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RESEARCH ARTICLE

Statistical and perceptual updating: correlated impairments in right brain injury

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Abstract It has been hypothesized that many of the cognitive impairments commonly seen after right brain damage (RBD) can be characterized as a failure to build or update mental models. We (Danckert et al. in Neglect as a disorder of representational updating. NOVA Open Access, New York, 2012a; Cereb Cortex 22:2745–2760, 2012b) were the first to directly assess the association between RBD and updating and found that RBD patients were unable to exploit a strongly biased play strategy in their opponent in the children's game rock, paper, scissors. Given that this game required many other cognitive capacities (i.e., working memory, sustained attention, reward processing), RBD patients could have failed this task for various reasons other than a failure to update. To assess the generality of updating deficits after RBD, we had RBD, left brain-damaged (LBD) patients and healthy controls (HCs) describe line drawings that evolved gradually from one figure (e.g., rabbit) to another (e.g., duck) in addition to the RPS updating task. RBD patients took significantly longer to alter their perceptual report from the initial object to the final object than did LBD patients and HCs. Although both patient groups performed poorly on the RPS task, only the RBD patients showed a significant correlation between the two, very different, updating tasks. We suggest these data indicate a general deficiency in the ability to update mental representations following RBD.

Keywords Right brain damage · Mental representations · Updating failures · Ambiguous figures

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Introduction

Strokes are common and rehabilitation outcomes are poor when strokes affect the right cerebral hemisphere (Appelros et al. 2002; Bowen and Lincoln 2007; Bowen et al. 1999; Cassidy et al. 1998; Nijboer et al. 2013; Ringman et al. 2004). Although impaired spatial attention (i.e., neglect) is certainly the core syndrome after right brain damage (RBD), there are other, non-spatial deficits that arise from RBD (Danckert et al. 2012a for an overview; Bartolomeo et al. 2012 for a discussion of the networks impaired in neglect), including prolongation of the attentional blink (Husain et al. 1997; Shapiro et al. 2002), impaired perception of time (Basso et al. 1996; Danckert et al. 2007; Merrifield et al. 2010), deficits of motor imagery (Danckert et al. 2002), decreased working memory capacity (Ferber and Danckert 2006; Husain et al. 2001), impaired statistical learning (especially when accompanied by neglect; for an overview, see Shaqiri and Anderson 2013; Shaqiri et al. 2013), impaired humor appreciation (Brownell et al. 1983) and alterations of Theory of Mind (Happé et al. 1999; Griffin et al. 2006). We have hypothesized that many of these apparently heterogeneous cognitive impairments reflect a failure to build, use or update representational models (Danckert et al. 2012a, b; Shaqiri and Anderson 2013; Shaqiri et al. 2013).

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Every day, we face the world with certain beliefs about the rules that govern our environment and the probable consequences of particular actions (Griffiths and Tenenbaum 2012). This process of modeling our environment requires a number of interdependent sub-processes. Through mere exposure and without explicit feedback, we implicitly learn environmental contingencies (i.e., statistical learning; Turk-Browne et al. 2009; Aslin and Newport 2012). There is evidence that young children and even newborns are able to detect regularities from the environment and to extract the transitional probabilities (Bulf et al. 2011; Fiser and Aslin 2002). Statistical learning in turn requires other processes such as priming, intact temporal processing and working memory (see Shaqiri and Anderson 2013; Shaqiri et al. 2013 for an overview). Based on these processes, we develop mental models of the world. These models compactly represent the rules and relationships of our world and allow us to make explicit predictions (e.g., if we go out in short pants in the middle of the Canadian winter, we will freeze); they also enable us to simulate "what-if" scenarios under different premises (e.g., if we are in Hawaii, it will be warm enough to wear shorts in January). Mental models contribute to a wide range of cognitive mechanisms including learning new skills from sparse data (Tenenbaum et al. 2011), modeling the mental states of others (Perner 1991; Vogeley et al. 2001) and mental simulation (e.g., counterfactual reasoning; Byrne 2002; Rafetseder and Perner 2010).

Critically, when incoming information does not match predictions generated by our models, we first need to detect this mismatch and then either abandon or update the current model. We conceive of updating as encapsulating both the recognition of a mismatch between expectations and observations, and the building of an alternative model; a process that may need several iterations to successfully complete (Danckert et al. 2012a, b; Hohwy 2012).

We have hypothesized that many of these diverse impairments after RBD can be considered disorders of model building and/or updating (Danckert et al. 2012a, b; Shaqiri and Anderson 2013; Shaqiri et al. 2013). A failure to appreciate humor, for example, can be construed as a failure to update, given that appreciating the punch line requires the detection of an incongruity between the expected and the actual information to resolve the inherent incongruity (Chan et al. 2012a, b; Samson et al. 2008). Similarly, the ability to build and update mental representations might also play a key role in Theory of Mind (i.e., modeling the mental states of others)—which has been consistently found to be impaired in patients with unilateral right hemisphere damage (Griffin et al. 2006; Happé et al. 1999; Winner et al. 1998; see Decety and Lamm 2007 for a meta-analysis of fMRI data on this point).

The notion that it is especially the right hemisphere that is involved in updating fits well with an older conception of the brain. Ramachandran (1995) considered the right hemisphere as a sort of "devil's advocate." In this conceptualization, the left hemisphere serves as an "interpreter" (Gazzaniga 1995) responsible for detecting and dealing with small, local anomalies (i.e., imposing consistency by ignoring or suppressing contrary evidence), while the right hemisphere monitors the *degree* of discrepancy and forces a shift when such a discrepancy is too large. Recently, Vocat et al. (2012) demonstrated an updating failure in RBD patients with anosognosia for hemiplegia (a syndrome in which patients deny their left-sided paralysis after right hemisphere brain damage), showing that these patients persisted in reporting their initial beliefs even when confronted with new, highly incongruent cues. This fits well with the notion that learning is accompanied by a transition in involvement from the right hemisphere responsible for learning at early stages (e.g., dealing with specific visual features, detecting novelty of stimuli) to the left hemisphere being specialized for processing patterns abstracted across stimuli required for conceptual learning (see Seger et al. 2000 for an overview). All this evidence supports the hypothesis that it is the right hemisphere that is involved in changing our mental models by detecting novel stimuli that do not fit within the constraints of the current model.

In prior work (Danckert et al. 2012b), we had participants play rock, paper and scissors (RPS) against a computer opponent that initially chose uniformly from the three options (i.e., 33 % rock, 33 % scissors, etc.) before ultimately switching to a strong bias, choosing one option 80 % of the time. We showed that RBD selectively disrupted the ability to exploit the biased strategy. Many RBD patients were unable to "beat" the computer at above chance levels even when the computer chose "paper" 80 % of the time. In contrast, controls and LBD patients rapidly recognized the biased play and adapted their choices accordingly. These data do not fully answer the question of *why* RBD patients typically failed to exploit the bias.

In our RPS task, participants needed to sustain their attention for a long period of time (i.e., 600 trials). For each of these 600 trials, they needed to process the reward value of a given trial (i.e., did they win, lose or tie) and they needed to keep track of their own plays. Sustained attention and working memory are known to be impaired after RBD (Bonato 2012; Ferber and Danckert 2006; Husain et al. 2001). It may be that RBD performance in our original study (Danckert et al. 2012a, b) reflected an impairment in one of these domains, as opposed to or in addition to a general updating impairment. Another account is that the RBD patients learned the statistics of the early block, which was uniformly random, and then failed to update this model when the computer opponent changed to biased play.

To evaluate among these possibilities, RBD and LBD participants and healthy controls (HCs) were asked to perform a shorter version (i.e., 410 trials) of the RPS task where the computer opponent chose 80 % "paper" right from the start. The computer then switched to an 80 % bias of playing "rock." A general failure to learn would predict that RBD patients should be impaired from the very first block. In contrast, if RBD patients can build a model of their opponent's initial play strategy, but are impaired when updating that model, such an impairment will be evident when transitioning from the first to the second bias.

