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RESEARCH ARTICLE

Differential neural activity patterns for spatial relations in humans: a MEG study

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Abstract Children learn the words for *above–below* relations earlier than for *left–right* relations, despite treating these equally well in a simple visual categorization task. Even as adults—conflicts in congruency, such as when a stimulus is depicted in a spatially incongruent manner with respect to salient global cues—can be challenging. Here we investigated the neural correlates of encoding and maintaining in working memory *above–below* and *left–right* relational planes in 12 adults using magnetoencephalography in order to discover whether *above–below* relations are represented by the brain differently than *left–right* relations. Adults performed perfectly on the task behaviorally, so any differences in neural activity were attributed to the stimuli's cognitive attributes. In comparing *above–below* to *left–right* relations during stimulus encoding, we found the greatest differences in neural activity in areas associated with space and movement. In comparing congruent to incongruent trials, we found the greatest differential activity in premotor areas. For both contrasts, brain areas involved in the encoding phase were also involved in the maintenance phase, which provides evidence that those brain areas are particularly important in representing the relational planes or congruency types throughout the trial. When comparing neural activity associated with the relational planes during working memory, additional right posterior areas were implicated, whereas the congruent-incongruent contrast implicated additional bilateral frontal and temporal areas. These findings are consistent with the hypothesis *left–right* relations are represented differently than *above–below* relations.

Keywords Left–right confusion · MEG · Congruency · Relational plane · Working memory · Encoding

Introduction

We live in a three-dimensional world in which we constantly make decisions regarding the spatial relations we share with the objects with which we interact. Yet, we sometimes confuse *left* and *right* spatial relations (Hannay et al. 1990; Jordan et al. 2006) despite never confusing other spatial relations, such as *above–below*, *up–down* or *forward–backward*. This differential confusion exists linguistically in children, as they learn the labels for these spatial relations, but it may not be present outside a linguistic context (Scott et al. 2015a). For example, children learn terms for *above–below* around the age of 3 years, but learn the terms for *left–right* around ages 6 or 7 years (Cox and Richardson 1985; Martin and Sera 2006). On the other hand, children are able to categorize things as "to the left" or "above" since early infancy (Gava et al. 2009; Quinn 2007). Categorizing and compartmentalizing space is important not just for navigating in a three-dimensional world, but for promoting other cognitive skills, such as structuring comparisons and quantification (Stieff et al. 2013; Uttal et al. 2013; Verdine et al. 2014; Vendetti et al. 2015). Although there is a wealth of behavioral data supporting the idea that differences exist between the *left–right* relational plane and other spatial relational planes (Cox and

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Richardson 1985; Landau and Hoffman 2005; Dessalegn and Landau 2008), there is a dearth of neural studies seeking evidence of such differences. In this study, we evaluated neural activity for *above–below* compared to *left–right* spatial judgments to investigate possible differences in neural representation of these two relational planes.

Human infants can recognize and categorize spatial relations (Gava et al. 2009; Quinn 2007). Infants can make correct visual matching judgments of *above*, *below*, *left* and *right* relative positions; yet, once they reach childhood they seem to have difficulty matching the relational category to the verbal label. Much of the literature concerning the development of spatial relational knowledge describes a "privilege" of the vertical axis (i.e., *above–below*)—especially the positive direction (i.e., "top" or "above")—in verbal labeling (Clark 1980; Cox and Richardson 1985; Landau and Hoffman 2005). This "privilege" can sometimes be found in children's non-linguistic matching performance where performance on the horizontal axis (i.e., *left–right*) is worse than performance on the vertical axis (i.e., *above–below*) in both typically developing children (Dessalegn and Landau 2008) and children with Williams syndrome (Landau and Hoffman 2005; Semel and Rosner 2003). It is also apparent that when observing an object, adults automatically assign a "top" to the object, although this judgment is somewhat dependent on the item's spatial orientation (e.g., Carlson et al. 2002). Therefore, the developmental literature suggests that *above–below* is treated differently from *left–right* in terms of attention and cognition, even in Williams syndrome, and this differential accessibility seems to persist into adulthood. What seems to develop, then, is the ability to label and remember spatial relations, rather than the ability to partition a space into categories, with the different relational planes following different trajectories. How this is realized in the brain is yet to be determined; however, we set out to describe the end state of these relations as represented by adult neural activity.

There has been little research on the neural correlates of encoding or remembering the spatial relations of *above*, *below*, *right* and *left*. The majority of studies investigating relational reasoning have focused on a general type of reasoning, such as analogical reasoning (Bunge et al. 2005; Wright et al. 2008) or matrix reasoning (Christoff et al. 2001; Crone et al. 2009; Baldo et al. 2010), or set out to differentiate between the different steps in the reasoning process (Krawczyk et al. 2011; Wendelken et al. 2012). Each of these studies has focused on the prefrontal cortex (PFC), and many have attempted to differentiate the specific areas within PFC that are responsible for specific aspects of reasoning. One study which did investigate neural correlates of spatial relations (Damasio et al. 2001) looked at the whole brain but relied on verbal retrieval, and did so in the context of object recognition and tool use. Furthermore, they did not differentiate between the different sets of relations (i.e., relational planes).

A recent study with monkeys (Goodwin et al. 2012), using a simple relational task similar to our own, directly compared *above–below* to *left–right* relations. In their study, two monkeys made simple relational judgments as their neural activity was recorded from prefrontal (along the principal sulcus) and parietal areas (along the intraparietal sulcus). The monkeys performed better at and had stronger neural activity—particularly in parietal areas—associated with *left–right* decisions compared to *above–below* decisions; however, it should be noted that both monkeys learned to differentiate *right* from *left* before learning *above* from *below* so the results may indicate an order of learning effect rather than a deeper evolutionary root of differential neural activity. These two possible outcomes represent a developmental effect and a phylogenetic effect, respectively: we will consider both possibilities in our results. Combined, these studies suggest that prefrontal areas should be activated in our spatial relational task, but it is not clear whether we will find differential activity in this area, as previous work has generally not compared activity associated with specific relations. The work of Goodwin et al. (2012) does suggest that we may find differential neural activity in parietal areas; however, their data acquisition was through single cell recording and relied on temporal differences, so these detailed techniques may not translate to similar findings in our study which used more holistic analyses and a different neural recording technique, magnetoencephalography (MEG).

