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Research report

Cortical and subcortical contributions to state- and strength-based perceptual judgments

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ABSTRACT

Perceptual judgments can be made on the basis of different kinds of information: *state-based* access to specific details that differentiate two similar images, or *strength-based* assessments of relational match/mismatch. We explored state- and strength-based perception in eleven right-hemisphere stroke patients, and examined lesion overlap images to gain insight into the neural underpinnings of these different kinds of perceptual judgments. Patients and healthy controls were presented with pairs of scenes that were either identical or differed in that one scene was slightly expanded or contracted relative to the other. Same/different confidence judgments were used to plot receiver-operating characteristics and estimate the contributions of state- and strength-based perception. The patient group showed a significant and selective impairment of strength-based, but not state-based, perception. This finding was not an artifact of reduced levels of overall performance, because matching perceptual discriminability levels between controls and patients revealed a double dissociation, with higher state-based, and lower strength-based, perception in patients vs. controls. We then conducted exploratory follow-up analyses on the patient group, based on the observation of substantial individual differences in state-based perception — differences that were masked in analyses based on the group mean. Patients who were relatively spared in state-based perception (but impaired in strength-based perception) had damage that was primarily in temporo-parietal cortical regions. Patients who were relatively impaired in both state- and strength-based perception had overlapping damage in the thalamus, putamen, and adjacent white matter. These patient groups were not different in any other measure, e.g., presence of spatial neglect symptoms, age, education, lesion volume, or time since stroke. These findings shed light on the different roles of right hemisphere regions in high-level perception, suggesting that the thalamus and basal ganglia play a critical role in state- and strength-based perception, whereas temporo-parietal cortical regions are important for intact strength-based perception.

1. Introduction

How do we detect changes in the environment? Imagine you are shown two photographs of a park and asked whether they are exactly the same or if something about the park was different in the two images. In some cases, you may be able to detect a specific difference—for example, a water fountain that is in one picture but not in the other. Alternatively, you may know that the pictures are different, but are unable to provide details about any specific change.

Thus, there are two kinds of information that can be used for perceptual change detection, which have been referred to as *state-based* and *strength-based* perception (Aly and Yonelinas, 2012; for related distinctions, see Fernandez-Duque and Thornton 2000; Rensink, 2000, 2004), Dehaene et al. (2006), and Howe and Webb (2014)). State- and strength-based perception have been studied by asking individuals to make same/different confidence judgments on pairs of images (e.g., pairs of scenes, faces, fractals, or objects; Aly and Yonelinas, 2012; Aly et al., 2013, 2014). Receiver-operating characteristic (ROC; Green and Swets, 1966; Macmillan and Creelman, 2005) analyses are then used to estimate the contributions of two kinds of perceptual decisions.

State-based perception is associated with high-confidence responses that are rarely in error; it is a discrete state that either occurs or does not, and when it does occur, it is associated with accurate

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awareness of specific details that differentiate two images. The probability of state-based perception is reflected in the upper *x*-intercept of ROCs (Fig. 1). Strength-based perception, on the other hand, is associated with a wider range of confidence responses; it is a continuously-graded signal associated with a feeling that something has changed, with little to no ability to report what that change was. The discriminability afforded by strength-based perception is related to the curvilinearity of ROCs (Fig. 1).

In previous studies, we have found that these two kinds of perception can be doubly dissociated, have different temporal dynamics, and are associated with distinct kinds of conscious experiences (Aly and Yonelinas, 2012; Aly et al., 2013, 2014). For example, state-based perception makes a greater contribution to tasks involving detection of discrete object changes (e.g., a water fountain that is present in one scene but absent in another), is associated with a rapid temporal onset, and subjective experiences are those of consciously perceiving specific, detailed differences. In contrast, strength-based perception makes a greater contribution to tasks involving global or relational change detection (e.g., a subtle manipulation of the distances between component parts of a scene), is associated with a gradual temporal onset, and subjective experiences are those of feeling as if a change has occurred but being unable to pinpoint what that change was (Aly and Yonelinas, 2012; also see Fernandez-Duque and Thornton, 2000; Rensink, 2000, 2004; Dehaene et al., 2006; Galpin et al., 2008; Busch et al., 2009, 2010; Howe and Webb, 2014; but see Simons et al., 2005).

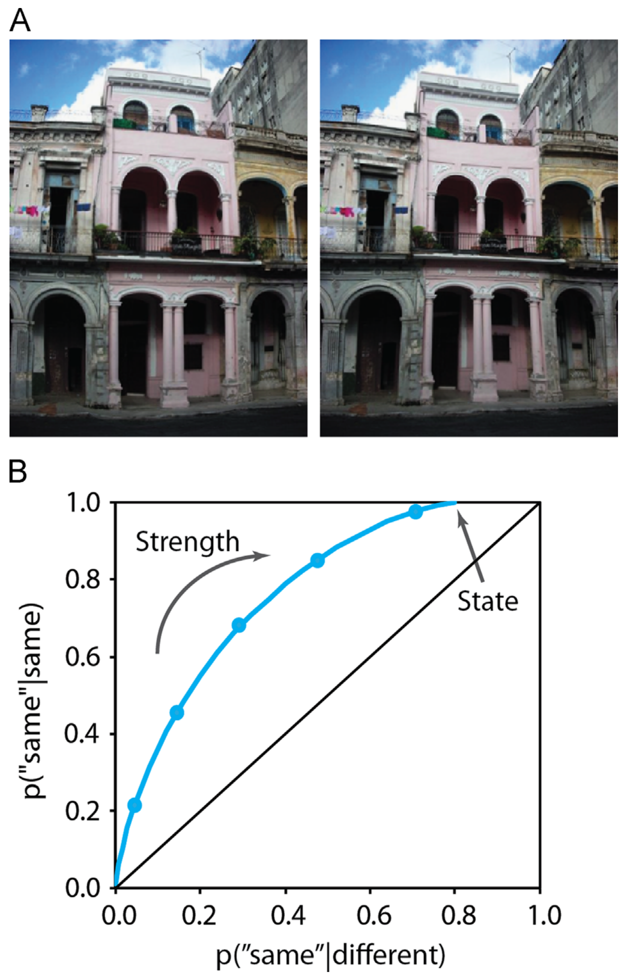

Fig. 1. Assessing state- and strength-based perception. Same/different judgments can be used to estimate the contributions of state- and strength-based perception. For example, participants could be shown pairs of scenes (A) that are either identical or different and asked to make same/different judgments using a confidence scale. In this example, the scenes are different: the image on the left is expanded outward while the image on the right is contracted inward. Same/different confidence ratings are subsequently used to plot receiver-operating characteristics (ROCs). A hypothetical ROC (B), depicting the pattern of results observed in variations of this task in prior studies, is shown here for illustration (Aly and Yonelinas, 2012; Aly et al., 2013, 2014). The left-most point on the ROC reflects the probability of a hit ("same" judgment when images are the same; *y*-axis) and a false alarm ("same" judgment when images are different; *x*-axis) for the most confident "same" response. Subsequent points reflect the cumulative hit and false alarm rates as confidence responses are added on, in order from highest-confidence "same" to highest-confidence "different". The upper *x*-intercept provides an estimate of the probability of state-based perception (further left = higher estimate); this is the point associated with high-confidence, correct "different" responses, with no errors. The degree of curvilinearity of the ROC provides an estimate of strength-based perception (more curved = higher estimate); this reflects the discriminability between equal-variance, signal-detection distributions for same and different items.

Thus, previous behavioral work on state- and strength-based perception has shown that perceptual decisions can be made on the basis of functionally dissociable processes or representations. State- and strength-based perception may reflect differences at early- to mid-level stages of perceptual representation (i.e., what information is represented in visual cortex, depending on the focus of attention) or later stages of decision-making (i.e., what information is used to inform the perceptual decision). While current data do not allow adjudication between these possibilities, it is clear that independent sources of information can be used to guide perceptual judgments.

In a previous neuropsychological study, we investigated the contribution of the hippocampus and surrounding medial temporal lobe (MTL) cortex to state- and strength-based perception (Aly et al., 2013). We tested patients with selective lesions to the hippocampus, bilaterally, and patients with more extensive unilateral MTL lesions that included the hippocampus and surrounding cortex. On each trial, patients and healthy controls were presented with a pair of scenes that were either identical or differed in that the center of one scene was expanded or contracted relative to the other (Fig. 1A). These changes alter the relational or configural information within the scenes without adding or removing any specific objects. Participants made same/different confidence judgments using a 1–6 scale, and these confidence responses were used to plot ROCs (Green and Swets, 1966; Macmillan and Creelman, 2005). The ROCs were in turn used to estimate state- and strength-based perception (see Fig. 1B for hypothetical data). The upper *x*-intercept of an ROC provides the probability that state-based perception has occurred, while the degree of curvilinearity is proportional to the contribution of strength-based perception (Aly and Yonelinas, 2012; see also Yonelinas, 1994).

Using this approach, we found that the patients were selectively impaired in strength-based perception (graded judgments of the overall configural or relational match/mismatch between images) but showed intact state-based perception (related to the ability to identify specific detailed differences between scenes; Aly and Yonelinas, 2012). This was true for patients with selective hippocampal lesions as well as those with more extensive MTL lesions. These data suggested that the hippocampus is critical for detecting configural or relational match/mismatch between complex scenes, but is not needed for state-based judgments based on identification of specific, item-level differences.