Given the possible confounds of the RPS task outlined above, we used a second task to measure updating. In this perceptual representation task—adapted from Christman et al. (2009)—pictures morphed over 15 successive presentations from one unambiguous object (e.g., rabbit) to another (e.g., duck). The idea is that the longer it takes a person to update from reporting object one to object two, the more contradicting evidence that is required. This task has several advantages over the RPS task: It does not place the same load on working memory as the RPS task. Essentially, participants only need the information in the image they are currently looking at to solve the task; remembering earlier images is not necessary. This task is a shorter task (i.e., 15 trials instead of over 400 or more for the RPS task), and thus there is less opportunity for fatigue, a loss of vigilance or impairments due to deficits of sustained attention. There is also no inherent reward signal involved in this task that the participant would need to process on a trial-by-trial basis as there is in the RPS task. Finally, the verbal reports in this task reflect the actual representation of the participant (e.g., "It is a rabbit."). In the RPS task, a particular choice could have different interpretations. (e.g., sometimes participants pick what they think will win, and sometimes they will make a choice in order to falsify an assumption).

Given that we believe many RBD dysfunctions reflect a common updating mechanism, we expect updating impairments to correlate across the two tasks and for RBD patients to have more severe impairments.

Methods

The experimental protocol was approved by the University of Waterloo's Office of Research Ethics. All participants gave informed written consent prior to participation. All assessments and tasks were done in the same order for each of the participants: Behavioral Inattention Test (BIT; Wilson et al. 1987), Montreal Cognitive Assessment (MoCa; Nasreddine et al. 2005), Rock–paper–scissors, ambiguous figures and the Berg card sorting task (BCST; see Piper et al. 2011 for validation testing).

Participants

Three groups of participants were tested in this study—RBD patients, LBD patients and HCs. Patients were recruited from our Neurological Patient Database (funded through the Heart and Stroke Foundation of Ontario). Fifteen individuals were tested in the RBD group. One RBD patient was excluded from the sample due to a MoCa score in the demented range (MoCa Score 11). The final RBD sample comprised 14 individuals (4 female) with a mean age of 66.08 years, ±9.24; Fig. 1a shows lesions for each patient. A detailed description of the demographics for the RBD group can be seen in Table 1. None of these patients had participated in our original study (Danckert et al. 2012b).

Thirteen LBD patients were tested; three of these patients were excluded because either they failed to give reliable reports in the RPS task (when asked on random occasions whether they had won or lost against the computer they showed chance performance) or they decided to quit the experiment. The final sample comprised 10 individuals (four females) with a mean age of 64.40 years, ±10.28). Two of these patients also participated in our original study (Danckert et al. 2012b; Table 2; Fig. 1b).

There was no significant difference for age, MoCa score and time since stroke or lesion volume between the RBD and LBD patients (all p's > .05 in independent sample t tests).

All brain-damaged patients were screened for the presence of neglect at the time of recruitment into our database and again prior to completing this experiment. Seven of the RBD patients showed neglect at initial screening, while only one showed signs of neglect at the time of testing. None of the LBD showed neglect—neither at the time of recruitment, nor at the time of testing.

Healthy controls were recruited from the Waterloo Research in Aging Participant Pool and were screened to exclude any history of past neurological or psychiatric illnesses. General level of cognitive functioning was assessed in all participants using the Montreal Cognitive Assessment (MoCa; Nasreddine et al. 2005). In accordance with the norms of the assessment, a cutoff point of a MoCa score higher than or equal to 26 was used for HCs. The sample of HCs comprised 11 individuals (5 female; mean age = 72.27 years, ±6.17). Their mean MoCa score was 27.81 (±1.40), which was significantly higher than the MoCa score of the 14 RBD patients (MoCa = 24.07 (±3.00) [$t(23) = 3.85$, $p < .01$]) and 10 LBD patients (MoCa = 22.00 (±4.22) [$t(19) = 4.33$, $p < .001$]). There was no significant difference in the MoCa score between LBD and RBD patients [$t(22) = 1.42$, $p > .15$]. All of the HCs completed all tasks.

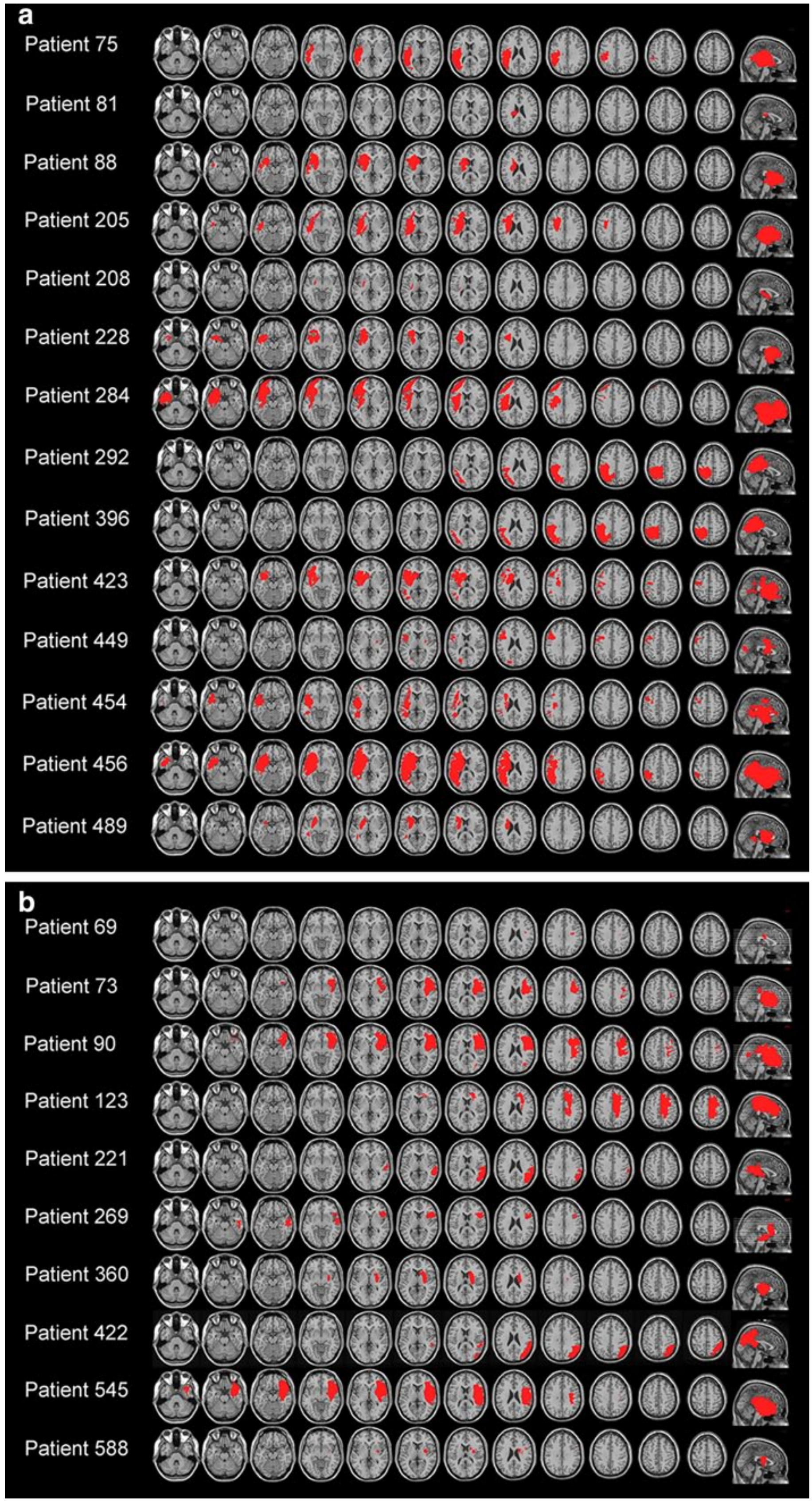

Fig. 1 Lesion tracings for all 14 RBD patients (**a**) and all 10 LBD patients (**b**) superimposed on an MNI template (see "Materials and Methods" section). Lesions are presented in a radiological convention (right hemisphere presented on the *left*)

