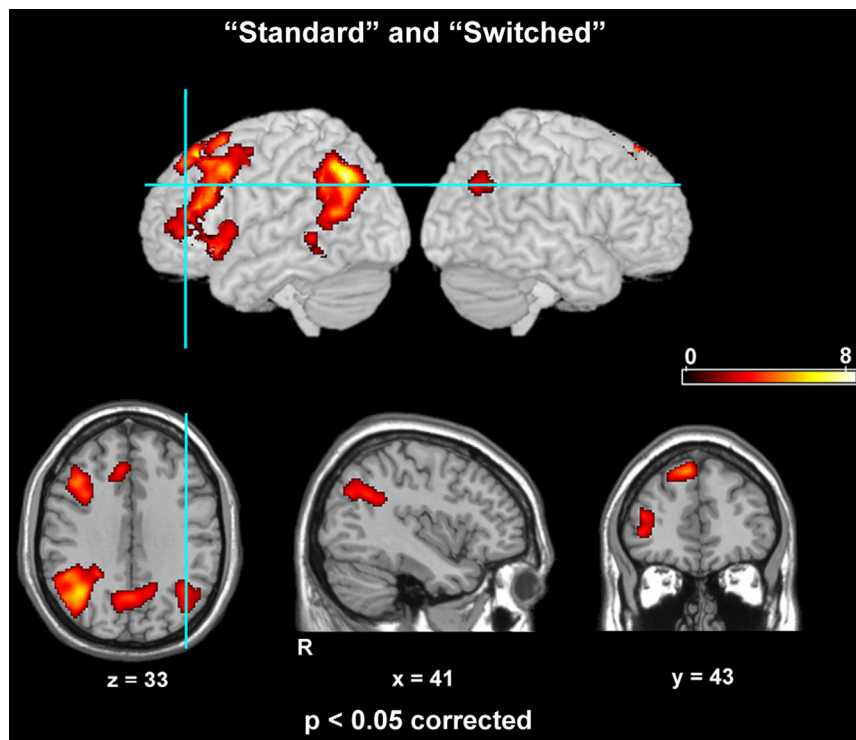


Fig. 1 – The brain network of deductive reasoning. The brain regions which were commonly activated while reasoning on the standard (SSC; “If I ..., then you ...”) and switched (WSC; “If you ..., then I ...”) “social contract” versions of the Selection-task ($p < 0.05$ corrected for multiple comparisons; see [Tables 1](#) and [2](#) for the detailed description of the activated regions in each of the two tasks). The activations largely overlap with those highlighted by a recent meta-analysis of 28 studies of deductive reasoning (see [Fig. 1b](#) in [Prado et al., 2011](#)).

Table 4 – The brain regions that were more strongly activated by “standard” than “switched” conditional rules ($p < 0.05$ corrected for multiple comparisons).

Cluster-size	Hemisphere	Anatomical region	MNI			t-value
			x	y	z	
2711	Right	Middle Cingulate Cortex (4a)	4	–30	50	4.29
	Right	Paracentral Lobule (4a)	14	–28	60	4.24
	Left	Middle Cingulate Cortex (5m)	–8	–38	52	3.77
	Right	Postcentral Gyrus (2)	22	–42	52	3.75
	Right	Postcentral Gyrus (3a)	26	–32	46	3.55
802	Right	Insula Lobe (OP2)	32	–24	20	4.64
	Right	Rolandic Operculum (OP1)	40	–28	20	4.6
	Right	Inferior Parietal Lobule (PFop)	46	–28	28	3.5
	Right	Postcentral Gyrus (OP4)	64	–16	18	3.41

–32, 54; [Fig. 2-bottom](#), red sphere). The converse comparison showed that the WSC task, compared with the SSC one, elicited higher activity in the medial superior frontal gyrus associated with external agency (BA 6; 6, 8, 60; [Fig. 2-bottom](#), green sphere).

3. Discussion

We used the “standard” and “switched” social contract versions of the Selection-task ([Wason, 1983](#)) to investigate the neural bases of human natural reasoning, beyond the formal

deductive operations performed by core-logic prefrontal regions ([Monti et al., 2007, 2009](#)). In line with previous studies ([Fiddick et al., 2004, 2005](#); [Sugiyama et al., 2002](#)), in both conditions the selection of the deontically correct responses (i.e. “benefit accepted” and “requirement non satisfied” cards, regardless of their logical category) was above 80%. This task thus provides an excellent opportunity to investigate the neural bases of human reasoning, while controlling for task difficulty and linguistic processing. By comparing activations associated with the standard and switched conditional rules, we thus aimed to highlight the relative weight of logical deductive operations vs. non-logical processes shaping their