Behaviorally, there is no difference in the performance of *above–below* judgments from *left–right* for human adults in a simple relational task (Hayward and Tarr 1995). Therefore, to capitalize on establishing differential neural activity in our study without the confound of differential performance, we used a simple spatial relational reasoning task. Furthermore, to make phylogenetic and developmental comparisons possible, we applied the same relational task that we developed for children (see Scott et al. 2015b), which was based on Goodwin et al.'s (2012) task used with monkeys. Therefore, our task required adults to encode the relation of a dot to a line, remember the relation for 3 s and then respond by reporting the relation via a button press. While adults performed the task, their neural activity was recorded using MEG.

In this study, we make four major comparisons. The first concerns the neural activity associated with two sets of spatial relations (*above–below* vs. *left–right*). Our broad prediction is that these relational planes require different levels of neural activity despite a lack of matching differential results in performance (i.e., adults should perform a simple relational task perfectly). Specifically, we expect to find areas of the brain that are differentially activated for one set of relations compared to the other set. Since few studies have explored a similar line of inquiry, we do not make predictions regarding specific areas of differential neural activity. We do, however, draw parallels to similar work when possible and align our results with previous findings. Our second comparison comprises congruent to incongruent—where the relative position of something does not match its global position—trials. Two common tasks that have been used to test congruency effects are the spatial Stroop (MacLeod 1991) and Simon (1969) tasks. Again, we align our results with previous findings regarding these congruency tasks. The third comparison concerns whether similar neural areas are used in making congruency and relational plane judgments. In this case, it may be that the relative relationship objects share in the *left–right* direction sometimes mismatches with the viewer's own egocentric frame of reference (Li and Gleitman 2002) and additional processing is necessary to overcome an initial judgment [e.g., change the frame of reference to map onto the object(s) to be judged] such that an incongruency exists in making the correct categorization. Therefore, we might find that similar neural areas are differentially activated in a congruent-incongruent comparison as for a spatial relational set comparison. Finally, one last comparison we draw is between the encoding and working memory (or maintenance) phases of the task. In the encoding phase, the stimulus is presented for 1 s. It is at this point in the trial when categorization should occur and there may be differential activation of attentional networks, such as the *dorsal attention network* or the *orienting network* (Pozuelos et al. 2014). In the working memory phase, the participant must maintain the spatial relation for 3 s before they are able to respond. It is during this point in the trial where we should see visuospatial working memory network activity. However, we expect to find continued (differential) activity in key brain areas that are the most responsible for one set of contrasts (e.g., *above–below* or congruent) over the other (e.g., *left–right* or incongruent).

Materials and methods

Participants

Twelve right-handed adults (age 27 ± 5 years, mean ± SD; 4 women and 8 men) participated in this study as paid volunteers. The Montreal Cognitive Assessment (MoCA) was administered to each participant to ensure they had normal cognitive functions; participants had an average score of 28 ± 1.6, out of 30 maximum. Handedness was assessed by the Edinburgh Inventory (Oldfield 1971); the average score was 85 ± 15.

Task design

Participants performed the same computerized nonverbal task used in our previous study (Scott et al. 2015a, b). In this study, a trial progressed as a series of three screens, followed by 1 s of empty black screen: (1) the stimulus appeared against a black background for 1 s ("stimulus encoding phase"), (2) replaced by static white noise for 3 s ("working memory phase") and (3) replaced by a response screen ("response phase") that disappeared after a response was given or after 5 s had passed (Fig. 1). The response screen comprised a single orange line against a black background where the line bisected the entire screen in the same direction as the line that had bisected the circle earlier in the trial. Responses were provided via a button box onto which the relations were directly mapped (i.e., right button = *right*, top button = *above*). No training was provided. Participants received only verbal instructions and received no feedback on any trial to avoid eliciting an experimentally irrelevant neural response. Responses were provided on every trial.

Equipment and experimental set-up

Participants performed the nonverbal task, while their neural activity was recorded using a 248-channel axial gradiometer MEG system (Magnes 3600WH, 4-D Neuroimaging, San Diego, CA). The MEG instrument was located in a shielded room to eliminate electromagnetic and environmental noise. Participants lay supine on a bed with their head inserted into the cryogenic helmet-shaped dewar which housed the 248 sensors. The MEG signal was sampled at 1017.25 Hz (band-filtered between 0 and 400 Hz). Environmental noise was eliminated using the manufacturer's proprietary software.

During trial presentation, the images were projected into the MEG room via a projector and periscope mirror system onto a screen that subtended approximately 10° of visual angle. The screen was positioned 62 cm in front of the participant. The button box was placed on participants' right sides, since all were right-handed. Participants were instructed to use only their pointer finger for pressing buttons. Finally, participants' eye positions were tracked using a nonmagnetic eye tracking system (RK-726PCI Pupil/Corneal Reflection Tracking System, model ETL-400, ISCAN, Inc., Burlington, MA). The system captured pupil/corneal reflection using a video feed (sampled at 60 Hz). Eye positions were calibrated before and after the experimental task.