Table 1 Patient demographics for the RBD group

ID	Gender	MoCa	Age	Months since stroke	Lesion	Neglect initially	Neglect at test	Lesion volume (voxels)	# of Trials in RPS	BCST	# pictures in AF task
75	M	22	60	45	Ins, F, O, P, T, RO	No	No	65,756	410	No	9.00
81	F	28	62	44	BG, Th	No	No	222	410	Yes	10.50
88	M	23	66	40	Ins, F, BG, T	No	No	48,445	64	Yes	11.75
205	M	27	58	29	Ins, F, O, T	Yes	No	41,506	410	No	
208	M	25	61	128	BG, T, RO	No	No	1,842	410	Yes	7.75
228	F	22	82	25	Ins, F, O, BG, T	Yes	No	38,168	86	Yes	8.25
284	F	25	70	17	Ins, F, O, BG, P, T, RO	Yes	No	125,495	37	No	12.75
292	M	28	50	24	Ins, F, BG, P, T, RO, Th, Cereb	Yes	No	131,810	410	Yes	6.75
396	M	18	85	18	F, O, BG, P, T, RO	Yes	Yes	84,156	360	No	11.75
423	M	25	58	7	Ins, F, BG, O, P, T, RO, Th	No	No	77,690	410	No	7.00
449	M	24	66	5	Ins, F, BG, O, P, T, RO	No	No	24,415	410	Yes	9.75
454	M	20	70	4	Ins, F, BG, O, P, T, RO, Th	Yes	No	43,832	410	Yes	10.00
456	F	27	65	3	Ins, F, BG, O, P, T, RO, Th	No	No	169,377	410	Yes	9.50
489	M	23	66	3	Ins, F, BG, T, RO, Th	Yes	No	17,110	301	Yes	7.75

Table 2 Patient demographics for the LBD group

ID	Gender	MoCa	Age	Months since stroke	Lesion	Lesion volume (voxels)	# pictures in AF task
69	F	26	76	43	F, BG, P, T	1,756	7.75
73	M	16	73	57	F, BG, O, P, T, RO	67,769	8.5
90	M	16	65	55	Ins, F, BG, O, P, T, RO	131,476	10.75
123*	F	20	60	295	Ins, F, BG, P	117,212	7.50
221*	M	23	47	66	IO, P, T, RO	33,064	4.50
269	F	21	72	41	Ins, F, O, P, T, RO	27,192	6.50
360	F	25	74	31	Ins, BG, T, Th	20,281	7.75
442	M	24	65	112	O, P, T, RO	50,171	5.50
545	M	20	48	2	Ins, F, BG, O, P, T, RO	128,583	10.00
588	M	29	64	2	Ins, F, BG	5,951	5.25

All LBD patients completed the RPS task (410 trials) and the BCST. None of the LBD patients showed signs of neglect

Sex: *M* male, *F* female, *Ins* insular, *F* frontal, *BG* basal ganglia, *O* occipital, *P* parietal, *T* temporal, *RO* rolandic operculum, *Th* thalamus, *Cereb* cerebellum

* LBD patients that participated in Danckert et al. (2012b)

The rock–paper–scissors task

Participants were asked to play the children's game RPS against a computer opponent and were instructed to try to win as many games as possible. Additionally, participants were instructed to attempt to determine whether the computer was employing a specific strategy. The task was adapted from our previous study (Danckert et al. 2012b) and modified for the purpose of this experiment. We programmed the task in Python using the PsychoPy library (Peirce 2009). We used pictures of the actual play items: rock, paper and scissors, rather than pictures of hand gestures to simplify the interpretation for participants. A trial began with two blue squares aligned vertically on a gray background in the center of the screen. Participants were informed that the top square represented the computer's choice and the bottom square represented the participant's choice (Fig. 2a).

After 500 ms, the color of the top square changed from blue to green. Participants were told that this color switch indicated that the computer had locked in its choice and that it was now their turn to choose the item they wanted to play. Participants could make their choice by selecting the "left" arrow key for "rock," the "down" arrow key for "paper" and the "right" arrow key for "scissors." Once a participant made his/her choice, both choices were revealed simultaneously, with the computer's choice revealed in the top square and the

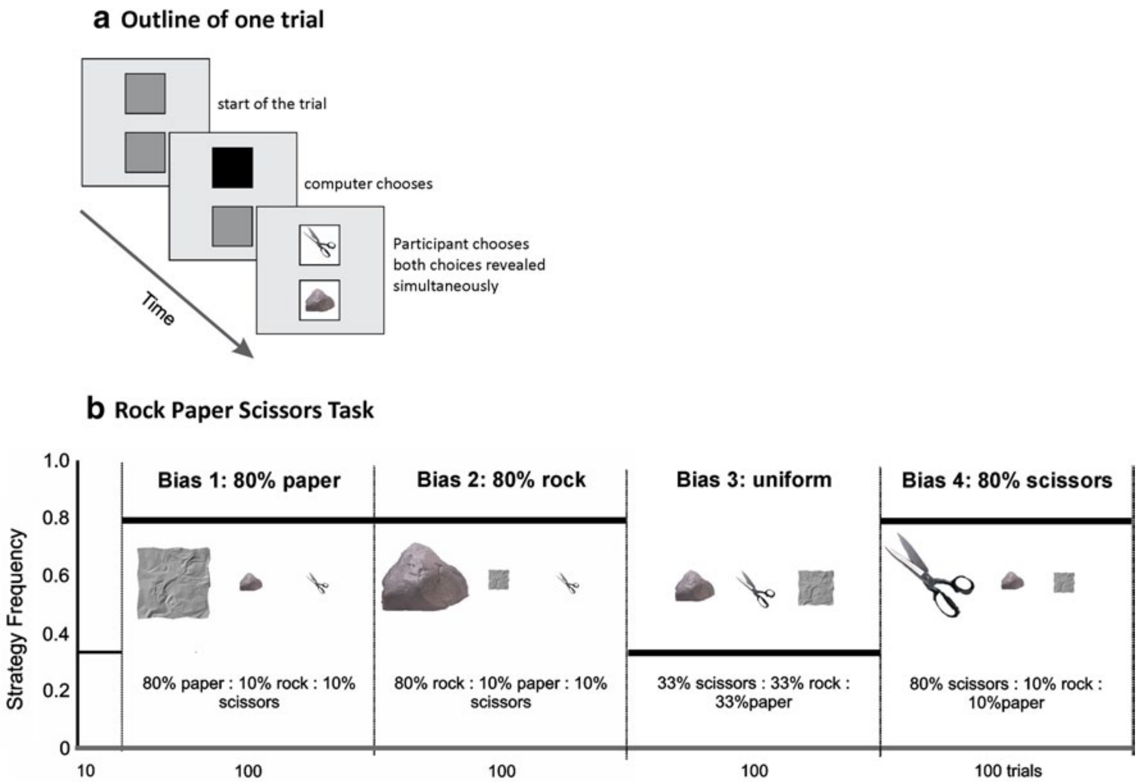

Fig. 2 **a** Schematic overview of the timeline of one trial. At the start of each trial, *two blue squares* were vertically aligned on a *gray background* in the center of the screen. The *top square* represented the computer's choice, and the *bottom square* represented the participant's choice. After 500 ms, the color of the top square changed from *blue* to *green* (here *displayed in black*), indicating that the computer had locked in its choice. Participants then made a choice, and both choices were revealed simultaneously (the computer's choice in the *top square* and the participant's choice in the *bottom square*). After viewing the results for 2 s, the next trial began. **b** Schematic overview over the different phases of the experiment. For the first 10 trials, the computer played randomly—each item was picked on one-third of trials. These trials were considered practice trials and were excluded from further analysis. In bias 1, the computer picked paper in 80 % of all cases, followed by bias 2 where rock was chosen by the computer in 80 % of all trials. In bias 3, each choice was picked by the computer uniformly before it switched to a final bias of 80 % scissors

participant's choice revealed in the bottom square. After 2 s, they were automatically moved to the next trial. No explicit feedback was given regarding the outcome of a given trial; however, prior to commencing the task, all participants were given instructions regarding the game's rules and all understood the task. Periodically throughout the task, patients were asked to repeat the rules (i.e., they were asked whether they or the computer won a particular trial) to ensure they still understood the nature of the task. Participants completed 410 trials consisting of 10 practice trials and 4 blocks of 100 trials (Fig. 2b). Participants were not informed that the strategy used by the computer opponent was fixed for a block of trials, or that it varied between blocks.