The MTL is just one of several regions that are likely to be critical for perceptual judgments on complex scenes. In a previous fMRI study (Aly et al., 2014), we examined whole-brain data to determine whether activity in different brain regions was differentially correlated with state- or strength-based perception. Individuals performed a task similar to that used in the MTL patient study, in which they viewed pairs of images and made same/different confidence judgments. These judgments were made using a scale that allowed individuals to report when state-based perception occurred, or, if it did not occur, to rate the confidence associated with strength-based perception. Activity in the supramarginal gyrus, posterior cingulate cortex, and precuneus was related to the occurrence of state-based perception, and was not modulated by varying confidence of strength-based perception. Activity in the fusiform gyrus, however, was sensitive to strength-based, but not state-based, perception. The lateral occipital complex showed both effects: that is, this region showed a graded increase in activity as confidence in strength-based perception increased, and showed an additional increase in activity for state-based judgments.

This study provides some insight into how state- and strength-based perception are supported by different brain regions, but, as with any fMRI study, it only indicates which regions are *correlated with* these different kinds of judgments, and does not indicate whether their activity is *necessary for* state- or strength-based perception. Thus, in the current study, we took a neuropsychological approach to determine which regions make necessary contributions to state- and strength-based perception.

In addition to this first exploratory aim, we also set out to test competing hypotheses about the role of lateral parietal cortex in state- vs. strength-based perception. The previous fMRI study (Aly et al., 2014) motivated the hypothesis that lateral parietal cortex — specifically, the supramarginal gyrus — might be critical for state- but not strength-based perception. Moreover, the "global neuronal workspace" model (Dehaene et al., 2006) proposes that an extended parietal-frontal network is critically involved in the threshold for conscious access; that is, this network shows a neural "ignition" that is related to conscious awareness of specific visual information. Insofar as state-based perception reflects a discrete signal indicating conscious awareness of detailed visual information, this would suggest a role for parietal regions in state-based perception (also see Lamme, 2003).

There are, however, reasons to predict that parietal cortex might be critical for strength-based perception. Our prior patient study implicated the hippocampus (and more generally, the MTL) in strength-based perception (Aly et al., 2013; also see Elfman et al., 2014). Due to the anatomical and functional connectivity between the hippocampus/MTL and parietal cortex (e.g., Kahn et al., 2008; Kravitz et al., 2011; Libby et al., 2012; Ranganath and Ritchey, 2012), one prediction is that patients with damage that includes parietal regions will show impairments in strength-based perception. Additionally, our findings relating strength-based perception to graded changes in confidence (Aly and Yonelinas, 2012) are reminiscent of the graded signals in monkey LIP neurons, which reflect continuous integration of sensory evidence in the service of perceptual decision-making (e.g., Shadlen and Newsome, 2001; Mazurek et al., 2003; Gold and Shadlen, 2007; Bollimunta et al., 2012). Although at different levels of analysis and different timescales, this parallel suggests that neural signals in parietal cortex may be related to perceptual judgments based on signals that vary in strength (for related fMRI work in humans, see Heekeren et al., 2006, Ploran et al., 2007, 2011; Kayser et al., 2010; Liu and Pleskac 2011).

Thus, our aims were twofold: (1) to explore which regions in the brain (outside of the MTL) are necessary for state-based and strength-based perception, and (2) to test competing hypotheses about the role of lateral parietal cortex in state- vs. strength-based perception. In order to examine these issues, we tested perceptual judgments in 11 stroke patients with right hemisphere lesions, which — considered as a group — included parietal, occipital, and temporal cortical regions, insula, thalamus, basal ganglia, and white matter in the vicinity of these cortical and subcortical structures (Fig. 2). Inclusion of patients with damage in heterogeneous regions allowed us to investigate the contributions of distinct brain areas to state- and strength-based perception, in addition to examining the specific hypotheses about the role of parietal cortex. Such an approach offers an important advance over our previous patient study, in which we only tested individuals with damage to the medial temporal lobe (Aly et al., 2013). We focus on right hemisphere structures because previous work has indicated that the right, more than the left, hemisphere plays a necessary role in visuospatial perception and attention (Mesulam, 1981).

We used a perceptual change detection task in which patients and healthy controls viewed pairs of scenes, presented sequentially, and indicated their confidence that the two were the same or different (Fig. 3). Differences consisted of a relational manipulation that slightly contracted or expanded the scenes relative to one another, changing the distances between component parts without adding or removing any particular object. Confidence ratings were used to plot ROCs and estimate the contributions of state- and strength-based perception.

In addition to the main behavioral analyses in which we examined state- and strength-based perception in the entire patient group, we conducted follow-up analyses in order to determine the roles of different right hemisphere regions in state- and strength-based perception. Specifically, we examined lesion overlap images for subgroups of patients depending on their behavioral performance. Such an analysis enabled us to test whether parietal cortical regions played a unique role in state- vs. strength-based perception: if this is indeed the case, patients who do not have damage in the parietal cortex should perform differently from those who do. Thus, we felt that this analysis would be useful in providing further insights into the neural correlates of state- and strength-based perception, and would be important in guiding future studies.

2. Materials and methods

2.1. Participants

The study was approved by the University of Liège Psychology ethics review board. All patients and healthy control participants gave their written informed consent prior to their inclusion in this study.

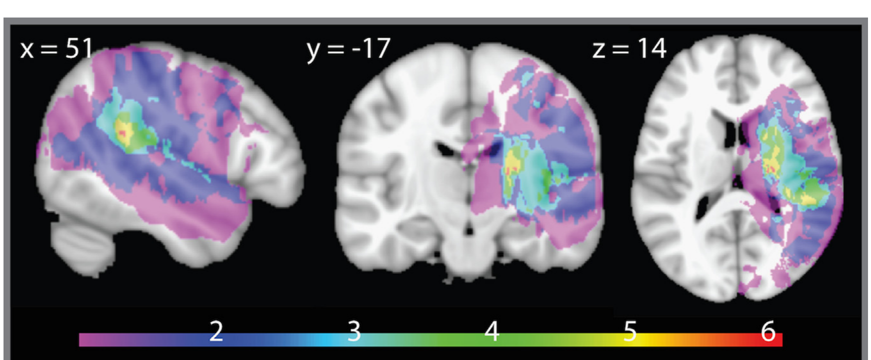

Fig. 2. Lesion overlap for all patients. The regions of greatest lesion overlap were the inferior parietal lobule (PFm), thalamus, superior longitudinal fasciculus (underlying the inferior parietal lobule), and corticospinal tract (adjacent to the thalamus and putamen). *x*, *y*, and *z* coordinates are in MNI space.

The patient group consisted of 11 patients with right hemisphere damage as a result of stroke. Patients were recruited at Centre Neurologique et de Réadaptation Fonctionnelle Fraiture, Hôpital Sainte-Ode, and University hospitals from Liège and Brussels in Belgium. All patients but one were in-patients. Exclusion criteria were bilateral lesions, evidence of previous neurological diseases, or psychiatric disorders.

Demographic information and the neuropsychological profiles of the patients are shown in Table 1. All but one patient showed symptoms of unilateral spatial neglect, as frequently observed after right-hemisphere stroke (see Karnath and Rorden (2012)). Neglect was assessed with the Batterie d'Evaluation de la Négligence unilatérale (BEN; Azouvi et al., 2002) and the line cancellation task (Albert, 1973). Patients were considered to have neglect if they had poor performance (i.e., errors or response times outside of the cut-off ranges; see Albert (1973) and Azouvi et al. (2002)) in one or more of these clinical tests assessing spatial attention. As an indicator of neglect severity, the proportion of spatial attention tests on which each patient was impaired and the proportion of scores that were impaired are shown in Table 1. Most patients completed all nine tests of spatial neglect (16 scores in total); two completed eight tests, and one patient completed seven tests.

CT or MRI scans were available for each of the 11 patients. For each patient, MRI or CT scans were first spatially normalized to MNI space using a specific MR or CT template optimized for individuals with ages similar to what is commonly seen in stroke, using the Clinical Toolbox in SPM8 (Rorden et al., 2012). This was done using SPM8 normalization routines with lesion cost function masking (Brett et al., 2001) in order to ensure that non-linear spatial transformations did not shrink the size of the brain lesion or distort the local healthy tissue. Next, areas of lesion

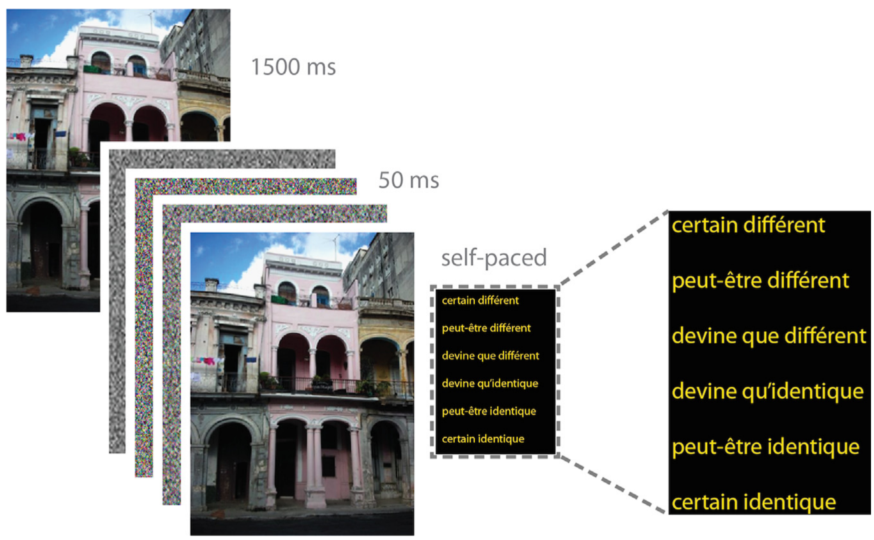

Fig. 3. Scene perception task. On each trial, participants viewed a pair of sequentially presented scenes, with a dynamic noise mask between them. They then made same/different judgments using a confidence scale [shown as presented to participants, in French. English translation (top to bottom): sure different, maybe different, guess different, guess same, maybe same, sure same]. There was no time limit for the response. This example is of a "different" trial: the first scene is expanded outward slightly and the second is contracted inward slightly. These changes alter the distances between components of the scene without adding or removing any objects.