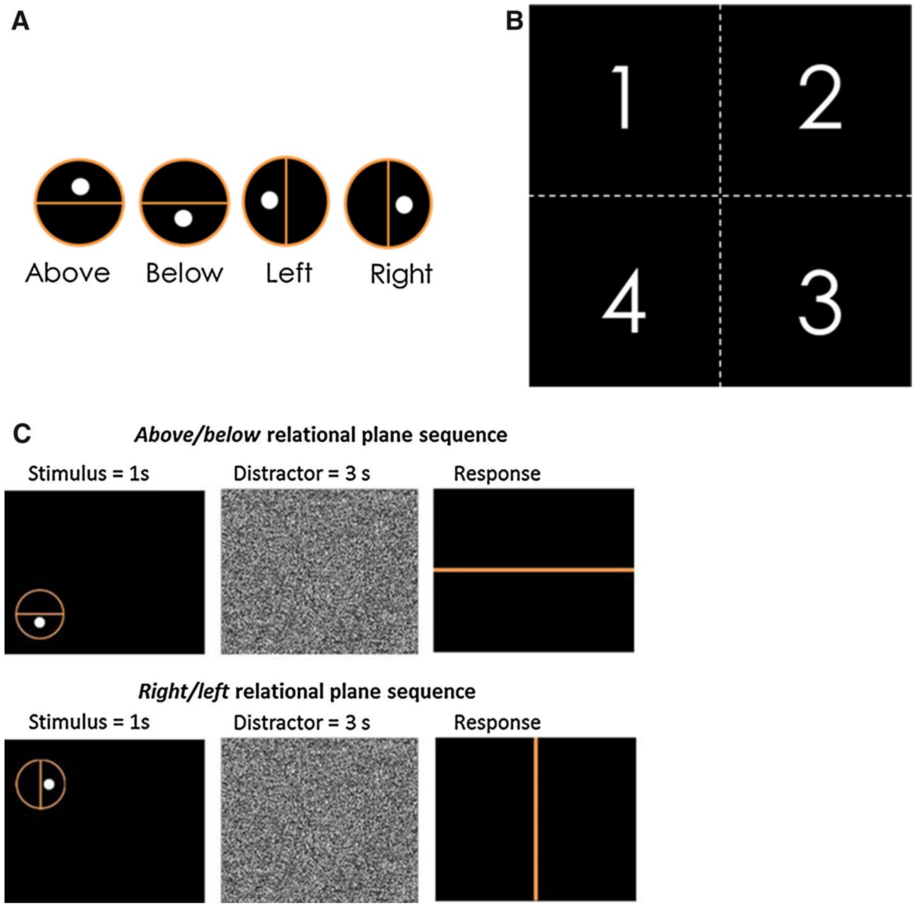

Fig. 1 Illustration of task. **a** Example of each of four spatial relation stimuli. **b** Each stimuli appeared in each subquadrant three times. **c** Progression of two trials: the *upper panel* illustrates a below congruent trial, and the *lower panel* illustrates a right incongruent trial (*NB*: this drawing is not to scale and does not reflect the actual stimulus size with respect to the computer screen). A portion of this figure was originally published in Scott et al. (2015b)

Data analysis

Task phase analysis

We analyzed neural activity recorded in the first two phases of the task (encoding phase and working memory phase—see above). To remove possible effects of the specific location of the stimulus and eye position in a trial, we performed a multiple linear regression where the MEG signal was the dependent variable and the *x*–*y* stimulus screen coordinates and the *x*–*y* eye position values were the independent variables. The residuals from that model were then averaged per task phase (for each individual separately to avoid pseudoreplication) and provided the stimulus- and eye-adjusted MEG signal values that were used in the following analyses of task effects.

Relations of neural activity to task parameters

The main objective of this study was to assess the relations of neural activity to two sets of spatial relations (i.e., relational planes) as well as to incongruency (as compared to congruency). We used the same statistical analyses to assess both effects. Specifically, we performed a univariate analysis of variance (ANOVA) for each MEG sensor for each trial, where MEG signal for the sensor was the dependent variable and the fixed factors (main effects) included the relational plane and congruency, each at two levels. This yielded two sets of comparisons, namely (1) differential activity for the *left–right* versus the *above–below* trials and (2) differential activity for congruent versus incongruent trials. In addition, subjects were included as random factors. Interactions were not included in the model as they are difficult to interpret.

Localization of neural activity

The low-frequency, sustained activity of interest in this study does not lend itself well to source reconstruction techniques, but the region of sensitivity for the gradiometer coil used here is substantially more compact than for magnetometer MEG coils or for EEG leads. To localize the neural source for MEG sensors that indicated differential activation, we recreated sensor space over the cortical space of a representative cortical surface reconstruction and noted the cortical area that each gradiometer coil was pointed toward. Our recording method primarily records only from the cortical surface and not from deeper structures. We used the

BESA/Brain Voyager package for the cortical surface reconstruction and to overlay sensor locations on that image and then rotated the brain/sensor space for each sensor to obtain a viewpoint that aligned the sensor with the neural area over which it was positioned, eliminating parallax error. There is a small region of maximum sensitivity for each gradiometer coil, around the identified cortical location for that coil. We report both the probable sulci and gyri over which the sensor was pointed. In this way, we could report the general area of the brain from which the neural signal originated, with the caveat that these are approximations. We used Damasio's (2005) brain atlas to identify the indicated brain areas.

Assessment of activity during the encoding phase

In this analysis, we evaluated the extent to which neural activity during the encoding phase rose above its standard error (determined across trials, after possible effects of eye position and stimulus position on the screen had been accounted for, as described in the section on *Task phase analysis* above). For that purpose, we calculated a signal-to-noise ratio (SNR) by dividing the mean by its standard error. Typically, a SNR > 2 would indicate the presence of appreciable activity above zero, i.e., the presence of an effect at the encoding phase.

Results

Behavioral performance

All participants performed the task without any errors. There was no significant advantage in reaction time for either relational plane (one-way ANOVA: $F_{1,574} = 2.13$, $p = .15$) or congruency type (one-way ANOVA: $F_{1,574} = .40$, $p = .53$).

Neural activity contrasts

F values taken from the univariate ANOVAs of each sensor were used to plot the comparison results in MATLAB. *F* values for relational plane effects and congruency effects are plotted as heatmaps in Figs. 2 and 3, respectively. Each heatmap is scaled to an overall maximum *F* value. Significance was set to $p < .05$, uncorrected for multiple comparisons since each comparison was planned. See Table 1 for the implicated brain areas and their associated significant F values as well as which condition has more positive values (with respect to valence from expected baseline activity—however, it should be noted that *more positive* value does not equate to *greater* activity level).