All blocks were completed in the same sequence for all participants. For the first block, the computer played a strongly biased strategy of choosing "paper" on 80 % of trials with each of the other two options chosen on 10 % of trials. Unannounced to the participant, the computer switched to a strong bias of 80 % "rock" for 100 trials, followed by 100 trials in which the computer's choices were uniform (i.e., each option chosen on 33 % of trials). For the final 100 trials, the computer chose "scissors" on 80 % of trials. The choice of 100 trial blocks was based on pilot data (Stöttinger et al. 2012), showing this length of trials was sufficient for learning and exploiting such a strong bias in choice probability. All HCs, nine of the RBD patients and nine of the LBD patients finished all 410 trials, and one LBD and two RBD patients quit the task after they completed at least two biases (more than 210 trials). Three of the RBD patients quit the task before they finished the first bias (i.e., less than 100 trials). These dropouts demonstrate the taxing nature of the RPS task for brain-damaged participants.

Ambiguous figures task

Four different ambiguous pictures were adapted for this task (Fig. 3c). Sets of fifteen images were created that began with an unambiguous version of one image and gradually morphed

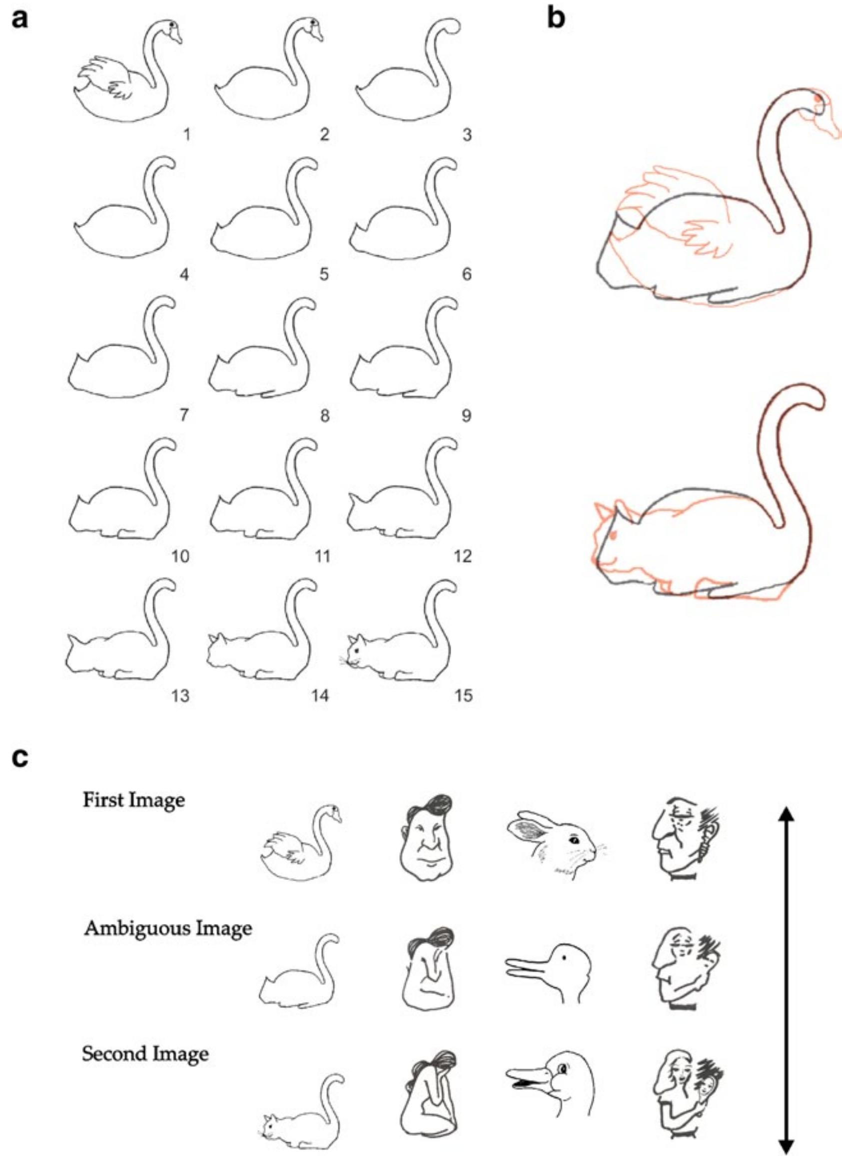

Fig. 3 **a** Swan/cat picture set, starting with a swan and then morphing gradually into a cat. *Picture 8* represents the ambiguous picture. **b** The ambiguous picture (image #8) overlaid on the initial and final pictures in the set to highlight that the ambiguous figures can be seen as either the initial or the final unambiguous image (in this case a swan or a cat). **c** First and last image for all four different picture sets

through the ambiguous image to an unambiguous version of an alternate image (Fig. 3a, b). Pictures (21 cm × 19.5 cm) were presented one at a time on a computer monitor. The "man's-face and kneeling-woman" and the "gypsy and girl" picture sets were taken from Fischer (1967a, b, respectively). Two additional pictures (Bernstein and Cooper 1997; Jastrow 1900) were used to generate two additional sequences with the intermediate images hand-drawn by the first author. In each picture set, one additional object (a circle, a spiral, a star or a triangle) was presented after the third and twelfth picture. These pictures served as "catch trials" to assess whether participants were simply perseverating on a single response.

Sequences could be presented in one of two orders. A Latin square design used four picture sets per participant and counterbalanced the sets and order of presentation across participants.

Participants were told they would see four different series of pictures; each series contained 17 images, and that the series would begin with the picture of a commonly known object. Participants were explicitly instructed that the pictures would change gradually with each presentation which would eventually result in a completely different object by the end of the series. Participants were told to verbally indicate what each picture was.

Responses were coded as "1" seeing the first object, "0" identifying the catch trials correctly and "2" seeing an object other than the initially presented object. Responses were accepted as correct if they generally matched either the first or second object (e.g., saying "duck" or "bird" in addition to "swan"). Except for a few rare responses, participants exclusively reported either the first or the second object. In very few occasions participants reported a different object (e.g., dinosaur following presentations of swans). In these cases answer were rated as 'seeing a second object'. Each presentation of a picture within a sequence was considered a single trial. The dependent variable was the sum of trials in which the participant reported seeing the first object. This number corresponds to the trial number where participants first switched—or updated—to the second object. A higher number indicates a longer time to update. All of the LBD patients and HCs and thirteen of the RBD patients completed the task.

Berg card sorting task (BCST)

We administered a brief computerized version of the Wisconsin Card Sorting task (i.e., the BCST (http://pebl.sourceforge.net/battery.html; see Piper et al. 2011 for validation). In this test, participants have to sort cards that differ according to color, number and shape according to an undivulged rule (i.e., match colors, shapes or numbers). For every single card, they are provided with feedback regarding correct performance. Unannounced to participants, the rule is shifted after 10 sequentially correct responses. The participant has to use the feedback provided to determine which criterion is now the correct one to sort by (Nelson 1976; Piper et al. 2011). In total, participants have to sort 64 cards. Nine of the RBD patients and all of the LBD patients and HCs completed the BCST.