Table 1
Demographic information and neuropsychological profiles for the right hemisphere stroke patients.

Patient #	Etiology	Time since stroke (months)	Age	Edu.	Gender	Neglect tests: proportion impaired	Neglect tests: proportion impaired scores	Preserved cognition domains	Impaired cognitive domains
12-10	Hemorrhage	6	75	6	M	0.38	0.33	WM,EM,Verbal fluency, naming	EF
18-16	Ischemia	3	66	14	M	0	0	WM, immediate recall in EM, visual EM, flexibility	Delayed recall in EM, inhibition
19-7	Ischemia	14	52	12	F	0.22	0.31	WM, EM	EF
3-10	Ischemia	2	65	12	M	0.11	0.06	WM, EM	EF, verbal fluency
7-10	Ischemia	2	51	12	M	0.11	0.13	WM, verbal EM	Visual EM, EF
6-3	Ischemia	0	67	16	M	0.78	0.63	WM	EM, EF, verbal fluency
12-4	Hemorrhage	4	78	9	F	0.67	0.44	Forward digit span, EM, verbal fluency	Backward digit span, EF
4-6	Ischemia	2	77	9	M	0.67	0.56	WM	EF (partly due to neglect)
10-16	Ischemia	3	73	12	M	0.78	0.75	WM	Visual EM
22-4	Ischemia	5	70	8	F	0.22	0.19	WM, EM, EF, verbal fluency	TMT time
23-10	Ischemia	2	65	9	M	0.63	0.50	Forward digit span	Mattis DRS, backward digit span

Neglect was assessed with the Batterie d'Evaluation de la Négligence unilatérale (BEN; Azouvi et al., 2002) and the line cancellation task (Albert, 1973). Working memory (WM) was assessed with forward and backward digit span. Episodic memory (EM) was assessed with verbal list learning (RL/RI-16; French version of Grober and Buschke (1987)), the California Verbal Learning Test, the Wechsler Memory Scale III, and the Doors subtest of the Doors and People test (Baddeley et al., 1994). Attention and executive function (EF) were assessed with the Trail Making Test, the Stroop task, the Test d'Evaluation de l'Attention (Zimmermann and Fimm, 1994), the key search task of the Behavioral Assessment of the Dysexecutive Syndrome, the Frontal Assessment Battery (Dubois et al., 2000) and the WAIS III digit symbol task. Language was assessed with verbal, semantic, and phonemic fluency tasks, and a naming task. In addition, the Mattis Dementia Rating Scale was administered. Each patient completed several, but not all, of these tests as part of the post-stroke clinical assessment, and the reported pattern of spared and impaired cognitive function is based on the tests that were administered to each patient. Gray shading indicates patients who were impaired in both state- and strength-based perception, while no shading indicates patients with only strength-based impairments (refer to Section 3 and Figs. 6 and 7).

were manually traced on the normalized structural image of the brain using PMOD software (http://www.pmod.com/technologies/index.html). Lesion overlap is shown in Fig. 2, and lesion descriptions for each patient are presented in Table 2. Maximal lesion overlap sites (determined using the MNI structural atlas and the Juelich Histological Atlas; Eickhoff et al., 2005) included the inferior parietal lobule (PFm), thalamus, superior longitudinal fasciculus (underlying the inferior parietal lobule), and corticospinal tract (adjacent to the thalamus and putamen).

Twenty-four healthy control participants took part in the study. They were community-dwelling, were recruited by word of mouth and had normal or corrected-to-normal vision. Control participants had no cognitive or psychiatric problems, were free of medication that could affect cognitive functioning, and reported being in good health. All controls had normal scores on the Mini-Mental State Examination (MMSE) and the Mattis Dementia Rating Scale.

Patients and controls did not differ in age [Patients: M=67.2 years, SD=9.1; Controls: M=69.7 years, SD=6.7; $t(33)=0.91$, $p=0.37$; 95% CI of difference in means: −8.04 to 3.08] or education [Patients: M=10.6 years, SD=3.1; Controls: M=12.9 years, SD=3.3; $t(33)=1.93$, $p=0.06$; 95% CI of difference in means: −4.69 to 0.13].

2.2. Materials, design, and procedure

The stimuli and task were adapted from Aly and Yonelinas (2012), Experiment 2A. The experimental stimuli were 160 colored photographs of buildings. An additional set of building images were used for practice trials. Two altered versions of each image were created in Adobe Photoshop. The first version was expanded outward slightly (using the "spherize" option, set at 15%); the second version was contracted inward slightly (using the "pinch" option, set at 15%). The 15% value was chosen based on pilot studies for the first series of behavioral experiments on state- and strength-based perception (Aly and Yonelinas, 2012). Those pilot studies were conducted to find the levels of distortion that avoided both floor and ceiling effects in terms of overall performance (measured as d'). Those levels of distortion were used in the current study.

These kinds of distortions keep the sizes of the images the same, but alter the global or relational information within the scenes (i.e., the relative distances of component parts) without adding or removing specific objects. Additionally, this manipulation leads to the largest changes at the center of the images, and gradually decreasing changes toward the periphery; the edges of the images are largely unaffected. This distortion does not manipulate the boundaries of the images, which may introduce confounds given the boundary extension phenomenon (in which individuals perceive or remember the boundaries of an image as extending further than they actually do; Intraub and Richardson, 1989; Intraub and Dickinson, 2008; also see Mullally et al., 2012, for a relevant patient finding). Thus, if the boundary extension effect happens with the current images, it should affect "same" and "different" trials similarly.

The task consisted of four practice trials and 160 experimental trials. Half of the trials were "same" trials, in which identical images were presented (i.e. the two pinched or the two spherized versions of a particular scene, with these trial types occurring equally often). The remaining half were "different" trials, in which the two altered versions of a scene were presented (i.e., the pinched version followed by the spherized version or vice versa; these trials occurred equally often). Pinched and spherized stimuli occurred equally often as the first and second images across trials. Two stimulus lists were created so that each scene was tested on both "same" and "different" trials across participants. "Same" and "different" trials were presented in a random order.

Patients were tested individually in an examination room at the hospital where they were in-patients, except for one patient who was tested at home. Control participants were assessed individually in a quiet room at home. All participants were native French speakers. Participants were told that they would be presented with pairs of very similar images, and they had to judge if the two images were the same or different.

The visual angle for presented stimuli was 3–5° at central vision, and participants sat 50 cm from the computer screen. On each trial, they viewed a red fixation cross for 1500 ms. This was followed by a scene for 1500 ms, a dynamic noise mask for 50 ms, and, finally, the corresponding identical (on "same" trials) or alternate (on "different" trials) version of the scene (Fig. 3). Participants then used a 6-point confidence scale (presented in French) to indicate how sure they were that the two scenes were the same or different. The confidence scale was presented vertically on the right hand side of the screen, to reduce the likelihood that patients would neglect half of the scale. Only verbal labels were provided (i.e., not numbers), to avoid potential distortion of a mental number line in the patients (Zorzi et al., 2002), which could affect the use of the confidence scale. Patients and controls verbally indicated their confidence response, which was entered by the experimenter. The second image and the scale stayed on the screen until a response was made; there was no time limit.

Before the experiment, participants were familiarized with the kinds of images and perceptual changes in the experiment. They viewed four pairs of images. Each pair consisted of a pinched and a spherized version of a scene. Participants examined the images to observe the differences between pairs, so that they would know the types of changes to expect in the experiment. Participants also completed four practice trials, with the same timing as the experimental trials, before beginning the actual experiment.

3. Results

Performance was examined by plotting confidence-based ROC curves. The leftmost point on the ROC is the probability of a hit (y-axis) and false alarm (x-axis) for the most confident "same" response, and subsequent points are the cumulative probabilities for hits and false alarms as responses of decreasing confidence are added. Parameter estimates of state- and strength-based perception are obtained using maximum likelihood estimation to find the curve that best fits the observed ROC points (Aly and Yonelinas, 2012; Aly et al., 2013, 2014; also see Yonelinas, 1994). This is done by varying the values of different parameters to find the ROC function that yields the highest log-likelihood. The parameters varied are the criterion points, the upper x-intercept, and the curvilinearity of the ROC. The upper x-intercept of the fitted ROC provides an estimate of the probability of state-based perception (higher estimates for intercepts that are shifted further to the left). The curvilinearity

Table 2
Lesion volume and description for each patient, based on CT or MRI scans.