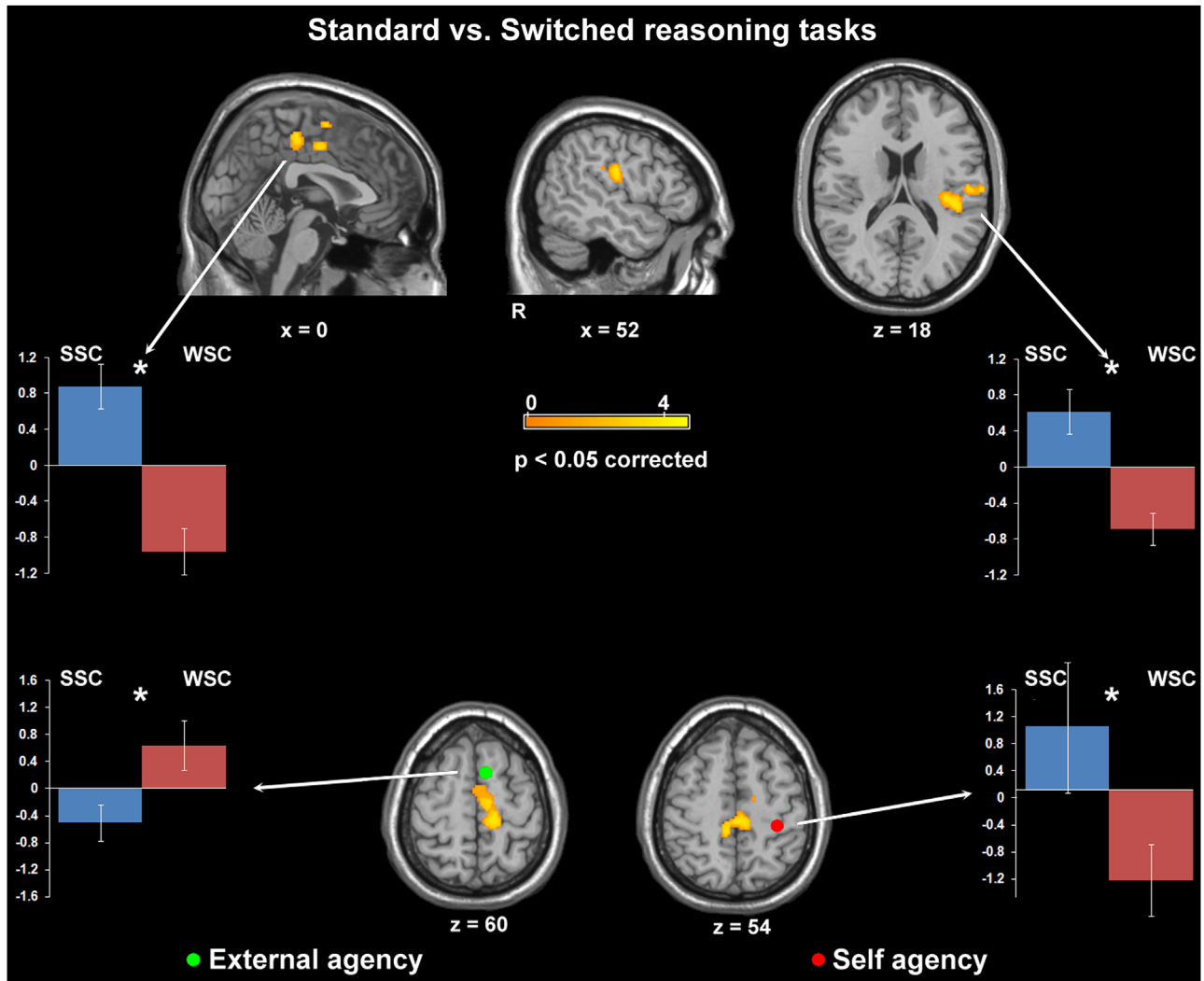


Fig. 2 – Reasoning on standard vs. switched conditional rules. Top: the medial parietal and right inferior parietal regions which were more strongly activated by the Standard (SSC), compared with the Switched (WSC), “social contract” versions of the Selection-task ($p < 0.05$ corrected for multiple comparisons). The histograms show the strength of neural activity (mean parameter estimates \pm standard error of the mean) in the same regions (blue columns: standard; pink columns: switched). Bottom: the histograms show the strength of neural activity in the regions-of-interest associated with external agency (medial superior frontal gyrus, 6, 8, 60; green sphere) and internal agency (right postcentral gyrus; 34, –32, 54; red sphere) in a recent meta-analysis (Sperduti et al., 2011) (blue columns: standard; pink columns: switched). Asterisks indicate a significant difference ($p < 0.05$) between SSC and WSC tasks.

semantic interpretation and the ensuing representational format (e.g. visuospatial or agency processes).