Relational plane effects: *above–below* versus *left–right* trials

For the encoding phase (Fig. 2, left panel), differential neural activity was found around the areas of the right cerebellum, right superior temporal gyrus and left temporal–parietal–occipital junction areas, particularly between the left superior temporal sulcus, anterior occipital sulcus and transverse occipital sulcus. For the working memory phase (Fig. 2, right panel), differential neural activity was found in 7 of the 9 areas above, notably the inferior parietal areas, right superior temporal areas, right cerebellum and along the left temporo-occipital junctions. Additional areas of differential activity during the working memory

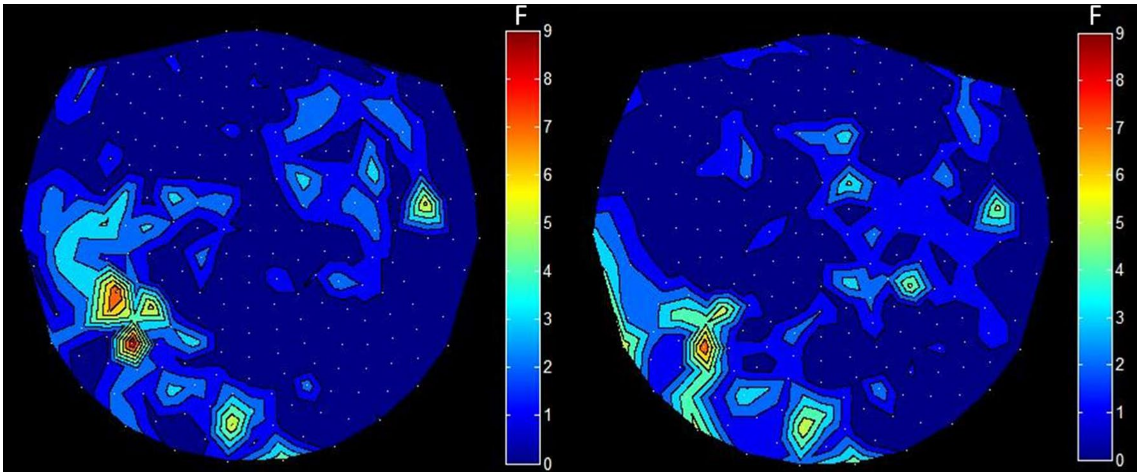

Fig. 2 *Above–below* trials versus *left–right* trials. Heatmap of *F* values representing differential neural activity for encoding (*left panel*) and working memory (*right panel*) phases of trials. The *top* of the figure is the front of the head; the *left* and *right sides* are the left and right sides of the brain, respectively

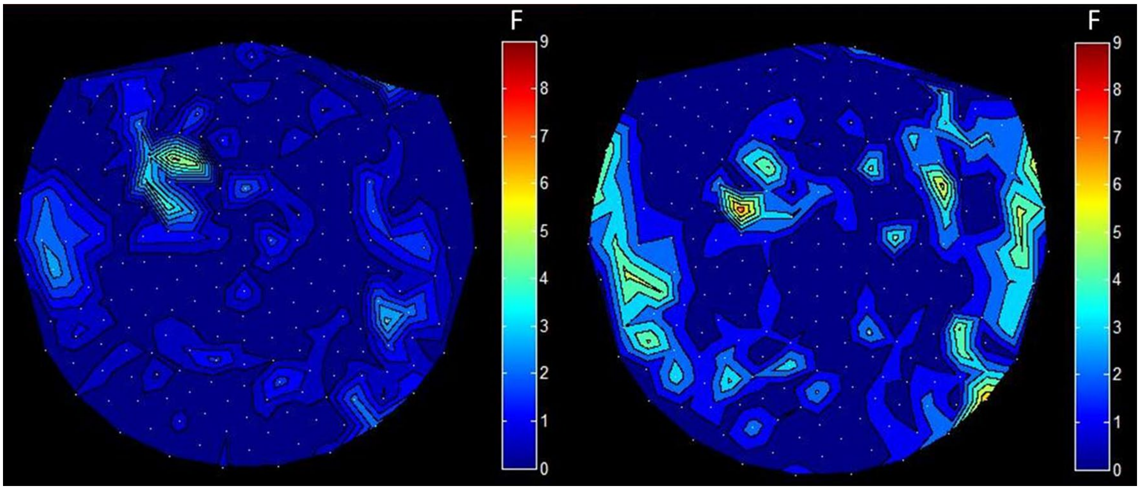

Fig. 3 Congruent versus incongruent trials. Heatmap of *F* values representing differential neural activity for encoding (*left panel*) and working memory (*right panel*) phases of trials. The *top* of the figure is the front of the head; the *left* and *right sides* are the left and right sides of the brain, respectively

phase included left inferior temporo-occipital areas, right superior frontal areas, and an area of the right parietal lobe. Unlike congruency contrasts, the strength of differences was slightly higher for the encoding phase than the working memory phase. In terms of which condition had the more positive values compared to expected baseline activity, *above–below* judgments were exclusively in left brain areas, whereas more positive values for *left–right* judgments compared to *above–below* were largely limited to right brain areas with the exception of the right cerebellum. This was true for both the encoding and working memory phases.

Congruency effects: congruent versus incongruent trials

For the encoding phase (Fig. 3, left panel), differential neural activity was found exclusively on the left side of the brain in two areas of the frontal lobe and one area of the parietal lobe. The frontal areas included precentral sulcus, over the most posterior areas of the middle frontal gyrus and possibly the most posterior and inferior portion of the superior frontal gyrus. This likely is premotor cortex. In the parietal lobe, the area involved was the supramarginal gyrus. For the working memory phase (Fig. 3, right panel), differential neural activity was mostly bilateral (but not symmetrical) and spread across similar frontal areas, inferior and posterior temporal areas, near the temporal–parietal–occipital junctions, and cerebellum. Two of the three areas above implicated in the encoding phase were also involved during the working memory phase. In terms of which condition had the more positive values compared to expected baseline activity, congruent judgments were more positive than incongruent trials in all (left brain) areas for the encoding phase of the task. On the other hand, for the working memory phase, incongruent judgments were almost exclusively more positive for left brain areas, whereas congruent judgments were almost exclusively more positive in right brain areas.