Patient	Lesion volume (% of cerebral volume)	Lesion Description
12–10	0.0245	thalamus, precuneus, posterior cingulate cortex, calcarine gyrus, posterior hippocampus
18–16	0.011	precuneus, superior parietal lobule, mid- and posterior cingulate cortex
19–7	0.02	supplementary motor area, superior frontal gyrus, precentral gyrus, middle and superior occipital gyrus, angular gyrus, precuneus, cuneus, mid cingulate cortex, caudate nucleus, thalamus, putamen, insula, hippocampus
3–10	0.0003	white matter near the right insula
7–10	0.049	caudate nucleus, globus pallidus, putamen, insula, superior temporal gyrus, amygdala, hippocampus, Rolandic operculum, supramarginal gyrus, postcentral gyrus; white matter in temporal areas
6–3	0.0161	calcarine gyrus, lingual gyrus, cuneus, fusiform gyrus, inferior occipital cortex
12–4	0.027	supplementary motor area, mid cingulate cortex, paracentral lobule, precuneus, superior parietal lobule; white matter in medial parietal lobe
4-6	0.073	precentral gyrus, middle frontal gyrus, Rolandic operculum, insula, superior temporal gyrus, angular gyrus, supramarginal gyrus, postcentral gyrus, putamen.
10-16	0.1423	thalamus, putamen, caudate nucleus, insula, middle and inferior temporal gyri, temporal pole, superior temporal sulcus, supramarginal gyrus, postcentral gyrus, precentral gyrus, inferior frontal gyrus; white matter in temporal and parietal regions
22-4	0.0046	putamen, thalamus, superior temporal gyrus
23-10	0.005	putamen, thalamus , caudate nucleus; white matter between putamen and caudate

Lesions were restricted to the right-hemisphere. Gray shading indicates patients who were impaired in both state- and strength-based perception, while no shading indicates patients with only strength-based impairments (refer to Section 3 and Figs. 6 and 7).

of the ROC reflects the discriminability afforded by strength-based perception (i.e., the difference between the strength distributions for "same" and "different" trials, in units of standard deviations).

Our first analyses treated the patients as a single group, albeit with the knowledge that there might be substantial variability across participants. First, we examined a standard measure of overall discriminability (d'), without respect to the distinction between state- and strength-based perception. To this end, all responses associated with a "same" judgment (i.e., sure, maybe, and guess same) were collapsed into a single "same" response, and all responses associated with a "different" judgment (i.e., sure, maybe, and guess different) were collapsed into a single "different" response. d' was then calculated based on the proportion of hits ("same" responses when the images were the same) and false alarms ("same" responses when the images were different). Patients were significantly impaired relative to controls on this measure of overall discriminability [Patients: $M=0.25$, $SD=0.43$; Controls: $M=1.01$, $SD=0.45$; $t(33)=4.68$, $p=0.00005$; 95% CI of difference in means: -1.09 to -0.43]. We next sought to determine whether this impairment in overall performance arose from a reduction in state-based perception, strength-based perception, or both.

Visual inspection of the aggregate ROCs for patients and controls (Fig. 4A) reveals that the patients' ROC is lower overall compared to that of controls, indicating a reduction in overall performance. Moreover, the patient ROC is relatively linear, in contrast to the curvilinear ROC of the controls; this is suggestive of an impairment in strength-based perception. Finally, the upper x-intercept of the patients' ROC is slightly reduced (shifted to the right) compared to that of controls, suggestive of a small reduction in state-based perception. These observations from the aggregate ROCs were confirmed by the average estimates of state- and strength-based perception from individual-participant ROCs (Fig. 4B). Strength-based perception was significantly impaired in the patients, with a nearly 85% reduction relative to controls [Patients: $M=0.09$, $SD=0.10$; Controls: $M=0.53$; $SD=0.30$; $t(33)=4.71$, $p=0.00004$; 95% CI of difference in means: -0.62 to -0.25]. In contrast, state-based perception was numerically, but not significantly, lower in the patients compared to controls [Patients: $M=0.18$, $SD=0.15$; Controls: $M=0.29$, $SD=0.21$; $t(33)=1.54$, $p=0.13$; 95% CI of difference in means: -0.25 to 0.04].

As performance nears the chance diagonal, ROCs will necessarily become more linear. To ensure that the large reduction in strength-based perception was not an artifact of lower performance, we compared patients and controls while matching overall performance in the two groups. In order to do this, we compared the highest-performing patients with the lowest-performing controls. From a median split on the basis of overall discriminability (measured with d'), we took the 12 lowest-performing controls (out of 24 total) and the 6 highest-performing patients (out of 11 total). These groups were not different in overall d' [Patients: $M=0.56$, $SD=0.05$; Controls: $M=0.62$, $SD=0.20$; $t(16)=0.73$, $p=0.47$; 95% CI of difference in means: -0.24 to 0.12].

Having matched overall performance, we examined state- and strength-based perception for group differences (Fig. 5). The ROCs for the two groups overlapped but crossed over, with a greater x-intercept for the patients' ROC, but increased curvilinearity for the controls' ROC (Fig. 5A). This pattern suggests a double dissociation in state- and strength-based perception across groups, and this double dissociation was confirmed in the average parameter estimates: patients had significantly higher estimates of state-based perception [Patients: $M=0.26$, $SD=0.10$; Controls: $M=0.13$, $SD=0.13$; $t(16)=2.12$, $p=0.05$; 95% CI of difference in means: 0.0–0.26], but significantly lower estimates of strength-based perception [Patients: $M=0.15$, $SD=0.09$; Controls: $M=0.41$, $SD=0.25$; $t(16)=2.39$, $p=0.03$; 95% CI of difference in means: -0.47 to -0.03]. This analysis with matched performance suggests that the impairment in strength-based perception for patients is not an artifact of lower overall performance; if it were, then matching performance would have eliminated all differences between the patients and controls. The cross-over pattern in the ROCs, however, suggests that there is a difference in the perceptual processes underlying performance in the patients vs. controls.

It is important to note that the preceding analysis does not suggest that right hemisphere damage *improves* state-based perception. Patients did *not* perform better than controls on state-based judgments in general (as seen in Fig. 4, there was a numerical *decrease* in state-based perception relative to the controls); the increase in state-based perception when matching for performance reflects differential use of perceptual signals in the patients and controls, but does not suggest that brain damage improves perceptual sensitivity overall.

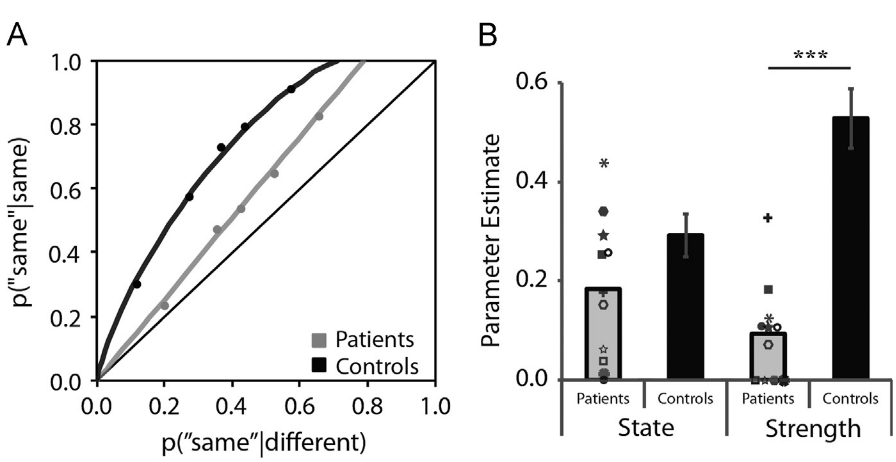

Fig. 4. State- and strength-based perception in patients and controls. (A) Aggregate ROCs for patients and controls on the scene perception task. The upper x-intercept reflects the probability of state-based perception, while the degree of curvilinearity provides an estimate of strength-based perception. The patient aggregate ROC was relatively linear, indicative of an impairment in strength-based perception, and also showed evidence of a reduction in state-based perception (upper-x intercept is shifted further to the right). (B) Average parameter estimates of state- and strength-based perception from individual ROC fits. Data for individual patients are shown overlaid on the patient mean. Patients showed significant impairments of strength-based perception, with all patients performing well below the control mean. In contrast, the overall patient group was not significantly impaired on state-based perception. State- and strength-based perceptions have different units (probability and d', respectively), so their parameter estimates are not directly comparable. Error bars depict ± 1 SEM. $^{***}p<0.001$.