3.1. The brain network of deductive reasoning

To this purpose, we first assessed the consistency of the present results with those described in previous studies. Both whole-brain and ROIs analyses supported the engagement of the left fronto-temporo-parietal network of deductive reasoning (see Fig. 1b in Prado et al., 2011), along with the right parietal cortex when reasoning on social contracts (Canessa et al., 2005; Fiddick et al., 2005). In addition, in both social tasks the left-sided activations in the inferior frontal cortex (BA 47) and inferior parietal cortex (BA 40) overlap with the coordinates of core-logic and support brain regions (Monti

et al., 2007), respectively. The latter regions, which are consistently activated in neuroimaging studies on deductive reasoning (Prado et al., 2011), have been suggested to support the deductive logic operations performed by core-logic rostralateral prefrontal cortex, by extracting, representing and manipulating in working-memory the formal structure of arguments. Our results strengthen this hypothesis in two ways. First, because these regions were commonly activated in the “descriptive” (DES), SSC and WSC tasks, all requiring the translation of linguistic arguments into a formal representational format despite their different contents. Second, because they were maximally activated, also involving the right inferior frontal cortex, in the DES task, in which the arbitrary content of the conditional rule increases the need for its processing in terms of logical categories. Indeed, the

same regions have been previously associated with conditional reasoning on arbitrary content, in particular while solving the modus tollens (“If P, then Q”; “not-Q”; then “not-P”; Noveck et al., 2004), which is the critical component of the logical processes underlying the Selection-task.

3.2. Reasoning on standard vs. switched conditional rules

Although the SSC and WSC tasks diverge in terms of their adherence to formal logic, differences between them at the neural level did not involve any of the prefrontal core-logic regions highlighted by Monti et al. (2007, 2009). We tested the alternative hypothesis that differential activity across the two types of social contract would involve parietal regions associated with visuospatial imagery processes coding egocentric vs. allocentric reference frames in social interactions.

In line with this hypothesis, the SSC task elicited stronger activity than the WSC one in the medial parietal cortex and right inferior parietal cortex. A similar right-lateralization in the fronto-parietal network of deduction is elicited by relational arguments, regardless of the presence of linguistic material (Prado et al., 2011), likely reflecting their visuospatial encoding (Knauff et al. 2003; Maguire et al., 1998; Molenberghs et al., 2012; Osherson et al., 1998; Sack et al., 2002). Indeed, both these regions are involved in mental imagery and rotation (Bien and Sack, 2014) as well as in self-agency and first-person perspective, i.e. with the centeredness of the subjective multimodal experiential space on one's own body, within an egocentric reference frame (Vogeley and Fink, 2003; see Maguire et al., 1998, 1999). A wealth of evidence shows that such a “minimal self” (Gallagher, 2000) – i.e., a clear instance of what has been considered elsewhere a form of goal-oriented, primitive, univocal, socially restricted, and yet significant variety of self (Pantaleo, 1997; Pantaleo and Wicklund, 2000; Pantaleo, Canessa, 2011; Wicklund, 1999; Wicklund and Pantaleo, 2012) – is crucial for people's instrumental relationships within their own physical and social environment. Critical neurobiological evidence, in this respect, comes from disorders of spatial cognition associated with right inferior parietal damage, such as impaired updating of egocentric spatial relationships in spatial neglect (Farrell and Robertson, 2000).

The differential activations across SSC and WSC tasks may thus suggest that, compared with the arbitrary content of “descriptive” rules, social interactions can be more easily represented in terms of well-defined (spatial) relationships between the agents involved in the conditional rule (i.e. antecedent and consequent). It is likely that this mapping cannot occur, unless greater cognitive resources are recruited, with “descriptive” conditional rules, which by definition entail an arbitrary relationship between the antecedent and the consequent.

Although no region survived a correction for multiple comparisons in the WSC vs. SSC contrast, our hypothesis was supported by ROIs analyses on coordinates reported in a recent meta-analysis on the neural bases of self-agency vs. external-agency (Sperduti et al., 2011). We selected coordinates for parietal and dorsomedial prefrontal cortex, as these regions have been previously associated with the coding of spatial/social relationships (see Vogeley and Fink, 2003). The

postcentral gyrus, associated with self-agency (Sperduti et al., 2011), was more strongly activated in the SSC than in the WSC task. The converse contrast highlighted the dorsomedial prefrontal cortex, which has been associated with external agency. In line with whole-brain results, these data support our hypothesis that standard and switched conditional rules may engage opposite, i.e. egocentric vs. allocentric, reference frames, although only the former emerged in whole-brain analyses. Such an asymmetry in the strength of related neural activity may reflect a greater effort needed for the adoption of an allocentric, compared with an egocentric, reference frame. This hypothesis fits with the fact that, although the difference is generally not significant, the standard task typically elicits higher performance than the switched one (e.g. Sugiyama et al., 2002).