SNR analysis of neural activity during the encoding phase

This analysis showed the greatest SNR in posterior and left-lateralized areas. Specifically, for the congruent trials, the largest SNRs were observed in the middle and superior temporal areas. For the incongruent trials, the largest SNRs occurred in the superior temporal and inferior parietal areas. While the *above–below* trials indicated little variation in activity across the brain, the *left–right* trials had strong effects in the superior temporal and inferior parietal areas.

The SNR for each sensor was plotted using MATLAB. Effects for each condition (*above–below*, *left–right*, congruent trials, incongruent trials) are plotted as heatmaps in Fig. 4. Each heatmap is scaled to an overall maximum value of 5.

Discussion

This study is the first to implicate differential neural activity for two sets of spatial relations. We also observed differential activity for congruent trials compared to incongruent trials. Some of the implicated brain regions for the two contrasts overlapped, although the precise sensor

Table 1 List of probable brain areas involved in contrasts

Contrast	Task phase	Sensor	Region	*F* value	Direction
Above–below versus left–right	Encoding	130	Left superior temporal sulcus; middle or superior temporal gyrus	4.1*	AB > RL
		132	Left superior temporal sulcus; inferior parietal lobule or lateral occipital area	8.1***	AB > RL
	Encoding and WM	101	Left transverse occipital sulcus/lateral occipital sulcus; angular gyrus	6.4*/5.7*	AB > RL
		133	Left transverse occipital sulcus; angular gyrus or superior occipital	4.2*/4.9*	AB > RL
		160	Left angular gyrus	7.1**/4.7*	AB > RL
		161	Left lateral occipital sulcus; lateral occipital gyrus	9.2***/8.0***	AB > RL
		172	Right superior temporal gyrus	6.3*/5.4*	AB < RL
		203	Left calcarine fissure; occipital pole	6.1*/5.9*	AB > RL
		239	Right cerebellum	4.9*/4.8*	AB > RL
	WM	16	Right middle frontal sulcus/longitudinal fissure; superior frontal gyrus	4.2*	AB < RL
		79	Right inferior parietal sulcus; inferior parietal lobule or temporo-occipito-parietal junction	5.3*	AB < RL
		183	Left calcarine fissure	4.9*	AB > RL
		186	Left or right lateral fissure	4.3*	AB > RL
		214	Left cerebellum	3.9*	AB > RL
		217	Left cerebellum	4.7*	AB > RL
		234	Left cerebellum	5.7*	AB > RL
		236	Left cerebellum	5.3*	AB > RL
Congruent versus incongruent	Encoding	41	Left precentral sulcus; middle frontal gyrus or precentral gyrus	5.1*	C > I
	Encoding and WM	22	Left precentral sulcus; middle or superior frontal gyrus	4.8*/5.1*	C > I
		43	Left postcentral sulcus; supramarginal gyrus	3.9*/7.7**	C > I
	WM	34	Right mid frontal sulcus or superior frontal sulcus; superior frontal gyrus	4.4*	C > I
		54	Right central sulcus; postcentral gyrus	4.5*	C > I
		114	Right central sulcus; precentral gyrus	6.4*	C > I
		148	Right inferior frontal gyrus	4.1*	C > I
		159	Left angular gyrus	5.0*	C < I
		162	Left transverse occipital sulcus; lateral occipital gyrus	4.2*	C < I
		169	Right lateral occipital sulcus/anterior occipital sulcus; temporo-occipital junction	5.1*	C > I
		180	Left inferior temporal gyrus	5.3*	C < I
		190	Right anterior occipital sulcus; lateral occipital gyrus or temporo-occipital junction	4.7*	C > I
		198	Left inferior temporal gyrus or fusiform gyrus	4.3*	C < I
		199	Left lateral occipital gyrus	5.2*	C < I
		209	Right inferior temporal gyrus or fusiform gyrus	5.0*	C > I
		210	Right inferior temporal sulcus; inferior temporal gyrus	5.5*	C > I
		225	Right cerebellum	3.9*	C > I
		231	Left lateral temporo-occipital sulcus; inferior temporal gyrus or temporo-occipital gyrus	4.9*	C < I
		232	Left lateral temporo-occipital sulcus; temporo-occipital gyrus or inferior temporal gyrus	5.6*	C < I
		242	Right cerebellum	7.0**	C > I
		246	Right inferior temporal gyrus	5.8*	C > I

This list is divided by task phase: encoding or working memory (WM). Cases where a brain region was involved in both phases are listed together on a single line and both *F* values are provided. Sensors which indicated significantly different activity between contrasts are included, as is the degree of significance