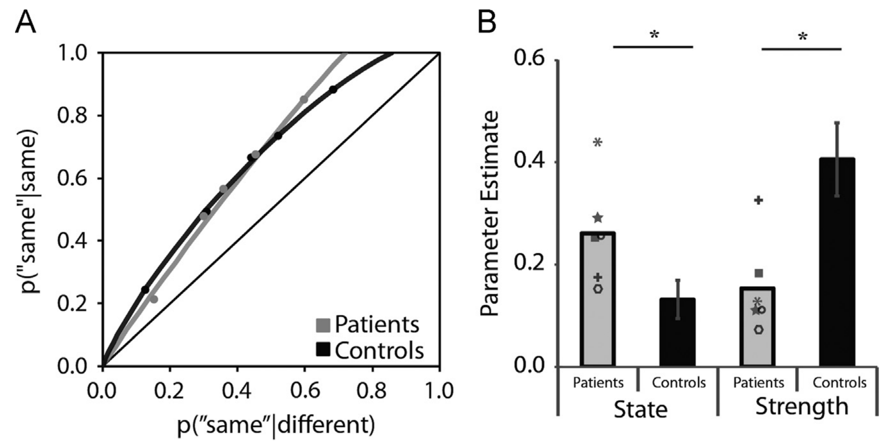

Fig. 5. State- and strength-based perception in patients and controls after matching for overall performance. (A) Aggregate ROCs overlapped but crossed over, suggesting a double dissociation in state- and strength-based perception. (B) Average parameter estimates of state- and strength-based perception from individual ROCs confirmed the double dissociation. Data for individual patients are shown overlaid on the patient mean. State- and strength-based perception have different units (probability and d', respectively), so their parameter estimates are not directly comparable. Error bars depict ± 1 SEM. $^{*}p<0.05$.

Thus, as a group, patients showed a significant impairment in strength-based perception, and not state-based perception. But the preceding analyses have overlooked the substantial individual differences in the patient group. An examination of the individual data points for the patients (Fig. 4B) shows that all patients had estimates of strength-based perception well below the control mean, but this was not the case for state-based perception. Rather, half of the patients were clustered above or around the control mean, while the other half showed evidence of impairment. To investigate this further, we divided the patients into two groups on the basis of estimates of state-based perception, such that the five patients who were closest to the control mean formed one group, and the remaining six patients, who were further away from the control mean, formed the other. In the former group, the estimate of state-based perception was $M=0.32$ ($SD=0.08$; compared to mean of controls $=0.29$), while in the latter group, this estimate was $M=0.07$ ($SD=0.07$).

We then examined the lesions and neuropsychological profiles of these two subgroups separately. This comparison revealed that the patients who were relatively impaired in state-based perception (as well as impaired in strength-based perception) had regions of lesion overlap at the thalamus, putamen, and white matter adjacent to those structures (Fig. 6). In contrast, the patients who had relatively spared state-based perception (but impaired strength-based perception) showed relative sparing of the thalamus and putamen, but had regions of lesion overlap at the inferior parietal lobule, anterior intraparietal sulcus, and insula (Fig. 7). Although there was generally little overlap in this latter group's lesion locations (for all regions of maximal overlap, this overlap was for only two of five patients), the lesions in this group tended to be cortical rather than subcortical, and primarily in temporal or parietal regions.

We next directly compared the lesions of these patient subgroups by subtracting them from one another. Fig. 8 shows the regions that are more often damaged in patients with deficits in both state- and strength-based perception (vs. those with only strength-based impairments); these regions include the putamen, thalamus, and adjacent white matter. Fig. 9 shows the regions that are more often damaged in patients with deficits in only strength-based perception (vs. those with both state- and strength-based impairments); these regions include cortical areas in and around the intraparietal sulcus.

The difference between these subgroups was specifically related to state-based perception (i.e., the basis for their division)—there was no difference between these subgroups in estimates of strength-based perception [Mann–Whitney $U=9.5$, $p=0.35$ $n_1=6$, $n_2=5$]. Moreover, there was no difference in the proportion of tests of spatial neglect at which they were impaired [$U=12$, $p=0.65$] or the proportion of scores on spatial neglect assessments that were associated with impairment [$U=10$, $p=0.43$]. Examining specific tests of neglect [i.e., overlapping figures, Bell cancellation, letter A cancellation, line cancellation, line bisection (5 and 20 cm lines), and text reading] revealed no differences between these subgroups in the number of left minus right misses or amount of deviation on line bisection [all $ps>0.42$ using the Mann–Whitney U test]. Finally, the subgroups were not different in age [$U=12.5$, $p=0.71$], education [$U=5$, $p=0.07$], time since stroke [$U=15$, $p=1$], or lesion volume [$U=9$, $p=0.33$].

Thus, the difference between patient subgroups in state-based perception does not seem to be a result of differences in severity of neglect, types of neglect tests on which performance is impaired, time since stroke, overall lesion size, or demographic factors. Instead, differences in state-based perceptual impairments in the two subgroups identified here are likely related to damage vs. sparing of subcortical structures (namely, thalamus and putamen, as well as the adjacent white matter). Thus, damage to the thalamus, putamen, and adjacent white matter impairs both state- and strength-based perception, while damage primarily focused at temporo-parietal cortical regions selectively impairs strength-based perception.

4. Discussion

Perceptual judgments can be based on different kinds of information (Fernandez-Duque and Thornton, 2000; Rensink, 2000, 2004; Dehaene et al., 2006; Galpin et al., 2008; Busch et al., 2009, 2010; Aly and Yonelinas, 2012; Howe and Webb, 2014). A useful distinction is between state-based judgments in which individuals have conscious access to specific, detailed information, and strength-based judgments, which are based on a graded sense of overall match/mismatch (Aly and Yonelinas, 2012). We tested a group of patients with heterogeneous lesions following right-hemisphere stroke, and found that the patient group considered as a whole was impaired in strength-based, but not state-based, perception. The deficit in strength-based perception was not an artifact of lower overall performance of the patients relative to controls, because matching control and patient performance revealed a double dissociation: patients showed increased reliance on state-based perception but impaired strength-based perception relative to controls.

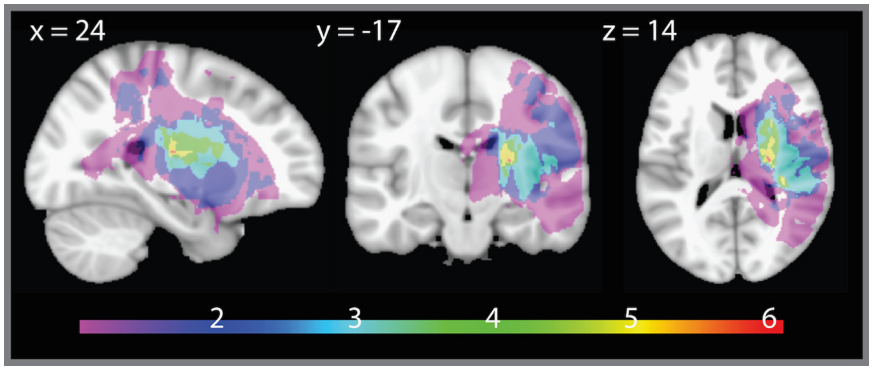

Fig. 6. Lesion overlap for the six patients who were impaired in state-based and strength-based perception. All six patients had damage at the corticospinal tract and thalamus. Additionally, five of the six patients had damage at the putamen and superior longitudinal fasciculus (adjacent to the inferior parietal lobule). *x*, *y*, and *z* coordinates are in MNI space.

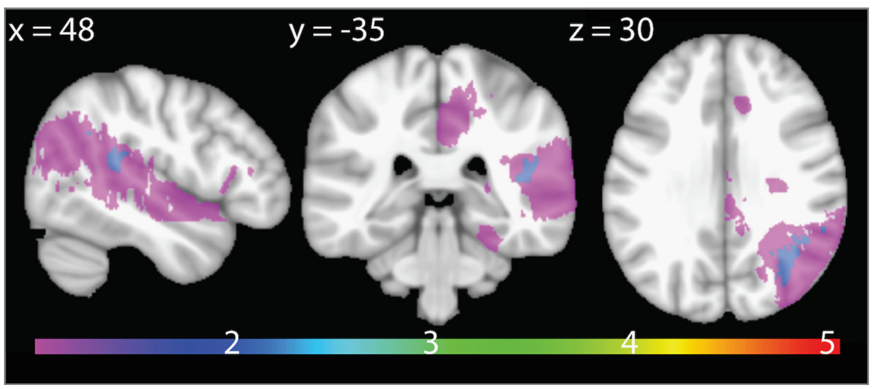

Fig. 7. Lesion overlap for the five patients who were impaired in strength-based perception but relatively spared in state-based perception. The regions of maximal overlap were the inferior parietal lobule (PFcm, PF, PFm, PGa, PGp), optic radiation, premotor cortex, anterior intraparietal sulcus (hIP1, hIP3), and insula. In all of these cases, the overlap was for two of five patients. The thalamus and putamen were spared in all but one patient. *x*, *y*, and *z* coordinates are in MNI space.

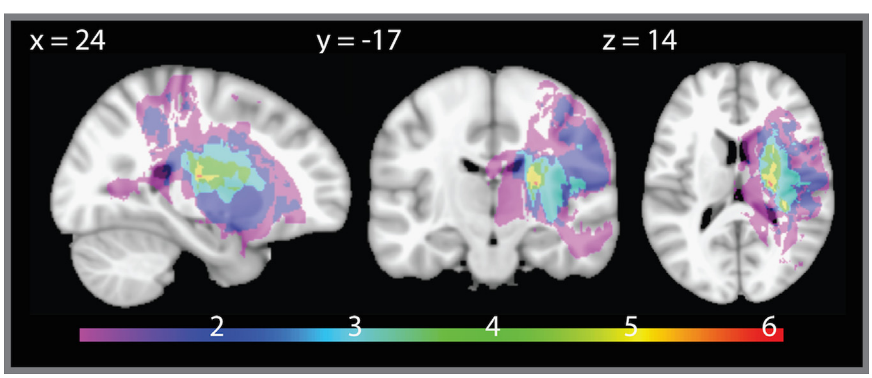

Fig. 8. Regions that are more often damaged in patients with deficits in both state- and strength-based perception (vs. those with just strength-based impairments). This image was obtained by subtracting the lesions of patients with selective strength-based deficits from the lesions of those impaired in both state- and strength-based perception. These regions include the putamen, thalamus, and adjacent white matter.