Our results thus suggest that human inferences engage visuospatial processes related with a sense of agency while acting in one's own environment, including the social one. Such processes may either overcome logic deductive operations via domain-specific reasoning mechanisms (Cosmides, 1989; Fiddick, 2004) or provide alternative inferential routes, e.g. in terms of the semantic interpretation of the arguments, thus resulting in higher deontical, rather than logical, accuracy. The latter view fits with a growing theoretical framework in the study of human reasoning, stressing the role of interpretative processes in charge of assigning a logical form to the conditional rule, i.e. “reasoning for, rather than from, an interpretation” (Stenning and van Lambalgen, 2001, 2004, 2008; see also Girotto et al. (2001)). These processes, related to understanding the semantics of the conditional rule, may result in a more straightforward interpretation (and consequently higher performance) of social contracts than descriptive rules. The recruitment of the right parietal cortex by standard vs. switched social contracts (and not by descriptive-abstract rules) may reflect a semantic interpretation in terms of spatial relationships between their interacting agents, and thus with reference to either an egocentric or allocentric perspective, respectively. This hypothesis may be tested via experimental designs explicitly separating the interpretation of the conditional rule from subsequent reasoning processes (e.g. Fiddick et al., 2005), particularly with techniques offering high temporal resolution.

3.3. Conclusions

In conclusion, we provide novel neural evidence reflecting the notion that human inferences often deviate from the rules of logical deduction. While core-logic brain regions in lateral and medial prefrontal cortex (Monti et al., 2007, 2009) play a key role in normative deductive inference, a wealth of evidence in the psychological literature (Wason, 1983; Manktelow and Over, 1991) shows that natural reasoning often follows alternative – possibly semantic-interpretative – routes, whose drives have been hotly debated for decades (see Cosmides, 1989; Fiddick et al., 2000; Sperber and Girotto, 2002; Stenning and van Lambalgen, 2004). Here we show that, in the human brain, such non-logic inferential routes intersect right parietal neural mechanisms underlying visuospatial processes which encode one's own subjective experience in either egocentric vs. allocentric frames, i.e. in terms of

either self-centered vs. other-centered social focal points. In line with the non-logical responses elicited by the social versions of the Selection-task, confirmed in the present study, these neural mechanisms appear to support (or redirect) our inferences, thus eliciting the well known “content effects” in deductive reasoning. Our data suggest that the resulting deductive inferences rely on visuospatial processes focusing one's own sense of self, at least when we are brought to act as decision-makers in apparently socially-meaningful circumstances.

4. Experimental procedure

4.1. Subjects

Fourteen right-handed (Oldfield, 1971) monolingual native speakers of Italian (7 females, 7 males; mean age = 23.6 years; standard-deviation (SD) = 1.64; range 21–26 years) took part in the experiment. All participants declared that they had little or no training in formal logic, and none had a history of neurologic or psychiatric disorders. Subjects gave informed written consent to the experimental procedure, which was approved by the local Ethics Committee.

4.2. Task

Subjects participated in three different versions of the Selection-task, namely descriptive (DES), standard social contract (SSC) and switched social contract (WSC), according to the terminology of Cosmides (1989, 2005). All tasks had the same structure, differing only in the content of the conditional rules. In the DES task, subjects were presented with conditional statements in the form “If P, then Q,” which described an arbitrary relation between two actions performed by a hypothetical member of an unknown tribe (e.g., “If one cracks walnut shells, then he drinks pond water”). In the SSC task, conditional rules described an exchange of goods proposed by an individual to four other individuals (e.g., “If I give you walnut shells, then you give me pond water”). In the WSC task, the conditional rule describing the exchange is switched (e.g., “If you give me pond water, then I give you walnut shells”). All the conditional rules were embedded in a story context, involving unfamiliar stimuli and impersonal situations pertinent to characters and objects proper to fictitious tribes, to ensure that subjects had not had any experience with those kinds of contexts. Such story specified that social contracts involved rationed goods, and that the people receiving the offer may thus be motivated to violate them. Following previous studies (e.g. Sugiyama et al., 2002; see Fiddick et al. (2000)), in all tasks subjects were then shown four cards, corresponding to the logical categories P, not-P, Q, and not-Q. For instance, given the social contract “If I give you X, then you give me Y”, the four cards reported “Has given X” (P), “Has not given X” (not-P), “Has given Y” (Q) and “Has not given Y” (not-Q) (see Supplementary Fig. 1). Participants were informed that (a) each card provided information about one of four people and (b) the two sides of the card provided information about the two parts of the conditional rule. Subjects were asked to indicate *all and only* the cards that need to be turned over to determine whether any of

the four people had violated the rule. For all tasks, the correct logical answer consists of choosing both the P and the not-Q cards because, whatever the content, only these cards can reveal a formal violation of the conditional rule. However, only in the SSC task these cards also allow to identify whether the social contract has been violated by any of the individuals receiving the offer. Instead, identifying such violation requires to turn the Q and not-P cards in the WSC task. The same stimuli were used in the three tasks, with the only difference among conditions being the kind of reasoning required of the subjects with reference to the content of the conditional rule. In fact, in the DES and SSC/WSC tasks, subjects had to reason in terms of, respectively, a possible violation of an arbitrary conditional rule or of a social contract.