* $p < .05$; ** $p < .01$; *** $p < .005$

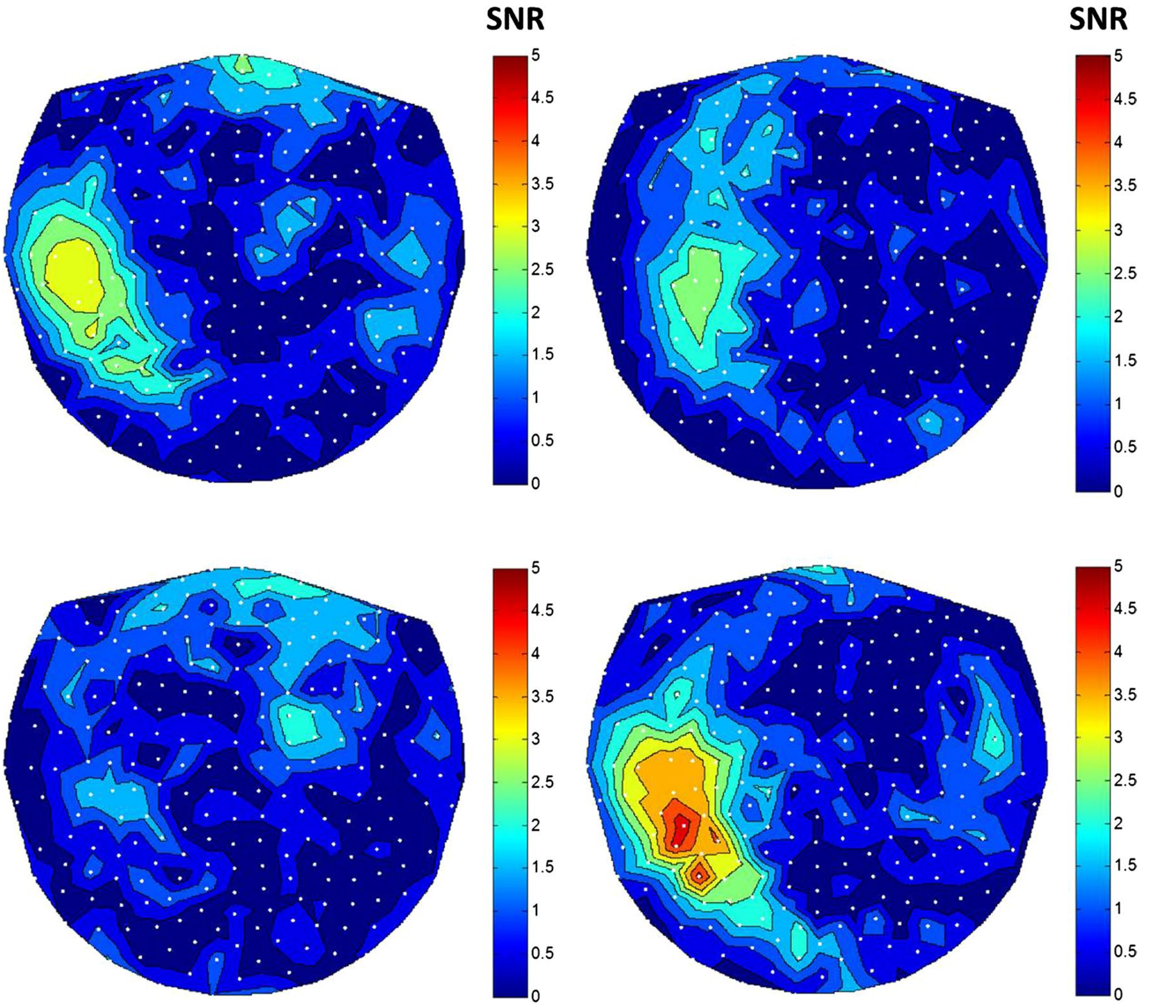

Fig. 4 Heatmap of SNR for each of four conditions: above–below trials (*bottom panel*, *left*), and left–right trials (*bottom panel*, *right*), congruent (*top panel*, *left*) and incongruent trials (*top panel*, *right*). Only the encoding phase was analyzed. The *top* of the figure is the front of the head; the *left* and *right sides* are the left and right sides of the brain, respectively

which indicated differential activity differed, thereby suggesting that the precise neural sources were likely different. For each contrast, most of the neural areas consistently showed differential activity across both the encoding and working memory phases of trials, strongly suggesting that these areas are especially important for making those judgments (i.e., relational plane or congruency). Overall, it was a rule rather than exception that the working memory phase included an expanded area of differential activity compared to the encoding phase. We use caution when assigning function to cortical areas since there is a rarely a one-to-one mapping (Price and Friston 2005), but would nevertheless expect to see differential neural activity if these areas were involved in the cognitive systems tapped for our task. It should be noted that from our results we cannot point to directionality in terms of which set of relations (or congruency type) drove the observed differences or in terms of neural activation versus deactivation. However, we can speak to whether these differences are due to separate cognitive systems or changes in activation within a single system based on our SNR analysis. Despite these small caveats, we can make a number of coherent conclusions, and align these to the current literature.

Relational plane contrasts

The two sets of spatial relations we examined have distinct neural signatures. This contrast indicated differential activity mostly over left occipital–parietal–temporal junction areas and cerebellar areas. Additional areas included parts of the right superior temporal gyrus, right frontal gyrus and right cerebellum. Left brain areas were exclusively in the direction of more positive values for *above–below* than for *left–right* judgments, whereas right areas were largely in the direction of *left–right* judgments having more positive residuals than *above–below* judgments (with the exception of the right cerebellum). However, *above–below* values were, for the most part, not greatly divergent from an expected baseline of activity, whereas *left–right* judgments engaged the left temporo-parieto-occipital junctions to a large degree. Together, these results suggest that these areas are central to the neural representation of these relations.

The importance of left inferior parietal lobule in categorical relations, generally, is supported in the literature (Amorapanth et al. 2009; Damasio et al. 2001; Franciotti et al. 2013), although we are the first to show that this area is differentially activated for different sets of spatial relations. Furthermore, our findings support the results of Damasio et al. (2001) for the importance of right inferior parietal lobule (in their study, the supramarginal gyrus) in spatial relational judgments. However, in our study the differential activity was due to working memory processes, whereas in their study it was due to differences from naming spatial relations using abstract shapes and naming spatial relations using implements. This suggests that our participants may have been accessing labels in this phase of the trial or otherwise doing something similar to Damasio et al.'s participants. Furthermore, Damasio et al. (2001) found neural activity specific to spatial relations in left frontal operculum, left posterior middle frontal gyrus, and left inferior temporal cortex (when subtracting the control condition from the spatial relations condition), left inferior temporal cortex (when subtracting activity from naming spatial relations using abstract shapes from naming spatial relations using tools/utensils), and left supramarginal gyrus (when subtracting the naming of implements from the naming spatial relations)—that we found differential activity in only a few of these areas suggests that only certain components of a *spatial relation* system are activated differentially for the different planes. We did not, however, match previous findings of left superior parietal activity or left posterior frontal (Amorapanth et al. 2009; Damasio et al. 2001) or middle frontal activity (Franciotti et al. 2013), although we found minimal difference in right frontal activity.