There were, however, substantial individual differences in behavioral performance in the patient group, which were masked by analyses of the group mean. An examination of lesion overlap images showed that patients with spared state-based perception but reduced strength-based perception had damage that was primarily focused around temporo-parietal cortical regions. In contrast, patients who showed evidence of impaired state- and strength-based perception had subcortical damage including the thalamus, putamen, and adjacent white matter. Importantly, these groups were not different in age, education, time since stroke, lesion volume, or the severity of spatial neglect symptoms. Thus, subcortical lesions that encroach on the thalamus and putamen are associated with impairments in both state- and strength-based perception, while temporo-parietal cortical lesions that spare subcortical structures are associated with selective deficits in strength-based perception.

It is important to note that temporo-parietal damage is sufficient, but not necessary, for strength-based perceptual impairments:

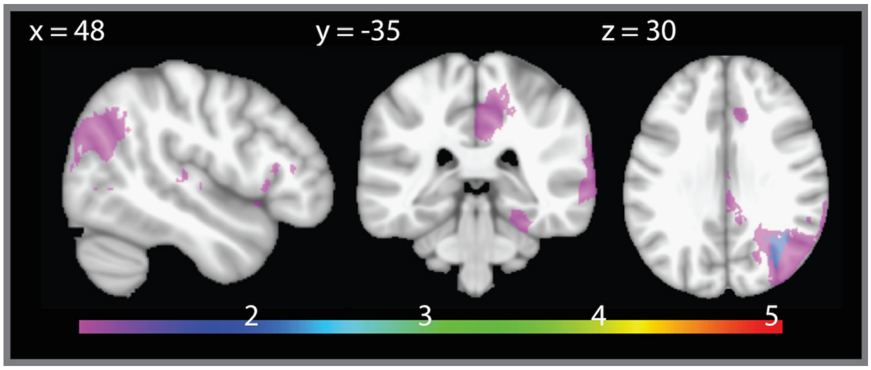

Fig. 9. Regions that are more often damaged in patients with selective deficits in strength-based perception (vs. those with both state- and strength-based impairments). This image was obtained by subtracting the lesions of patients with state- and strength-based deficits from the lesions of those with selective strength-based impairments. These regions include cortical areas in and around the intraparietal sulcus.

patients with thalamic and/or basal ganglia damage and spared temporo-parietal cortical areas also showed deficits in strength-based perception (in addition to impaired state-based perception). Thus, temporo-parietal regions are just one of several regions whose damage can result in impaired strength-based perception (also see Aly et al., 2013).

In previous behavioral work (Aly and Yonelinas, 2012), we found that state-based perception played a larger role in tasks involving detection of discrete object changes (e.g., a tree that is present in one scene but absent in another), was associated with a rapid temporal onset, and was accompanied by conscious awareness of specific details that had changed. In contrast, strength-based perception played a larger role in tasks involving detection of relational or global changes (i.e., the changes used in the current study), was associated with graded changes in confidence over time, and was accompanied by a sense of something having changed without awareness of what the specific change was (also see Rensink, 2000, 2004). Below, we (1) discuss the findings of the current study with respect to prior studies of state- and strength-based perception, (2) consider how patients' spatial neglect symptoms may have contributed to the observed deficits, and, finally, (3) speculate about the specific roles of temporo-parietal and subcortical structures in these kinds of visual change detection.

4.1. Relation to prior studies of state- and strength-based perception

In a previous study, we examined state- and strength-based perception in patients with selective lesions of the hippocampus or more extensive unilateral medial temporal lobe lesions that included the hippocampus and the surrounding cortex (Aly et al., 2013). We found that these patients showed selective deficits in strength-based perception. In the current study, patients with damage around temporo-parietal cortical regions showed this same pattern of results (i.e., impaired strength-based perception but intact state-based perception). This similarity in performance across patient groups with distinct lesion sites may be related to the anatomical and functional connectivity between the hippocampus/medial temporal lobe and parietal cortex (e.g., Kahn et al., 2008; Kravitz et al., 2011; Libby et al., 2012; Ranganath and Ritchey, 2012). That is, these regions may be part of a network that is important for, among other functions, representations of complex scenes or contexts (Ranganath and Ritchey, 2012), and damage to any part of this network may result in similar behavioral deficits. Importantly, however, the same behavioral deficit might arise from different underlying impairments: e.g., an impaired ability to form or maintain precise relational representations (following damage to the hippocampus) or an impaired ability to continuously integrate or accumulate sensory information over time or across saccades (following damage to parietal regions).

Interestingly, in an fMRI study with healthy adults (Aly et al., 2014), activity in the supramarginal gyrus, bilaterally, was increased for state-based perception and was not modulated by varying levels of strength-based perception. While this pattern of results suggested that this region in the lateral parietal cortex might be necessary for state-based perception, the current results are not consistent with that view. Rather, damage including (and in the vicinity of) the supramarginal gyrus impaired strength-based but not state-based perception. A potential caveat is that we did not have patients with selective and complete damage to the supramarginal gyrus; testing patients with more selective lesions within parietal cortex will be necessary to make more specific claims about the roles of parietal subregions.

Finally, our previous (Aly et al., 2013) and current findings show an interesting relationship to work done in similar patient populations in the domain of recognition memory. Recognition memory performance can be separated into the contributions of state-based memory (high-confidence recollection of specific details) or strength-based memory (assessments of the strength of familiarity; see Yonelinas, 2002). Patients with focal hippocampal lesions show selective deficits in state-based memory (i.e., recollection; see Yonelinas et al., 2010 for review) and strength-based perception (Aly et al., 2013). Interestingly, a recent study found that patients with damage including the lateral parietal cortex and intra-parietal sulcus made fewer high-confidence memory judgments than controls (Hower et al., 2014); such a pattern may suggest an impairment in state-based memory. In the current study, patients with similar lesion locations showed impairments in strength-based perception. Thus, hippocampal and parietal damage lead to selective impairments in state-based memory but strength-based perception (for related work, see Elfman et al., 2014). As mentioned above, this similarity in performance across patient groups with different sites of damage may be related to the connectivity between the hippocampus and parietal cortex (e.g., Kahn et al., 2008; Kravitz et al., 2011; Libby et al., 2012; Ranganath and Ritchey, 2012).

4.2. Spatial neglect and impairments in state- or strength-based perception

The task used in this study was designed as a test of high-level scene perception, but perceptual judgments depend on the ability to attend to task-relevant information. Thus, reduced task performance could be related to impairments in "perception" or "attention", though it would be difficult or impossible to disentangle these cognitive processes in the current task. Because 10 of the 11 patients tested showed symptoms of unilateral spatial neglect on neuropsychological tests (as commonly observed after damage to right-hemisphere temporo-parietal cortex, thalamus, or basal ganglia; for review, see Mesulam 1999; Halligan et al., 2003; Husain and Rorden 2003; Corbetta and Shulman 2001; Karnath and Rorden 2012), it is important to consider how their pattern of performance on the scene perception task can be informed by the kinds of deficits observed in this population of patients.

In the current study, stimuli were presented sequentially (rather than simultaneously on the left and right hand sides of the screen; c.f. Aly et al., 2013) to avoid neglect of one image in each pair; moreover, the scale was presented vertically on the right-hand side of the screen and without any numerical labels, in an attempt to prevent neglect or distortion of half of the scale or a corresponding mental number line (Zorzi et al., 2002). While these task manipulations minimized any potential impairment as a result of neglect of the left side of (body-centered) space, such spatial attentional deficits may have still contributed to performance. For example, if neglect was based on image-centered coordinates (see Mesulam, 1999; also see Bisiach and Luzzatti, 1978), then half of each scene might have been unattended. Detection of relational changes (which can be the basis for strength-based decisions) might have therefore been more difficult, because this relies on a representation of how component parts of the overall scene are related to one another. In contrast, detection of relatively local differences (which can be the basis for state-based decisions) may be less impaired, because such judgments could be made on the basis of features in the attended right half of each image. This is especially true for the perceptual manipulations used in the current study, because differences, when present, were in both left and right halves of each image. Thus, this is one way in which strength-based perception might be impaired more than state-based perception in patients with unilateral spatial neglect.

Alternatively, the deficits observed might be related to aspects of attention other than the lateralized deficits, including sustained attention, selective attention, and salience detection—all of which can be impaired in patients with spatial neglect (Husain and Rorden, 2003), and all of which are likely important in the current task. Sustained and selective attention is important to maintain focus over the course of many trials and attend to the task-relevant scene information; salience detection is necessary for noticing differences between scenes that are largely identical, and learning to attend to parts of the scene that are more diagnostic for change detection (i.e., the center rather than the edges). Difficulties in any of these aspects of attention would be expected to affect both state- and strength-based responses, however, rather than just one or the other. Thus, such attentional deficits are unlikely to explain the performance of patients who showed *selective* impairments in strength-based perception (i.e., those patients with primarily temporo-parietal cortical lesions), but may have contributed to the performance of those who showed impairments in both state- and strength-based perception (i.e., those patients with subcortical lesions).