A matching task was used as a baseline, in which either a descriptive or a social contract rule was presented (e.g., “If I give you walnut shells, then you give me pond water”). Each baseline task consisted of exactly the same conditional sentences presented in the corresponding reasoning task. However, the content of the subsequent four cards was partially different from reasoning trials. In baseline task, indeed, two of them showed the name of objects actually mentioned in the sentence (e.g., walnut shells and pond water) whereas the other two cards showed the name of objects not present in the sentence (e.g., granite rocks and carrot roots). The baseline task was to select all and only the cards of the former kind. According to a classic “cognitive subtraction” logic, the aim of the baseline was to control for visuo-perceptual and linguistic processing, as well as for motor response requirements.

4.3. Procedure

We used a block-design paradigm, with 16 trials for each of the three reasoning tasks (subdivided in four scanning sequences). In each trial, a conditional rule was presented for 5 s and was followed by a group of four cards, which remained on the screen for 20 s during which subjects could select the cards by pressing a four-button keyboard. The presentation time of the stimuli during functional scanning was calibrated based on response times measured in a behavioral pilot study. The left–right order of the cards corresponding to the four possible logical categories (P, not-P, Q, not-Q) was counterbalanced across trials. Each task was preceded by specific instructions lasting 12 s, and was paired with a baseline task which had the same structure and stimuli except that subjects had only 10 s to select the cards. The order of presentation of the tasks was counterbalanced across the four scanning sequences, and the order of the sequences was counterbalanced across subjects.

Before being positioned in the scanner, subjects received a brief training to ensure that they had understood the instructions and the stories we used to introduce the tasks. In addition, they were instructed to perform the task throughout its 20-s period and double-check their answers to ensure accuracy if they finished before the cards were removed from view. Visual stimuli were viewed via a back-projection screen located in front of the scanner and a mirror placed on the head-coil.

4.4. fMRI data acquisition

Anatomical T1-weighted and functional T2*-weighted magnetic resonance (MR) images were acquired with a 1.5-T whole-body scanner (General Electric Medical Systems, Milwaukee, WI). Functional images were acquired using a T2*-weighted gradient-echo, echo planar pulse sequence (30 contiguous slices parallel to the anterior-posterior commissure (AC-PC) line covering the whole brain, repetition time (TR)=4 s, echo time (TE)=60 ms, flip-angle=90°, field-of-view (FOV)=280 × 280 mm², matrix=64 × 64, slice thickness=4 mm, in-plane resolution=4.38 × 4.38 mm²). Each scanning sequence comprised 149 sequential volumes, for 596 volumes in total for each subject. A high-resolution T1-weighted anatomic scan (3D, spoiled gradient recalled (SPGR) pulse sequence, 124 slices, TR=600 ms, TE=20 ms, slice thickness=1.5 mm, in-plane resolution=0.78 × 0.78 mm²) was also acquired for each subject.

4.5. fMRI data pre-processing and statistical analyses

Image pre-processing and statistical analyses were performed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>), implemented in Matlab v7.4 (Mathworks, Inc., Sherborn, MA) (Worsley and Friston, 1995). We discarded the first 6 volumes of each functional run to allow for T1-equilibration effects. All remaining 572 volumes from each subject were then spatially realigned to the first volume of the first scan and unwarped, spatially normalized and resampled in 2 × 2 × 2 mm³ voxels, and spatially smoothed with a 8-mm full-width half-maximum (FWHM) isotropic Gaussian kernel. The resulting time series across each voxel were high-pass filtered to 1/128 Hz, and serial autocorrelations modeled as an AR(1) process.

The results related to reasoning on standard social contracts (SSC) vs. descriptive (DES) conditional rules have been previously described in a smaller sample of 12 participants (Canessa et al., 2005). In line with the aim of the present study, here we compare and discuss only the activations elicited by the SSC and WSC tasks. We used statistical parametric mapping to highlight the brain regions showing significantly stronger activity in each reasoning task compared with its baseline, as well as those showing significant differences between the two social contract tasks (i.e. direct comparisons between SSC and WSC, after baseline subtraction). Statistical maps were generated using a random-effect model, implemented in a 2-levels procedure.

At the first level, single-subject fMRI responses were modeled in a design-matrix comprising the onset of trials belonging to the single reasoning tasks and their baselines, with duration equal to the response times of single trials. We modeled only trials with correct responses (P and not-Q in DES and SSC tasks, Q and not-P in WSC task), while those with incorrect or missed responses were modeled in a regressor of no interest. In order to balance epoch-length across regressors, in a separate control analysis we specified a duration of 10 s for all reasoning and baseline trials, while the last 10 s of each reasoning trial were modeled in a regressor of no interest (see Supplementary Tables 1–4). In both analyses, regressors modeling epochs were convolved with a canonical hemodynamic response function (HRF), and parameter

estimates for all regressors were obtained by maximum-likelihood estimation.