In comparison with other studies, it has been suggested that the right superior temporal gyrus (STG) subserves spatial awareness and encoding (Karnath et al. 2005) as well as shifting attention (Yantis and Serences 2003), while the left STG contributes to language processing: any of these attributes could explain why STG was differentially activated in our study, but future investigations are needed to address this issue. Differential activation of left temporal–parietal areas could be explained by increased activity for *left–right* judgments compared to *above–below* since this area (the angular gyrus, specifically) has been implicated in *left–right* confusion (Gerstmann 1940; Hirnstein et al. 2009). This finding may be due specifically to *left–right* incongruent trials if these trial types required additional processing that *above–below* incongruent and *left–right* congruent trials did not require, possibly due to automaticity of those other judgments. Our parietal findings are in accord with those of Goodwin et al. (2012), which indicated stronger neural activity for one set of relations over the other. Their results (Goodwin et al. 2012) pointed to stronger activity for *left–right* judgments—the spatial relations learned first for two monkeys—than for *above–below* judgments. However, Goodwin and colleagues also reported differential activity in prefrontal areas: areas which we did not find any differential activity. In fact, prefrontal areas were not implicated in either of our contrasts. Further work needs to be conducted to ensure these differences in neural activity cannot be attributed to differential linguistic processing (e.g., retrieving the relational labels more quickly for one relational set or not at all for the other set).

Left-lateralized specialization for categorical spatial relations (and right lateralization for coordinate spatial relations) appears to be well supported in the literature (Amorapanth et al. 2009; Baciu et al. 1999; Kosslyn et al.1998; Niebauer 2001; Slotnick et al. 2001). For example, in an MEG study by Franciotti et al. (2013) left inferior parietal lobule appeared to be particularly important for categorical judgments, while right inferior parietal lobule was differentially activated within coordinate judgments. Furthermore, a study by Amorapanth et al. (2009) suggested greater activity in superior and inferior parietal cortices (especially on the left) and posterior middle frontal cortices bilaterally when participants were asked to attend to the categorical spatial relations compared with the identity of objects; they verified the left lateralization of categorical relations with a lesion study. We similarly found a leftward bias in differential neural activity for our categorical judgment task. In comparing the divergence of activity levels for *above–below* and *left–right* judgments, it appears that the significant differences in activity levels can be attributed to *left–right* judgments. Our finding that *above–below* judgments were associated with more positive residuals in the left hemisphere and that *left–right* judgments were associated with more positive residuals in the right hemisphere lends further support to the idea of differential hemispheric involvement for different spatial relations.

An effect of the order of label acquisition?

Previous work has suggested an order of acquisition effect on neural activity. For example, Fiebach et al. (2003) found differential activity in the lateral inferior prefrontal cortex and precuneus for later-learned and earlier-learned words, respectively. Recall that Goodwin et al. (2012) found differential activity for *above–below* compared to *left–right* judgments in two monkeys and that children learn the labels for *above–below* before they learn the labels for *left–right*. Furthermore, some researchers have suggested that language acquisition begins in the right hemisphere earlier in life, but shifts to the left hemisphere such that early-learned words continue to be processed later in life predominately by the right hemisphere while later-learned words are processed by the left hemisphere (Bowers et al. 2013). In fact, the right hemisphere has been implicated in certain cases of recovering from aphasia, although only for certain types of lesions (Anglade et al. 2014). Our finding of hemispheric differences in direction of residual values may add to this story; however, additional research with comparisons of level of activity compared to baseline activity is necessary before strong conclusions may be drawn. Overall, it appears our findings support a developmental (or order of acquisition) story rather than a phylogenetic one for *left–right* confusion. Although there may not be anything inherently difficult about *left–right*, there may be an inherited bias toward better performance on earlier-learned items than later-learned ones. However, it cannot be discounted that *left–right* judgments require choosing and applying the correct frame of reference, while *above–below* judgments do not and this added effort may contribute to human performance bias as much as an order of acquisition effect: such a distinction needs to be explored further in future efforts.

Congruency contrasts

The congruency contrast implicated areas that have been previously shown to be involved in overcoming incongruencies as well as areas associated with motor planning and visual spatial working memory. Areas previously indicated for overcoming incongruency—as tested by Simon and spatial Stroop tasks—include supplementary motor area, visual association areas, inferior temporal cortex, inferior parietal areas and inferior frontal areas (Peterson et al. 2002). However, one study investigating neural areas activated by the Simon task indicated similar, but adjacent areas: presupplementary motor area, superior parietal lobule and cuneus (Wittfoth et al. 2006). Although we did not find differential activity in all the areas implicated in previous studies, we did find overlap in most of these (cortical) areas. Furthermore, the areas implicated in our study have been linked to object-based and perspective-based transformations, including the areas in occipital, temporal, parietal and posterior frontal cortices, and a substantial portion of the cerebellum (Zacks and Michelon 2005), which may be important in adjusting category assignment.

For the encoding phase of the task, specifically, premotor areas were differentially activated which suggests that some motor planning was affected more for one congruency type than the other. According to the change in activity analyses, congruent trials appear to have elicited little activity away from the expected (random) activity level, while incongruent trials had a much larger activity SNR; therefore, it appears that the incongruent trials drove the substantial differences in these areas. It is interesting to note that although congruent trials had more positive values with respect to baseline activity compared to incongruent trials during the encoding phase, this relationship switched during the working memory phase but only for the areas additionally activated: the areas implicated in the encoding phase continued to show more positive values for congruent judgments.

The additional neural areas activated in the working memory phase including bilateral temporo-occipital areas as well as the right cerebellum and parts of the right superior frontal gyrus and left angular gyrus. Bilateral temporo-occipital areas, including fusiform and inferior temporal gyri, have been implicated in survey encoding (Shelton and Gabrieli 2002), topographical memory (Corkin 2002) and object processing (Damasio et al. 2001): it may be that incongruent trials necessitate these kinds of additional processing (or strategies) in order to make the correct judgment, whereas congruent trials are processed and remembered automatically and without further processing. Both the left supramarginal and left angular gyri have been implicated in *left–right* confusion (Gerstmann 1940; Hirnstein et al. 2009), but it is not clear whether *left–right* incongruent judgments are driving this result considering these same neural areas also showed differential activity in the relational plane contrast. Finally, superior frontal sulcus, which divides the middle and superior frontal gyri, is associated with working memory (Klingberg et al. 2002), and although the same sensors were not implicated in both contrasts (relational plane and congruency), these sensors were adjacent to each other suggesting that a similar function may have been performed in each condition.

Overlap in congruency and relational plane contrasts?