4.3. Parietal cortex, spatial representations, and accumulation of sensory evidence

The parietal cortex has been implicated in various aspects of spatial processing, including spatial attention and perception (Mesulam, 1999; Halligan et al., 2003; Behrmann et al., 2004; Thiebaut de Schotten et al., 2005; Hutchinson et al., 2009; Verdon et al., 2010; Kravitz et al., 2011; Cabeza et al., 2012; Ranganath and Ritchey, 2012; Geng and Vossel, 2013). Parietal regions may therefore be important for strength-based perception because this kind of perception depends more on relational or spatial representations than state-based perception, which can be based on identification of local or item-level details (Aly and Yonelinas, 2012).

The inferior parietal lobule plays an important role in maintaining stable representations of space across saccades (see Husain and Rorden, 2003; Verdon et al., 2010). Strength-based perceptual judgments may place a large demand on the ability to maintain such a stable spatial representation because judgments of relational match/mismatch would benefit from knowledge of where scene components are relative to one another. In contrast, state-based judgments can be made on the basis of identifying relatively local differences (Aly and Yonelinas, 2012), and, as such, need not depend as much on maintaining a stable spatial representation across saccades. This is particularly important in the context of the current study because participants were free to move their eyes, and had enough time to make several saccades over each image. Thus, the contribution of the parietal cortex to strength-based perception may be related to its role in maintaining stable spatial representations of the environment.

In a previous study, we found that strength-based perception was associated with graded evidence accumulation; that is, in a task that depended largely on strength-based perception, individuals gradually increased their confidence in a same/different judgment over time. Furthermore, these graded changes in confidence were correlated with estimates of strength-based perception from an ROC analysis (Aly and Yonelinas, 2012). Neural activity in the lateral intraparietal area has been studied extensively in the context of perceptual decision-making tasks, and activity in these neurons has been related to continuously-graded integration of sensory evidence (e.g., Shadlen and Newsome, 2001; Bollimunta et al., 2012; see Gold and Shadlen, 2007) as well as the degree of confidence in perceptual decisions (Kiani and Shadlen, 2009). In humans, BOLD activity in the parietal cortex — specifically, the intraparietal sulcus and inferior parietal lobule — has similarly been related to accumulation of sensory evidence in the service of perceptual decision-making (e.g., Heekeren et al., 2006; Ploran et al., 2007, 2011; Kayser et al., 2010; Liu and Pleskac, 2011). Although on markedly different timescales and levels of analysis, these behavioral and neural results raise the possibility that graded signals in parietal areas may be related to graded levels of strength-based perception. The current finding that damage to the intraparietal sulcus and inferior parietal lobule is associated with a deficit in strength-based perception lends support to this idea, and future studies investigating the relationship between graded evidence accumulation and strength-based perception will be important.

4.4. Thalamic and basal ganglia contributions to attention and perceptual awareness

Patients with damage that included the thalamus and/or the putamen showed impairments in both state- and strength-based judgments, raising the possibility that these subcortical structures play a role in high-level perceptual processing more generally. A potential caveat is that, of the six patients with reduced state- and strength-based perception, three also had damage in cortical areas, with the region of maximal overlap in the cortex being the inferior parietal lobule. Nevertheless, the remaining three patients had lesions confined to the vicinity of the thalamus, putamen, and adjacent white matter, and these patients performed just as poorly as the ones with more extensive damage that included the cortex. Thus, it seems from these data that damage to the thalamus and/or putamen is sufficient to impair both state- and strength-based perception. Moreover, these data show that damage to temporo-parietal cortical areas is also sufficient, but not necessary, for strength-based impairments (also see Aly et al., 2013).

The thalamus is often referred to as the "gateway" to the cortex, because information from nearly all senses (except olfaction) has to pass through the thalamus on the way to primary sensory cortices. Thalamic lesions may therefore disrupt the integrity of visual information relayed to the cortex and, as a result, impair high-level perception. The thalamus is also critical for states of vigilance as well as various aspects of visuospatial attention, and activity in the thalamus is modulated by attention (e.g., Crick, 1984; Rafal and Posner, 1987; Guillery et al., 1998; Dehaene et al., 2006; McAlonan et al., 2008; Saalmann and Kastner, 2009). Moreover, although the basal ganglia are often studied in the context of motor learning or control, these structures also play an important role in visual perception (see Pribram, 1977; Brown et al., 1997) and attentional regulation, including shifting attention or focusing on task-relevant information in the face of competing information (e.g., Downes et al., 1989; Sharpe, 1990; Kermadi and Boussaoud, 1995; Ravizza and Ivry, 2001; see Brown et al., 1997). Accordingly, damage to the thalamus or basal ganglia might impair visuospatial attention, selective attention, or high-level perceptual processing, leading to reductions in both state- and strength-based decisions in this task.

It is important to consider whether general inattentiveness could account for the performance of patients with thalamic damage. That is, could deficits in state- and strength-based perception be related to a reduced level of general vigilance or arousal in this group? This seems unlikely, because these patients were not different from those without subcortical damage on several neuropsychological measures, including the proportion of spatial neglect tests or scores that were impaired and performance on specific tests of spatial neglect. Additionally, each of the patients in this group showed evidence of spared cognitive functions on several neuropsychological tests (see Table 1; refer to Table 2 for lesion descriptions). Thus, deficits in high-level perception on this task were not secondary to generally reduced attention or arousal. That said, an important avenue for future research is an examination of the extent of perceptual impairments in these patients. The current study was geared toward exploring high-level scene perception in the context of a change detection task, but this may be just one of many perceptual deficits that result after right hemisphere subcortical damage.

5. Conclusions

Perceptual change detection can be based on different kinds of information: conscious access to local, detailed information (state-based perception), or graded signals reflecting a sense of relational match/mismatch (strength-based perception). In the current study, we show that right temporo-parietal cortical regions play a critical and selective role in strength-based perception, while the integrity of the right thalamus, putamen, and adjacent white matter is necessary for intact state- and strength-based perception. This work adds to a growing body of evidence that highlights the utility of separating different kinds of conscious perceptual experiences, which have different functional characteristics and neural underpinnings. Distinguishing between these kinds of perception will be critical for elucidating the multifaceted nature of visual experiences and their complex neural bases.

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References

Albert, M.L., 1973. A simple test of visual neglect. Neurology 23, 658–664.
Aly, M., Ranganath, C., Yonelinas, A.P., 2013. Detecting changes in scenes: the hippocampus is critical for strength-based perception. Neuron 78, 1127–1137.
Aly, M., Ranganath, C., Yonelinas, A.P., 2014. Neural correlates of state- and strength-based perceptions. J. Cogn. Neurosci. 26, 792–809.
Aly, M., Yonelinas, A.P., 2012. Bridging consciousness and cognition in memory and perception: evidence for both state and strength processes. PLoS One 7, e30231. http://dx.doi.org/10.1371/journal.pone.0030231 (1–16).
Azouvi, P., Samuel, C., Louis-Dreyfus, A., Bernati, T., Bartolomeo, P., Beis, J.M., et al., 2002. Sensitivity of clinical and behavioral tests of spatial neglect after right hemisphere stroke. J. Neurol. Neurosurg. Psychiatry 73, 160–166.
Baddeley, A.D., Emslie, H., Nimmo-Smith, I., 1994. Doors and People: A Test of Visual and Verbal Recall and Recognition. Thames Valley Test Company, Flempton, Bury St. Edmunds.
Behrmann, M., Geng, J.J., Shomstein, S., 2004. Parietal cortex and attention. Curr. Opin. Neurobiol. 14, 212–217.
Bisiach, E., Luzzatti, C., 1978. Unilateral neglect of representational space. Cortex 14, 129–133.
Bollimunta, A., Totten, D., Ditterich, J., 2012. Neural dynamics of choice: single-trial analysis of decision-related activity in parietal cortex. J. Neurosci. 32, 12684–12701.
Brett, M., Leff, A.P., Rorden, C., Ashburner, J., 2001. Spatial normalization of brain images with focal lesions using cost function masking. NeuroImage 14, 486–500.
Brown, L.L., Schneider, J.S., Lidsky, T.I., 1997. Sensory and cognitive functions of the basal ganglia. Curr. Opin. Neurobiol. 7, 157–163.
Busch, N.A., Dürschmid, S., Hermann, C.S., 2010. ERP effects of change localization, change identification, and change blindness. NeuroReport 21, 371–375.
Busch, N.A., Fründ, I., Herrmann, C.S., 2009. Electrophysiological evidence for different types of change detection and change blindness. J. Cogn. Neurosci. 22, 1852–1869.
Cabeza, R., Ciaramelli, E., Moscovitch, M., 2012. Cognitive contributions of the ventral parietal cortex: an integrative theoretical account. Trends Cogn. Sci. 16, 338–352.
Corbetta, M., Shulman, G.L., 2011. Spatial neglect and attention networks. Annu. Rev. Neurosci. 34, 569–599.
Crick, F., 1984. Function of the thalamic reticular complex: the searchlight hypothesis. Proc. Natl. Acad. Sci. USA 81, 4586–4590.
Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., Sergent, C., 2006. Conscious, preconscious, and subliminal processing: a testable taxonomy. Trends Cogn. Sci. 10, 204–211.
Downes, J.J., Roberts, A.C., Sahakian, B.J., Evenden, J.L., Morris, R.G., Robbins, T.W., 1989. Impaired extra-dimensional shift performance in medicated and unmedicated Parkinson's disease: evidence for a specific attentional dysfunction. Neuropsychologia 27, 1329–1343.
Dubois, B., Slachevsky, A., Litvan, I., Pillon, B., 2000. The FAB: a frontal assessment battery at bedside. Neurology 55, 1621–1626.
Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., et al., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. NeuroImage 25, 1325–1335.
Elfman, K.W., Aly, M., Yonelinas, A.P., 2014. Neurocomputational account of memory and perception: thresholded and graded signals in the hippocampus. Hippocampus, http://dx.doi.org/10.1002/hipo.22345, in press.
Fernandez-Duque, D., Thornton, I.M., 2000. Change detection without awareness: do explicit reports underestimate the representation of change in the visual system? Vis. Cogn. 7, 323–344.
Galpin, A., Underwood, G., Chapman, P., 2008. Sensing without seeing in comparative visual search. Conscious. Cogn. 17, 658–673.
Geng, J.J., Vossel, S., 2013. Re-evaluating the role of TPJ in attentional control: contextual updating? Neurosci. Biobehav. Rev. 37, 2608–2620.
Gold, J.I., Shadlen, M.N., 2007. The neural basis of decision making. Annu. Rev. Neurosci. 30, 535–574.
Green, D.M., Swets, J.A., 1966. Signal Detection Theory and Psychophysics. Wiley, New York.
Grober, E., Buschke, H., 1987. Genuine memory deficits in dementia. Dev. Neuropsychol. 3, 13–36.
Guillery, R.W., Feig, S.L., Lozsádi, D.A., 1998. Paying attention to the thalamic reticular nucleus. Trends Neurosci. 21, 28–32.
Halligan, P.W., Fink, G.R., Marshall, J.C., Vallar, G., 2003. Spatial cognition: evidence from visual neglect. Trends Cogn. Sci. 7, 125–133.
Heekeren, H.R., Marrett, S., Ruff, D.A., Bandettini, P.A., Ungerleider, L.G., 2006. Involvement of human left dorsolateral prefrontal cortex in perceptual decision making is independent of response modality. Proc. Natl. Acad. Sci. USA 103, 10023–10028.
Howe, P.D.L., Webb, M.E., 2014. Detecting unidentified changes. PLoS One 9, e84490. http://dx.doi.org/10.1371/journal.pone.0084490 (1–9).