At the second level, the resulting contrast images from all subjects entered paired t-tests to assess group effects. For each comparison of interest (e.g. SSC vs. baseline), this process produced a statistical parametric map of the t-statistics at every voxel. We also performed a Conjunction-null (Nichols et al., 2005) analysis to identify clusters that were significantly activated by both SSC and WSC tasks. Maxima were reported in the MNI (Montreal Neurological Institute; Evans et al., 1993) space for clusters exceeding a threshold of $p < 0.05$ corrected for multiple comparisons (Friston et al., 1996; Hayasaka et al., 2004). The location of activation foci was determined in the stereotaxic space of Talairach and Tournoux (1988) after correcting for differences between the latter and the MNI coordinate systems with a nonlinear transformation (see <http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml>).

4.6. Regions-of-interest (ROIs) analysis

Based on our experimental hypothesis, we aimed to assess the consistency of the present results with previously published data on the neural bases of deductive reasoning, reasoning on social contracts, logical inference and agency attribution in social interactions. To this purpose, in different sets of ROIs analyses we assessed the neural activations in the SSC and WSC tasks in terms of the brain regions previously associated with (a) deductive reasoning in 28 previous related studies, i.e. meta-analytic results by Prado et al. (2011); (b) deductive reasoning on social contracts vs. descriptive conditional rules, i.e. replication of data by Canessa et al. (2005); (c) reasoning on social contracts vs. precautionary rules (Fiddick et al., 2005); (d) “logical” deductive operations, i.e. “core logic” and “support regions” of Monti et al. (2007); (e) agency processes, i.e. meta-analytic results on 1st vs. 3rd person agency attribution by Sperduti et al. (2011).

For all these analyses, we first used the SPM-toolbox Marsbar (<http://marsbar.sourceforge.net>) to manually define ROIs as 4-mm radius spheres centered on the MNI coordinates of the key regions reported in the above studies (see Supplementary Table 5a–e). Then, we used the toolbox REX (<http://web.mit.edu/swg>) to extract from these ROIs task-specific parameter estimates for off-line statistical analyses. In the latter, we used two-tailed two-sample t-tests to assess whether a given ROI was significantly activated in a given task (compared with its baseline), or whether it was differentially activated by SSC vs. WSC tasks. Within each set of ROIs analysis we employed a statistical threshold of $p < 0.05$ corrected for multiple comparisons using False-Discovery-Rate (FDR; Benjamini, 2010).

Acknowledgments

We wish to thank two anonymous reviewers for their insightful suggestions. This study was financially supported by a Ministero dell'Istruzione, dell'Università e della Ricerca, MIUR Grant (PRIN 2010XPMFW4_008 “I meccanismi neurocognitivi alla base delle interazioni sociali”) to Stefano F. Cappa. CC was financially supported by the Fondazione Cariplo Grant “Formazione Post-universitaria di Eccellenza in Medicina

Molecolare". The funding sources had no role in any phase of the study. The authors declare no competing financial interests. Authors' contributions: planned and designed the study: NC, AG, SFC; collected data: NC, AG; analyzed data: NC, CC; obtained funding: GP, SFC; wrote the paper: NC, GP, SFC.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.brainres.2014.06.001>.