Lesion tracing and overlay analysis

Although the number of brain-damaged subjects was small, we employed lesion overlay analyses to determine the common regions of damage associated with poorest performance on our tasks. We used the same procedures as we did in our prior work (Danckert et al. 2012b). Lesions were manually traced from computed tomography (CT) images on a slice-by-slice basis (Analyze AVW software; Biomedical Imaging Resource, Mayo Foundation, Rochester, MN). Lesions were defined as hypointense or hypodense signal compared with the surrounding parenchyma. Individual tracings were transformed to the International Consortium for Brain Mapping (ICBM152) template (http://www.bic.mni.mcgill.ca/ServicesAtlases/HomePage). After brain tissue extraction (Brain Extraction Tool software; http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/BET; Jenkinson et al. 2005) and registration (Automatic Image Registration version 5.2.5 software; http://bishopw.loni.ucla.edu/AIR5) using spatial normalization and warping models for template matching, the resulting images, after inspection, were transformed into lesion maps. The proportion of each anatomical region involved in each patient's lesion was estimated using the MRIcro single-subject Colin template (http://www.cabiatl.com/mricro/). Individual brain lesions were then superimposed using the same software allowing for lesion overlay analyses. Lesions are overlaid on the ICBM152 template from which Talairach coordinates were extracted.

Results

Performance on the rock, paper and scissors task

LBD patients built models to a lower degree than RBD patients and HCs

For each participant, we calculated mean optimal play rates in block 1. An optimal play rate was determined by how frequently participants played the optimal (i.e., "scissors") choice. We conducted an analysis of variance on groups of 10 trials (within subject) and participant group (between subjects). Optimal plays increased significantly during the first block [$F(9,261) = 15.69$, $p < .001$, $\eta^2 = .35$]. There was a significant main effect for participant group [$F(2,29) = 3.74$, $p < .05$, $\eta^2 = .21$. While RBD patients and HCs demonstrated similar proportions of optimal plays [$F(1,17) = 1.37$, $p > .25$, $\eta^2 = .08$], LBD patients demonstrated a significantly smaller proportion of optimal plays compared with HCs [$F(1,19) = 7.45$, $p < .05$, $\eta^2 = .28$], and tended to play the optimal choice to a smaller degree than RBD patients [$F(1,19) = 3.53$, $p = .08$, $\eta^2 = .16$] (Fig. 4a).

RBD and LBD patients were equally impaired on model updating

We analyzed the proportion of trials in the second block for which participants played the block 1 former optimal choice—choices that now had become suboptimal. We compared the proportion of these suboptimal choices to the proportion of trials for which they played the new, block 2, optimal choice. In other words, these analyses provide a metric of successful updating (i.e., abandoning the previous optimal strategy of block 1 together with adopting the new optimal response of block 2). We submitted these two dependent variables separately to an analysis of variance.

Optimal block 2 plays increased significantly over the block [$F(9,261) = 11.41$, $p < .001$, $\eta^2 = .28$] (Fig. 4b). The significant main effect for participant group [$F(2,29) = 4.03$, $p < .05$, $\eta^2 = .22$] was due to a significant difference between HCs and brain-damaged patients [HCs vs. LBD $F(1,19) = 8.44$, $p < .01$, $\eta^2 = .31$; HCs vs. RBD $F(1,20) = 5.52$, $p < .05$, $\eta^2 = .22$]. There was no significant difference between LBD and RBD patients [$F(1,19) = .02$, $p > .90$, $\eta^2 = .001$].

A similar analysis for playing block 1 optimal choices (i.e., the now suboptimal choice of scissors) in

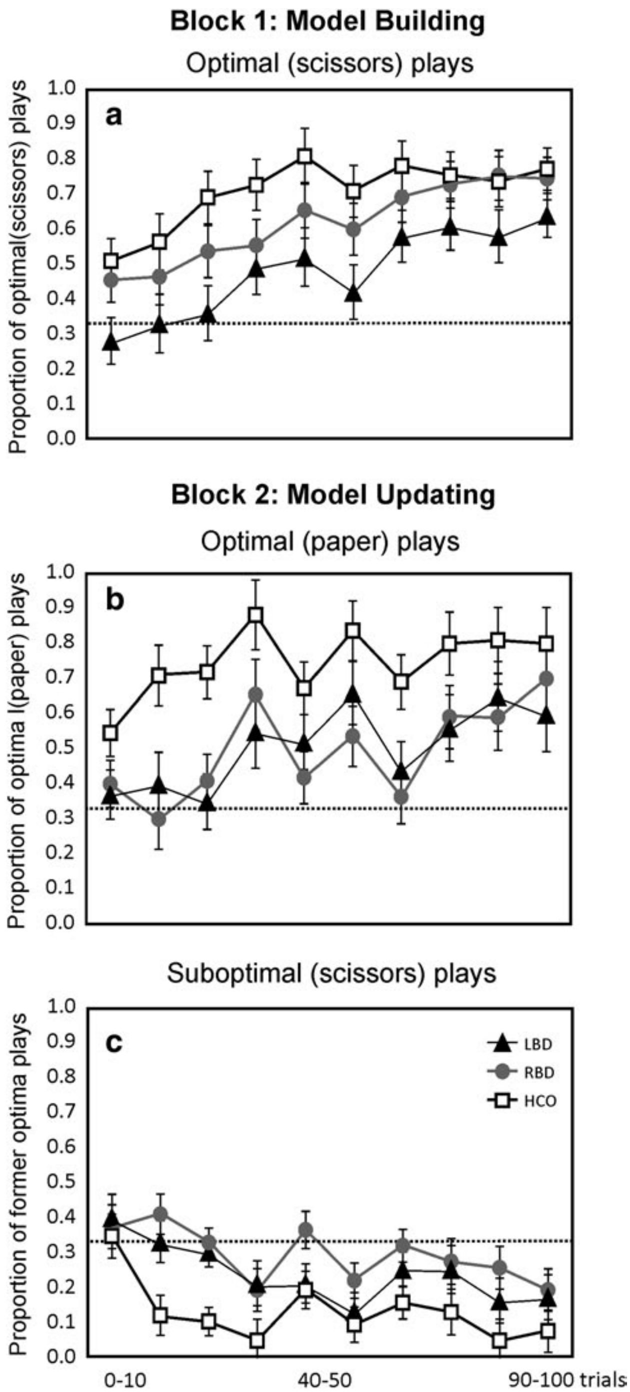

Fig. 4 Mean proportion of optimal plays in block 1 (4A), optimal plays in block 2 (4B) and suboptimal plays in block 2. The *horizontal dashed line* represents chance performance. *Error bars* are standard errors of the mean. *Gray circles* represent performance of RBD patients, *white rectangles* represent the performance of HCs, and *black triangles* represent performance of LBD patients

block 2 showed a significant decrease across the block [$F(9,261) = 7.92$, $p < .01$, $\eta^2 = .21$] as well as a significant difference between participant groups [$F(2,29) = 5.01$, $p < .05$, $\eta^2 = .26$]. This significant main effect for group came about because of a significant difference between HCs and brain-damaged patients [HCs vs. LBD $F(1,19) = 9.37$, $p < .01$, $\eta^2 = .33$; HCs vs. RBD $F(1,20) = 7.82$, $p < .05$, $\eta^2 = .28$]. There was no significant difference between LBD and RBD patients [$F(1,19) = .69$, $p > .40$, $\eta^2 = .04$] (Fig. 4c).

LBD patients were significantly worse than HCs by the end of the experiment

For every participant, we calculated how frequently they played the optimal choice (i.e., "rock") in block 4. Optimal plays increased significantly during the last block [$F(9,234) = 15.77$, $p < .001$, $\eta^2 = .38$] with a significant difference between participant group [$F(2,26) = 4.25$, $p < .05$, $\eta^2 = .25$]. This main effect for participant group is due to a significantly lower overall proportion of optimal choices for LBD patients compared with HCs [$F(1,18) = 9.97$, $p < .01$, $\eta^2 = .36$]. No other effects were significant.