Hower, K.H., Wixted, J., Berryhill, M.E., Olson, I.R., 2014. Impaired perception of mnemonic oldness, but not mnemonic newness, after parietal lobe damage. Neuropsychologia 56, 409–417.
Husain, M., Rorden, C., 2003. Non-spatially lateralized mechanisms in hemispatial neglect. Nat. Rev. Neurosci. 4, 26–36.
Hutchinson, J.B., Uncapher, M.R., Wagner, A.D., 2009. Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. Learn. Mem. 16, 343–356.
Intraub, H., Dickinson, C.A., 2008. False memory 1/20th of a second later: what the early onset of boundary extension reveals about perception. Psychol. Sci. 19, 1007–1014.
Intraub, H., Richardson, M., 1989. Wide-angle memories of close-up scenes. J. Exp. Psychol.: Learn. Mem. Cogn. 15, 179–187.
Kahn, I., Andrews-Hanna, J.R., Vincent, J.L., Snyder, A.Z., Buckner, R.L., 2008. Distinct cortical anatomy linked to subregions of the medial temporal lobe revealed by intrinsic functional connectivity. J. Neurophysiol. 100, 129–139.
Karnath, H.-O., Rorden, C., 2012. The anatomy of spatial neglect. Neuropsychologia 50, 1010–1017.
Kayser, A.S., Buchsbaum, B.R., Erickson, D.T., D'Esposito, M., 2010. The functional anatomy of a perceptual decision in the human brain. J. Neurophysiol. 103, 1179–1194.
Kermadi, I., Boussaoud, D., 1995. Role of the primate striatum in attention and sensorimotor processes: comparison with premotor cortex. NeuroReport 6, 1177–1181.
Kiani, R., Shadlen, M.N., 2009. Representation of confidence associated with a decision by neurons in the parietal cortex. Science 324, 759–764.
Kravitz, D., Saleem, K.S., Baker, C.I., Mishkin, M., 2011. A new neural framework for visuospatial processing. Nat. Rev. Neurosci. 12, 217–230.
Lamme, V.A.F., 2003. Why visual attention and awareness are different. Trends Cogn. Sci. 7, 12–18.
Libby, L.A., Ekstrom, A.D., Ragland, J.D., Ranganath, C., 2012. Differential connectivity of perirhinal and parahippocampal cortices within human hippocampal subregions revealed by high-resolution functional imaging. J. Neurosci. 32, 6550–6560.
Liu, T., Pleskac, T.J., 2011. Neural correlates of evidence accumulation in a perceptual task. J. Neurophysiol. 106, 2383–2398.
Macmillan, N.A., Creelman, C.D., 2005. Detection Theory: A User's Guide, ed. 2 Cambridge University Press, New York.
Mazurek, M.E., Roitman, J.D., Ditterich, J., Shadlen, M.N., 2003. A role for neural integrators in perceptual decision making. Cereb. Cortex 13, 1257–1269.
McAlonan, K., Cavanaugh, J., Wurtz, R.H., 2008. Guarding the gateway to cortex with attention in visual thalamus. Nature 456, 391–394.
Mesulam, M.M., 1981. A cortical network for directed attention and unilateral neglect. Ann. Neurol. 10, 309–325.
Mesulam, M.M., 1999. Spatial attention and neglect: parietal, frontal, and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. Philos. Trans. R. Soc. Lond. B: Biol. Sci. 354, 1325–1346.
Mullally, S.L., Intraub, H., Maguire, E.A., 2012. Attenuated boundary extension produces a paradoxical memory advantage in amnesic patients. Curr. Biol. 22, 261–268.
Ploran, E.J., Nelson, S.M., Velanova, K., Donaldson, D.I., Petersen, S.E., Wheeler, M.E., 2007. Evidence accumulation and the moment of recognition: dissociating perceptual recognition processes using fMRI. J. Neurosci. 27, 11912–11924.
Ploran, E.J., Tremel, J.J., Nelson, S.M., Wheeler, M.E., 2011. High quality but limited quantity perceptual evidence produces neural accumulation in frontal and parietal cortex. Cereb. Cortex 21, 2650–2662.
Pribram, K., 1977w. New dimensions in the functions of the basal ganglia. In: Shagass, C., Friedhoff, I. (Eds.), Psychopathology and Brain Dysfunction. Raven Press, New York.
Rafal, R.D., Posner, M.I., 1987. Deficits in human visual spatial attention following thalamic lesions. Proc. Natl. Acad. Sci. USA 84, 7349–7353.
Ranganath, C., Ritchey, M., 2012. Two cortical systems for memory-guided behavior. Nat. Rev. Neurosci. 13, 713–726.
Ravizza, S.M., Ivry, R.B., 2001. Comparison of the basal ganglia and cerebellum in shifting attention. J. Cogn. Neurosci. 13, 285–297.
Rensink, R.A., 2000. Seeing, sensing, and scrutinizing. Vis. Res. 40, 1469–1487.
Rensink, R.A., 2004. Visual sensing without seeing. Psychol. Sci. 15, 27–32.
Rorden, C., Bonilha, L., Fridriksson, J., Bender, B., Karnath, H.-O., 2012. Age-specific CT and MRI templates for spatial normalization. NeuroImage 61, 957–965.
Saalmann, Y.B., Kastner, S., 2009. Gain control in the visual thalamus during perception and cognition. Curr. Opin. Neurobiol. 2009 (19), 408–414.
Shadlen, M.N., Newsome, W.T., 2001. Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. J. Neurophysiol. 86, 1916–1936.
Sharpe, M.H., 1990. Distractibility in early Parkinson's disease. Cortex 26, 239–246.
Simons, D.J., Nevarez, G., Boot, W.R., 2005. Visual sensing is seeing: why "mindsight", in hindsight, is blind. Psychol. Sci. 16, 520–524.
Thiebaut de Schotten, M., Urbanski, M., Duffau, H., Volle, E., Lévy, R., Dubois, B., Bartolomeo, P., 2005. Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. Science 309, 2226–2228.
Verdon, V., Schwartz, S., Lovblad, K.O., Hauert, C.A., Vuilleumier, P., 2010. Neuroanatomy of hemispatial neglect and its functional components: a study using voxel-based lesion-symptom mapping. Brain 133, 880–894.
Yonelinas, A.P., 1994. Receiver-operating characteristics in recognition memory: evidence for a dual-process model. J. Exp. Psychol.: Learn. Mem. Cogn. 20, 1341–1354.
Yonelinas, A.P., 2002. The nature of recollection and familiarity: A review of 30 years of research. J. Mem. Lang. 46, 441–517.
Yonelinas, A.P., Aly, M., Wang, W.-C., Koen, J.D., 2010. Recollection and familiarity: Examining controversial assumptions and new directions. Hippocampus 20, 1178–1194.
Zimmerman, P., Fimm, B., 1994. Tests d'évaluation de l'attention (TEA): Manuel d'utilisation. Psychologische Testsysteme, Würselen.
Zorzi, M., Priftis, K., Umiltà, C., 2002. Neglect disrupts the mental number line. Nature 416, 138–139.