REFERENCES

- Benjamini, Y., 2010. Discovering the false discovery rate. *J. R. Stat. Soc.: Ser. B (Stat. Methodol.)* 72 (4), 405–416.
- Bien, N., Sack, A.T., 2014. Dissecting hemisphere-specific contributions to visual spatial imagery using parametric brain mapping. *Neuroimage* 94, 231–238.
- Canessa, N., Gorini, A., Cappa, S.F., Piattelli-Palmarini, M., Danna, M., Fazio, F., 2005. The effect of social content on deductive reasoning: an fMRI study. *Hum. Brain Mapp.* 26 (1), 30–43.
- Charron, S., Koechlin, E., 2010. Divided representation of concurrent goals in the human frontal lobes. *Science* 328 (5976), 360–363.
- Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J.K., Holyoak, K.J., 2001. Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage* 14 (5), 1136–1149.
- Cosmides, L., 1989. The logic of social exchange: has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition* 31 (3), 187–276.
- Cosmides, L., Tooby, J., Fiddick, L., Bryant, G.A., 2005. Detecting cheaters. *Trends Cogn. Sci.* 9 (11), 508–510 (505–506; author reply).
- Ermer, E., Guerin, S.A., Cosmides, L., Tooby, J., Miller, M.B., 2006. Theory of mind broad and narrow: reasoning about social exchange engages ToM areas, precautionary reasoning does not. *Soc. Neurosci.* 1 (3–4), 196–219.
- Evans, A.C., Collins, D.L., Mills, S.R., Brown, E.D., Kelly, R.L., Peters, T.M., 1993. 3D statistical neuroanatomical models from 305 MRI volumes. *Proc. IEEE Nucl. Sci. Symp. Med. Imaging Conf.*, 1813–1817.
- Farrell, M.J., Robertson, I.H., 2000. The automatic updating of egocentric spatial relationships and its impairment due to right posterior cortical lesions. *Neuropsychologia* 38 (5), 585–595.
- Fiddick, L., 2004. Domains of deontic reasoning: resolving the discrepancy between the cognitive and moral reasoning literatures. *Q. J. Exp. Psychol. A* 57 (3), 447–474.
- Fiddick, L., Cosmides, L., Tooby, J., 2000. No interpretation without representation: the role of domain-specific representations and inferences in the Wason selection task. *Cognition* 77 (1), 1–79.
- Fiddick, L., Spampinato, M.V., Grafman, J., 2005. Social contracts and precautions activate different neurological systems: an fMRI investigation of deontic reasoning. *Neuroimage* 28 (4), 778–786.
- Fodor, J., 2000. Why we are so good at catching cheaters. *Cognition* 75 (1), 29–32.
- Friston, K.J., Holmes, A., Poline, J.B., Price, C.J., Frith, C.D., 1996. Detecting activations in PET and fMRI: levels of inference and power. *Neuroimage* 4 (3 Pt 1), 223–235.
- Gallagher, I.I., 2000. Philosophical conceptions of the self: implications for cognitive science. *Trends Cogn. Sci.* 4 (1), 14–21.
- Gigerenzer, G., Hug, K., 1992. Domain-specific reasoning: social contracts, cheating, and perspective change. *Cognition* 43 (2), 127–171.
- Giroto, V., Kemmelmeier, M., Sperber, D., van der Henst, J.B., 2001. Inept reasoners or pragmatic virtuosos? Relevance and the deontic selection task. *Cognition* 81, B69–B76.
- Goel, V., 2007. Anatomy of deductive reasoning. *Trends Cogn. Sci.* 11 (10), 435–441.
- Hayasaka, S., Phan, K.L., Liberzon, I., Worsley, K.J., Nichols, T.E., 2004. Nonstationary cluster-size inference with random field and permutation methods. *Neuroimage* 22 (2), 676–687.
- Johnson-Laird, P.N., 1995. Mental models, deductive reasoning, and the brain. In: Gazzaniga, M.S. (Ed.), *The Cognitive Neurosciences*. MIT Press, Cambridge, MA, pp. 999–1008.
- Knauff, M., Fangmeier, T., Ruff, C.C., Johnson-Laird, P.N., 2003. Reasoning, models, and images: behavioral measures and cortical activity. *J. Cogn. Neurosci.* 15 (4), 559–573.
- Legrenzi, P., 2004. Willem Doise e la Scuola di Ginevra [Willem Doise and the Geneva School]. *G. Italiano Psicol.* 4, 683–695.
- Maguire, E.A., Burgess, N., Donnett, J.G., Frackowiak, R.S., Frith, C.D., O'Keefe, J., 1998. Knowing where and getting there: a human navigation network. *Science* 280 (5365), 921–924.
- Maguire, E.A., Burgess, N., O'Keefe, J., 1999. Human spatial navigation: cognitive maps, sexual dimorphism, and neural substrates. *Curr. Opin. Neurobiol.* 9 (2), 171–177.
- Manktelow, K., Evans, J.S. B.T., 1979. Facilitation of reasoning by realism: effect or non-effect? *Br. J. Psychol.* 70, 477–488.
- Manktelow, K.I., Over, D.E., 1991. Social roles and utilities in reasoning with deontic conditionals. *Cognition* 39 (2), 85–105.
- Molenberghs, P., Sale, M.V., Mattingley, J.B., 2012. Is there a critical lesion site for unilateral spatial neglect? A meta-analysis using activation likelihood estimation. *Front. Hum. Neurosci.* 6, 78.
- Monti, M.M., Osherson, D.N., Martinez, M.J., Parsons, L.M., 2007. Functional neuroanatomy of deductive inference: a language-independent distributed network. *Neuroimage* 37 (3), 1005–1016.
- Monti, M.M., Parsons, L.M., Osherson, D.N., 2009. The boundaries of language and thought in deductive inference. *Proc. Natl. Acad. Sci. U. S. A.* 106 (30), 12554–12559.
- Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. *Neuroimage* 25 (3), 653–660.
- Noveck, I.A., Goel, V., Smith, K.W., 2004. The neural basis of conditional reasoning with arbitrary content. *Cortex* 40 (4–5), 613–622.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Osherson, D., Perani, D., Cappa, S., Schnur, T., Grassi, F., Fazio, F., 1998. Distinct brain loci in deductive versus probabilistic reasoning. *Neuropsychologia* 36 (4), 369–376.
- Pantaleo, G., 1997. Explorations in Orienting vs. Multiple Perspectives. Pabst Science Publishers, Lengerich.
- Pantaleo, G., 2004. Il conflitto socio-cognitivo stimola la coesistenza psicologica di prospettive multiple? [Does socio-cognitive conflict stimulate the psychological coexistence of multiple perspectives?] *G. Italiano Psicol.* 4, 737–743.
- Pantaleo, G., Canessa, N., 2011. 'Prospettive multiple', comportamento prosociale e altruismo: oltre la Civiltà dell'empatia. ['Multiple perspectives', prosocial behavior, and altruism: Beyond the Age of Empathy]. In: Boca, S., Scaffidi Abbate, C. (Eds.), *Altruismo e comportamento prosociale: Temi e prospettive a confronto*. Franco Angeli, Milano, pp. 186–240.