Discussion

To evaluate whether RBD performance in our previous study was due to a learning impairment or an updating impairment, we had HCs and LBD and RBD patients play against a computer opponent that chose one option 80 % of the time from the beginning of the task. Results of block 1 showed that RBD and HCs were able to learn to exploit the strong bias of the computer opponent; both groups appreciated the strong bias of the computer and adapted their choice probabilities accordingly, suggesting that RBD patients are able to represent regularities in the world and to build a mental model of the opponent's play. When the computer subsequently switched to a different bias in block 2, RBD patients were significantly worse at updating their play strategy. RBD patients needed significantly longer than controls to adopt the new optimal response for block 2 and to abandon the now suboptimal strategy that had prior utility during block 1. Eventually, RBD patients were able to update similarly to controls in block 4. Hence, data from this experiment fit with the assumption that RBD patients in our initial study learned in the first part of the experiment that the computer's choices were uniformly random, and then failed to update this model when the computer opponent eventually changed and picked one choice 80 % of the time.

Based on the findings of our previous study (Danckert et al. Danckert et al. 2012a, b), we expected LBD patients to perform at the same or higher level than HCs. However, LBD patients performed significantly worse than HCs throughout the experiment. They not only failed to learn the first bias to the same degree than HCs, but were also picking the optimal choice at a significantly lower level than HCs by the end of the experiment. At first sight, it might seem that RBD and LBD patients are similarly impaired in updating, given that their performance in bias 2 is virtually identical for both patient groups. At this point, it is worth emphasizing that while RBD patients are only worse than HCs in Bias 2 (i.e., when they need to update), LBD patients are always worse than HCs. These results clearly suggest that LBD patients fail the task for different reasons than RBD patients.

One explanation to account for these data is the difference in working memory capacity between participant groups in our two studies (measured in one of the subscales of the MoCa) [$F(2,32) = 4.39$, $p < .05$, $\eta^2 = .22$]. The MoCa has a component that requires remembering and repeating 5 words. HCs remembered on average 4.09 ± 1.14 correctly, compared with 3.43 ± 1.09 items for RBD patients and 2.2 ± 2.15 for LBD patients. LBD patients remembered significantly fewer words than HCs [$t(19) = 2.48$, $p < .05$] and tended to remember fewer words than RBD patients [$t(22) = 1.66$, $p = .12$]. No such difference was found in our previous study (Danckert et al. 2012a, b). Our original study made use of the mini-mental status examination (MMSE). Of the 3 possible items in the MMSE, RBD remembered 2.6 ± .70 compared with 2.2 items in LBD patients [$t(18) = 1.10$, $p > .25$]. In fact, although the MMSE and MoCa are not equivalent, the patients in our original study had an average MMSE of 27.60 (±1.65) out of 30 (compared with a MoCa score of 22.00 (±4.22) out of 30 in our current study) suggestive of a generally higher level of functioning in the LBD patients of our initial study. Additionally, in the current version of the task, both choices—the participant's choice and the choice of the computer—were revealed for only 2 s before they were automatically moved to the next trial. In our original study (Danckert et al. 2012a, b), the next trial was initiated by the participant pressing the space bar. In the old task, participants could still see both choices while they processed who won the trial, while in the current version participants had to rely on their working memory. Hence, the current version of the task was probably more demanding of WM resources.

While the performance of LBD patients in the RPS task most likely reflects a general cognitive impairment due to a more impaired working memory, RBD patients performance reflect an updating impairment only. RBD patients *can* build a mental model of the opponent's play to the same degree than HCs. They, however, fail to update that model to the same level as HC when the computer switches to a different bias. To assess the generality of updating deficits after RBD, we used a second task to measure updating—a task that was less complex and therefore less confounded with other cognitive capacities.

Performance in the ambiguous figures task

All participants correctly identified all eight catch trials (two trials per picture set). This excluded perseveration as an explanation for performance. The sum of "first object reports" was submitted to a mixed design repeated-measures analysis of variance with the within-subject factor of order of presentation of sequences and a between-subjects factor of participant group (RBD, LBD and HCs). This analysis showed a significant main effect for participant group [$F(2,31) = 11.44$, $p < .001$, $\eta^2 = .43$]: RBD patients needed on average 9.42 (SD = 1.91) pictures to see the second object compared with 7.40 (SD = 2.02) pictures in LBD patients and 5.95 (SD = 1.35) in HCs. RBD patients needed significantly more pictures than LBD patients [$F(1,21) = 6.03$, $p < .05$, $\eta^2 = .22$] and HCs [$F(1,22) = 25.43$, $p < .001$, $\eta^2 = .54$] to see the second object (Table 3 displays the responses of one RBD patient, one LBD patient and one HC). LBD patients tend to have a slightly higher number of "first object reports" than HCs [$F(1,19) = 3.76$, $p = .07$, $\eta^2 = .17$] (Fig. 5). No other effect was significant.

Is performance across the two tasks related?

Updating performance was correlated across all participants. Overall, there was a correlation between updating performance in the RPS task and updating in the ambiguous figures tasks (Fig. 6). The average number of first object reports correlated negatively with the proportion of optimal plays employed in block 2 [$\tau = -.36$, $p < .01$] and positively with the proportion of suboptimal plays employed in block 2 [$\tau = .42$, $p < .01$]. The longer the participants persisted in reporting seeing the first image in the ambiguous figures task, the longer they took to successfully update in the RPS task (i.e., abandoning the suboptimal strategy of block 1 early, together with adopting the new optimal response of block 2). The correlations calculated separately for all three participant groups showed a similar, although only marginally significant pattern for RBD [optimal plays $\tau = -.36$, $p = .15$; suboptimal plays $\tau = .45$, $p = .07$] and HC [optimal plays $\tau = -.38$, $p = .11$; suboptimal plays $\tau = .40$, $p = .10$]; these correlations were not evident in the LBD group [optimal plays $\tau = -.14$, $p > .55$; suboptimal plays $\tau = .11$, $p > .60$] (Fig. 6). No significant correlation was found between learning the bias of block 1 in the RPS task and updating in the ambiguous figures task [$\tau = -.08$, $p > .55$].

The Berg card sorting task (BCST) performance: results are not due to perseveration

The results for both patient groups are presented in Table 4. There was no significant difference in any of the metrics

Table 3 Verbal reports of two participants (RBD and healthy control) addressing the changes in the 'girl/gypsy' picture set

#	Pictures	RBD participant	LBD participant	Healthy control
1		**Lady looking into a mirror**	**Lady with a hand mirror**	**Woman looking in the mirror**
2		**Lady looking into a mirror**	**Lady with a hand mirror**	**Same thing**
3		**Lady looking into a mirror**	**Lady with a hand mirror**	**Same thing**
4		**Lady looking into a mirror**	**Lady with a hand mirror**	**Woman looking in the mirror**
5		**Lady looking into a mirror**	**Lady with a hand mirror**	**woman's face is changing**
6		**Something is going around her waist**	Man's face, or an ugly lady	**Same thing**
7		**Looks in a different direction**	Older man	Turning into a profile of man's face
8		**Mirror looks toward us**	Cartoon man	Can see both woman and man
9		**Woman holding a baby**	Tired old man	Same thing

Table 3 continued

#	Pictures	RBD participant	LBD participant	Healthy control
10		**Woman holding a baby, mouth of the baby is open**	Even older tried man	Man's face more predominant
11		**Woman holding a baby**	Even older tried man	Same thing
12		**Baby looking at the mother. Maybe choking**	Old man	Strongly man's face
13		Guy	Older person	More of man's face
14		Guy, sleeping	Older person	Same thing
15		Guy, ear	Old man	Same thing; can still see resemblance of a woman's face