- Pantaleo, G., Wicklund, R.A., 2000. Multiple perspectives: social performance beyond the single criterion. *Z. Sozialpsychologie* 31, 231–242 (Special Issue on Motivation Gains in Groups).
- Prado, J., Chadha, A., Booth, J.R., 2011. The brain network for deductive reasoning: a quantitative meta-analysis of 28 neuroimaging studies. *J. Cogn. Neurosci.* 23 (11), 3483–3497.
- Rips, L., 1994. *The Psychology of Proof*. MIT Press, Cambridge, MA.
- Rypma, B., Prabhakaran, V., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1999. Load-dependent roles of frontal brain regions in the maintenance of working memory. *Neuroimage* 9 (2), 216–226.
- Sack, A.T., Hubl, D., Prvulovic, D., Formisano, E., Jandl, M., Zanella, F.E., 2002. The experimental combination of rTMS and fMRI reveals the functional relevance of parietal cortex for visuospatial functions. *Brain Res. Cogn. Brain Res.* 13 (1), 85–93.
- Sperber, D., Girotto, V., 2002. Use or misuse of the selection task? Rejoinder to Fiddick, Cosmides, and Tooby. *Cognition* 85 (3), 277–290.
- Sperduti, M., Delaveau, P., Fossati, P., Nadel, J., 2011. Different brain structures related to self- and external-agency attribution: a brief review and meta-analysis. *Brain Struct. Funct.* 216 (2), 151–157.
- Stenning, K., van Lambalgen, M., 2001. Semantics as a foundation for psychology: a case study of Wason's selection task. *J. Log., Lang. Inf.* 10, 273–317.
- Stenning, K., van Lambalgen, M., 2004. A little logic goes a long way: basing experiment on semantic theory in the cognitive science of conditional reasoning. *Cogn. Sci.* 28, 481–529.
- Stenning, K., van Lambalgen, M., 2008. *Human Reasoning and Cognitive Science*. Bradford Book, Cambridge MA. MIT Press.
- Stone, V.E., Cosmides, L., Tooby, J., Kroll, N., Knight, R.T., 2002. Selective impairment of reasoning about social exchange in a patient with bilateral limbic system damage. *Proc. Natl. Acad. Sci. U. S. A.* 99 (17), 11531–11536.
- Sugiyama, L.S., Tooby, J., Cosmides, L., 2002. Cross-cultural evidence of cognitive adaptations for social exchange among the Shiwiari of Ecuadorian Amazonia. *Proc. Natl. Acad. Sci. U. S. A.* 99 (17), 11537–11542.
- Talairach, J., Tournoux, P., 1988. *Co-planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System – an Approach to Cerebral Imaging*. Medical Publishers. Thieme, New York.
- Tanaka, S., Honda, M., Sadato, N., 2005. Modality-specific cognitive function of medial and lateral human Brodmann area 6. *J. Neurosci.* 25 (2), 496–501.
- Vogeley, K., Fink, G.R., 2003. Neural correlates of the first-person-perspective. *Trends Cogn. Sci.* 7 (1), 38–42.
- Volz, K.G., Schubotz, R.I., von Cramon, D.Y., 2005. Variants of uncertainty in decision-making and their neural correlates. *Brain Res. Bull.* 67 (5), 403–412.
- Wason, P., 1983. Realism and rationality in the selection task. In: Evans, J.S.B.T. (Ed.), *Thinking and Reasoning: Psychological Approaches*. Routledge, London, pp. 44–75.
- Wicklund, R.A., 1999. Multiple perspectives in person perception and theorizing. *Theory Psychol.* 9, 667–678.
- Wicklund, R.A., Pantaleo, G., 2012. The role of the professor. *Psicol. Soc.* 3, 355–376.
- Worsley, K.J., Friston, K.J., 1995. Analysis of fMRI time-series revisited—again. *Neuroimage* 2 (3), 173–181.