Bold lines represent first object reports

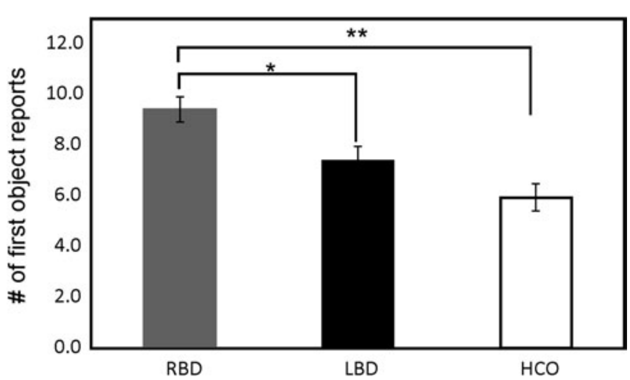

Fig. 5 Mean number of first object reports for RBD (*gray bar*), LBD (*black bar*) and HCs (*white bar*) averaged over all four picture sets. The *error bars* represent standard error of the mean *$p < .05$; **$p < .01$

between LBD and RBD patients, nor between patients and HCs. One LBD and one RBD patient never managed to sort at least one category correctly. Perseveration errors for both patient groups were well within the range of a normative sample of healthy older controls when the analysis was restricted to those patients who at least sorted one category correctly (Piper et al. 2011).

Lesion overlay

Lesion overlay analysis for all RBD patients showed that ten of fourteen patients had an overlap in the insula (Fig. 7; bottom panel). Five of the seven RBD patients who performed at or above the median on the ambiguous figures task (i.e., those most impaired on the task) had common involvement of the insula (426 shared voxels),

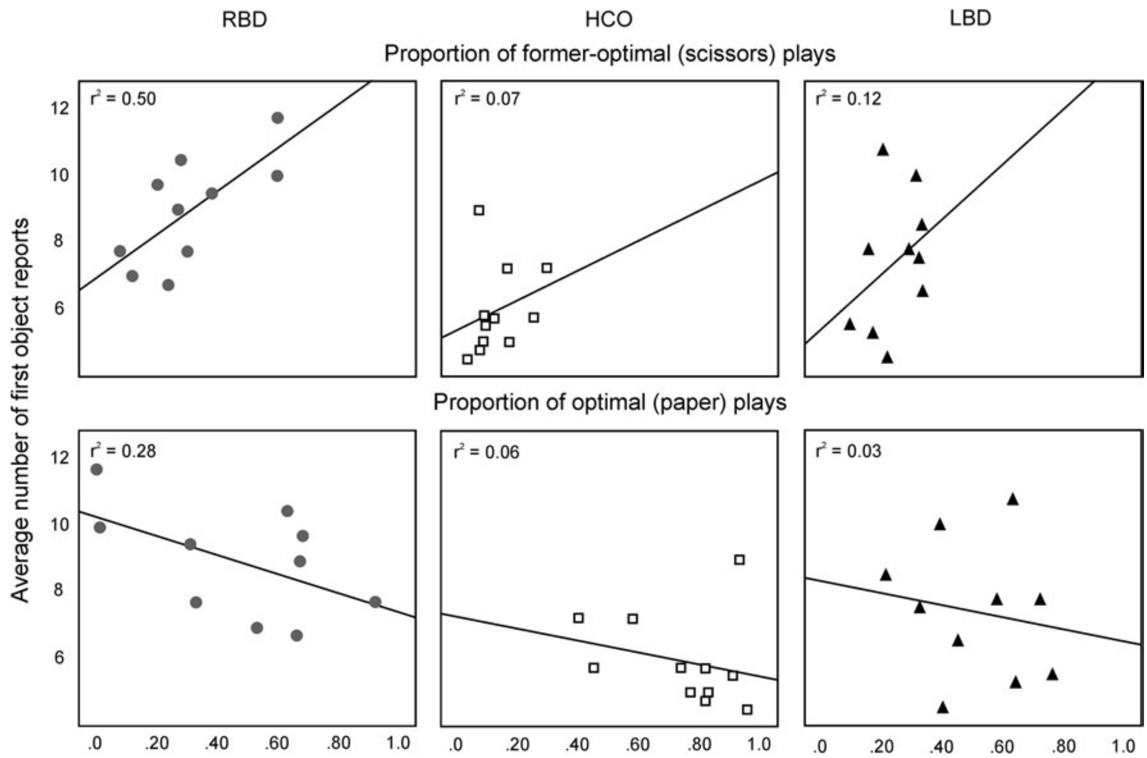

Fig. 6 Correlation of updating performance in the ambiguous figures (*y* axes) and RPS tasks measured by the proportion of optimal plays in block 2 (*lower panel*) and by the proportion of suboptimal plays in block 2 (*upper panel*). *Gray circles* represent RBD patients, *black triangles* represent LBD patients, and *white squares* represent healthy controls

the fontal inferior operculum (79 shared voxels) and the rolandic operculum (31 shared voxels). The five patients that performed below the median had no significant overlap in their lesions. There was no significant difference in lesion volume between RBD patients performing above the median and RBD patients performing below the median on the ambiguous figures task [$t(12) = .42$, $p > .65$].

Only five of the LBD patients showed an overlay in their lesions; the overlay was mainly in the white matter and in a highly restricted region of the insula (five shared voxels; Fig. 7; top panel). There was no significant difference in lesion volume between RBD patients and LBD patients [$t(22) = .18$, $p > .85$].

General discussion

Right brain damage results in a highly heterogeneous pattern of cognitive impairments. We have hypothesized that many of these diverse impairments can be considered disorders of model building and updating. Previously, we compared LBD, RBD and HCs on their ability to detect and exploit biases in the game rock, paper and scissors (Danckert et al. 2012b). The RBD patients typically failed to notice transitions and did not exploit a pronounced bias (80 %). The present report explores in more detail why RBD patients were unable to do so. Analysis of their play in the first block of RPS in the present experiment showed an equivalent performance in the RBD and HC groups demonstrating that these RBD participants could detect a statistical bias and exploit it. However, when the computer switched its bias to a different item, the RBD patients, as a group, took longer to begin exploiting the new bias and persisted with a now suboptimal choice more so than did HCs (Fig. 4).

LBD patients performed worse throughout the task. This contrasts with our previous findings showing that LBD patients even outperformed HCs in a different version of the RPS task (Danckert et al. 2012a, b). This mismatch is most likely due to a more severely impaired LBD patient group in the current study. Although the RPS task provided us with valuable insights into model building and updating (Filipowicz et al. 2013; Stöttinger et al. in press; Danckert et al. 2012b), the task might be more complex than ideal (Sato et al. 2002). One can perform poorly on the RPS task for a multitude of reasons—only one of which is a failure to update. To assess the generality of updating deficits after RBD, we used a simpler task that did not require the same degree of working memory, sustained attention or reward processing and required a shorter period of time. In addition, the behavior of participants (i.e., the verbal reports)

Table 4 Berg card sorting task results for both patient groups

	RBD	LBD	*p*	*t*
Categories completed	2.56 (1.74)	2.30 (1.42)	.35	>.70
Trials to complete first category	20.22 (16.73)	27.40 (19.85)	−.85	>.40
Correct responses	40.44 (10.63)	42.60 (11.20)	−.43	>.65
Total errors	23.56 (10.63)	21.40 (11.20)	.43	>.65
Perseveration responses	20.11 (10.04)	14.60 (7.90)	1.34	>.15
Perseveration errors	11.44 (7.35)	7.00 (4.22)	1.64	>.10
Non-perseveration errors	12.11 (10.45)	14.40 (14.26)	−.40	>.65
Unique errors	1.00 (1.32)	1.40 (.84)	−.80	>.40

One participant in each group failed to sort even one category correctly

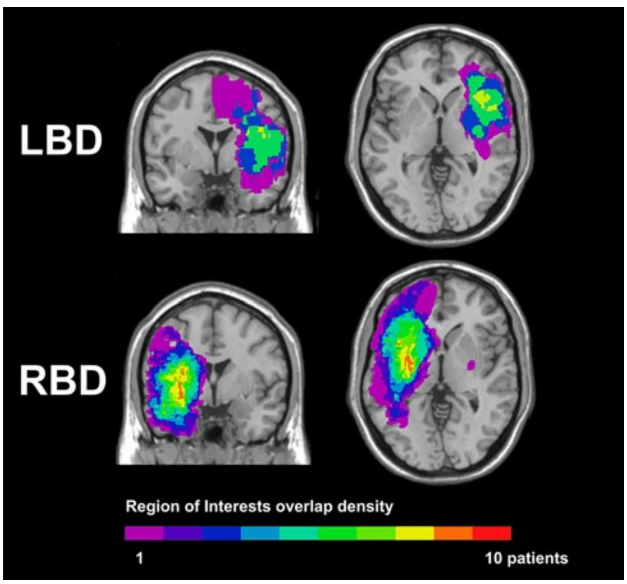

Fig. 7 Lesion overlay maps for 5 of the 10 LBD patients (*top panel*) and for 10 of the 14 RBD patients (*bottom panel*). *Shading* indicates the amount of overlap, ranging from 1 patient to 10 patients

represented a genuine report of their actual mental models (e.g., "It is a rabbit."). We found that the RBD impairment for updating per se was replicated in the ambiguous figures task. RBD patients needed significantly more contradicting evidence (i.e., additional morphed pictures) to see the second object compared with LBD patients and HCs. Only three LBD patients needed as many pictures as most RBD patients (i.e., >9 pictures)—two of these patients had severe aphasia which might contribute to the poor performance on this task.

Together, our results show that right brain injury results in an updating impairment; and this impairment is more general than simply defective statistical estimation, working memory and sustained attention (Bonato 2012; Ferber and Danckert 2006; Husain et al. 2001; Miller et al. 2005; Roser et al. 2011; Vickery and Jiang 2009; Wolford et al. 2000, 2004).

Reversible, ambiguous or bistable figures like the Rubin's face/vase picture or the Necker cube have been widely used in research paradigms since the 1800s (Long and Toppino 2004 for an overview). These objectively stable pictures typically produce a multistable experience, or rivalry, for an observer: when looking at these pictures, people continuously alternate between two mutually exclusive interpretations (e.g., from a vase to a face and vice versa; Long and Toppino 2004; Kleinschmidt et al. 1998). Studies using fMRI and EEG while participants view ambiguous figures have demonstrated involvement in frontal and parietal areas in perceptual switches between the two conflicting percepts (Lumer et al. 1998; Kleinschmidt et al. 1998), especially within the right inferior parietal sulcus (Britz et al. 2009; Zaretskaya et al. 2010). By using TMS (Zaretskaya et al. 2010) and EEG (Britz et al. 2009), it has been shown that the activity within the right parietal cortex precedes the switch and does not represent merely a consequence of the change in percept. There is also evidence that neglect patients have significantly longer dominance times during binocular rivalry (i.e., images persist for longer durations; Bonneh et al. 2004).

While no definitive conclusions can be drawn from a lesion overlay analysis in such a small group of RBD patients, results highlighted an area—the right insula—that was also commonly damaged in a separate group of patients reported in our original study (Danckert et al. 2012b). The insula is assumed to be involved in representing salient information, the current "conscious state," and in switching between large-scale neural networks (Craig 2009; Menon and Uddin 2010). One view is that the insula serves as a comparator that detects mismatches between predicted and actual sensory feedback (Spinazzola et al. 2008; Jones et al. 2010). The insula, however, is not the only area likely to be important. Other research shows that the putamen is also a reasonable candidate for updating, as it has been reported to be involved in learning, including stimulus–action–reward associations (Haruno and Kawato 2006), evaluating reward values in reinforcement learning paradigms (e.g., Bischoff-Grethe et al. 2009; Seger et al. 2010) and implicit sequence learning (Rauch et al. 1995). Lesions in stroke patients, however, reflect vascular anatomy and not functional networks. The common involvement of the insula in brain-damaged patients might partially reflect the fact that the insula is commonly injured in middle cerebral artery strokes due to its immediate vicinity to the middle cerebral artery (Fink et al., 2005). Hence, future work using different techniques (e.g., functional neuroimaging) will be necessary to clearly delineate the anatomical network responsible for updating internal representations.

Perseveration is not the source of the behavioral differences between RBD, LBD and HC participants seen here. There was no difference in the number of perseveration errors in the BCST between either of the participant groups. In addition, all participants in the ambiguous figures task—including RBD participants—were perfectly able to report all catch trials correctly. In a similar vein, performance of RBD patients also cannot be explained by perceptual/attentional impairments after RBD. When the computer switched from favoring "paper" 80 % of the time to favoring "rock" 80 % of the time, RBD patients were able to notice this change within 10 trials (i.e., their "scissors" plays dropped from 75 % to 37 % [$t(10) = 4.67$, $p < .01$]). Furthermore, all participants typically reported perceived differences between the pictures in the ambiguous figures task, even if their ultimate interpretation did not change. Contrary to HCs and LBD patients, RBD patients tended to interpret these changes in favor of the first object (Table 3). This is a non-trivial point. The instructions for this task explicitly drew participants' attention to the fact that the pictures would change from one presentation to the next. Hence, it is not an inability to detect change per se that is evident in this data, but that RBD patients needed longer to interpret the perceived changes within the context of a new mental representation than did HCs.

One could argue that the updating impairment in RBD patients reflects more generalized cognitive impairments, for example, the well-known deficit of global processing following RBD (Fink et al. 1997; Robertson and Delis 1986). While this represents a potentially plausible account for the ambiguous figures data, it cannot account for a failure to update in our RPS task, given that no local/global perceptual elements are involved in this task. Similarly, the updating impairment in RBD patients does not simply reflect a generalized cognitive impairment, or an impairment in set shifting. There was no difference in the overall MoCa scores, months since stroke, lesion volume or a difference in any metric of the BCST between RBD and LBD patients.

Whether playing RPS or interpreting simple line drawings, RBD participants reveal impaired updating that is correlated across tasks. The emerging picture is that the right hemisphere is dominant for the function of building and updating mental representations. When incoming observations are contrasted against an established mental representation or model, it is the right hemisphere that signals discrepancies and prompts a shift to a new representation when that discrepancy is too large. The right hemisphere as "updater" is in accordance with other data on the role of the right hemisphere in the modeling the mental states of others and in evaluating and updating beliefs (Perner et al. 2006; Vogeley et al. 2001; see Corbetta et al. 2008; Decety and Lamm 2007 and Mitchell 2008 for an overview and Happé et al. 1999; Griffin et al. 2006 for Theory of Mind impairment after right brain injury) and in evaluating and updating beliefs (Chistman et al. 2008 for an overview; Vocat et al. 2012).

Poorer rehabilitation prospects are statistically associated with neglect arising from RBD (Appelros et al. 2002; Bowen and Lincoln 2007; Bowen et al. 1999; Cassidy et al. 1998; Nijboer et al. 2013; Ringman et al. 2004). As lasting improvements are not achieved with spatially targeted therapies, it would seem that non-spatial impairments represent the true barriers to successful therapy after RBD (Danckert in press; Danckert et al. 2012a; Shaqiri and Anderson 2013; Shaqiri et al. 2013; Striemer et al. 2013). We have hypothesized that many of the impairments seen in neglect can be considered disorders of model building and updating (Danckert et al. 2012a, b; Shaqiri and Anderson 2013; Shaqiri et al. 2013). Our findings contribute to a better understanding of the right hemisphere's contribution to the foundational human skill of mental model building and updating, and suggest that rehabilitation treatments targeting updating impairments may be useful after RBD.

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