In comparing the neural activity contrasts, our analyses of the degree of change from expected baseline activity suggests that similar neural areas may be tapped by left–right judgments as for congruent and incongruent trials; specifically, temporal and inferior parietal areas. However, the extent to which these “overlapping” areas are driven exclusively by left–right judgments is yet to be determined considering that the two congruency conditions include left–right judgments (i.e., if *left–right* judgments are sufficiently valenced, then *above–below* trials would simply diminish the strength of the signal, which could be what we are seeing in Fig. 4). One reason to make such a comparison is that similar areas of differential activity would be expected if symmetry was a factor in left–right confusion (Brandt and Mackavey 1981; however, see Sholl and Egeth 1981 for opposing behavioral evidence). At this point, we cannot conclude that there is significant overlap in cognitive resources for making relational plane and congruency judgments, since the results could be driven exclusively by *left–right* judgments as both *above–below* and *left–right* judgments are included in these analyses and since the congruent and incongruent trials had similar levels of associated activity. Further research should be conducted in response to this possibility.

If there is no true overlap in *left–right*, congruent and incongruent judgments, then this could be due to a lack of complex stimuli in our study: our stimuli were simple and did not have (biologically) relevant axes onto which a canonical top could be assigned or front–back could be distinguished. Future work should consider if similar differences are found for oriented faces, bodies or other biologically relevant stimuli. One proposition regarding why *left–right* relations are confused is that symmetry tends to occur across the *horizontal* direction rather than the *vertical* direction, especially in nature, and the human visual system is adapted to detect *left–right* symmetry (Brandt and Mackavey 1981). This theory rests on the explanation that asymmetry in neural functioning (hemispheric specialization) provides better discrimination ability (in Brandt and Mackavey 1981; Mach 1959; Corballis and Beale 1970). It should be the case, then, that *left–right* reasoning may tap into the same neural areas used in reasoning about incongruencies; however, we did not find this in our study.

Overlap of encoding and working memory phases

Our finding of a consistency in differential activity across encoding and working memory phases indicates neural areas that are imperative for representing one condition over the other. For the congruency contrast, one of the left premotor areas and an area of the left supramarginal gyrus were consistently differentially activated. Similarly for the dimension contrast, nearly all the areas differentially activated in the encoding phase were also differentially activated in the working memory phase. These areas, in particular, should be further examined in future work that is focused on congruency (perhaps as it relates to relational complexity) or spatial relations.

In looking at those areas that were only implicated in either the encoding or the working memory phase, it may be that different attentional networks are activated for the two contrasts. For example, one such network is the *dorsal attention network* which is thought to be responsible for focusing attention on a task via top-down processing and consists of bilateral intraparietal sulcus and frontal eye fields (Farrant and Uddin 2015). Another is the orienting network which comprises the superior parietal cortex, temporoparietal junction and frontal eye fields (Pozuelos et al. 2014). Although we did not find differential activity that could be attributed to attentional network activation, we did find activation of a portion of a general visuo-spatial working memory network during the working memory phase, which consisted of bilateral visual association cortex (Ruff et al. 2003). Future work will focus on parsing the working memory phase into smaller timespans (i.e., dividing the working memory phase into three equal time bins) since previous work has suggested that different cognitive processes within working memory follow specific and often short-lived timeframes (Wang et al. 2015). Therefore, the extent to which encoding and working memory phases truly overlap must be further explored.

No prefrontral cortex contribution?

Many studies of relational reasoning have focused on the connections between prefrontal cortex (PFC) and parietal areas, and these fronto-parietal connections are well documented and central to spatial encoding in both humans (Krawczyk 2012; Wendelken et al. 2015) and monkeys (Chafee et al. 2007; Goodwin et al. 2012). Our current analysis did not concentrate specifically on these connections or their temporal coordination as previous studies have done, but we will investigate these in future analyses. In terms of localization, prefrontal areas were not differentially involved in either of our experimental contrasts even though parietal areas were activated. There also did not appear to be activity outside the baseline in prefrontal areas.

Left PFC has been regarded as an important center for judgments of relational complexity (fronto-polar cortex; Bunge et al. 2005), for manipulating self-generated information and integrating the outcomes of two or more cognitive operations (rostrolateral PFC; Christoff et al. 2001; Crone et al. 2009), as well as for evaluating whether relations match (monitoring and manipulating representations held in working memory) and mediating reasoning processes by supporting analogical mappings (dorsolateral PFC; Bunge et al. 2005). The lack of differentiated activity in our study suggests that these cognitive resources were not tapped more for one contrast than for the other; the performance results corroborate this conclusion. In particular, we expected prefrontal activation for incongruent trials; the fact that we did not find differential activity compared to congruent trials suggests either that our task was too easy to tap this cognitive resource, that our participants were not applying a strategy that required PFC participation, or that our analyses could not detect differences (e.g., if differences are only apparent in the temporal information of the neural signals).

Conclusions

Considering our overall findings more generally, and in the context of other studies, our conclusions add to the current literature on relational reasoning. The main contribution is that we offer new evidence of differential neural activity for two sets of spatial relations. Due to our approach, it is unclear whether differences are due to increases or decreases from a baseline of activity, such that one set of relations (or one type of congruency) drove our results; however, we do have evidence, from our SNR analyses, that differences are due to activity within a single system rather than distinct systems, at least for the congruency contrasts. Since *above-below* trials showed little activity above zero, it is possible that these judgments are supported by a separate cognitive system from *right-left* judgments. Further work is needed. In terms of localization of neural signals, fMRI or other neural imaging technique would contribute more precise supporting evidence. Future steps should also include investigating the strength and timeline of connectivity across brain regions. We predict that *left–right* relations likely require increased activity in the indicated areas compared to *above–below* if these relations are truly more difficult (Laeng et al. 2011). Furthermore, to get closer to the answer of whether *left–right* relations are the more difficult relations to judge, a future study should require participants to respond as fast as possible rather than allowing a response delay as in our study: faster response times for *above–below* judgments would be expected if *left–right* judgments are more difficult. The current analysis was the first of its kind, so few a priori hypotheses were formed regarding what neural areas should show differential neural activity. This was largely the case because there were no precedents to suggest differential neural activity for *above–below* versus *left–right* judgments; therefore, further inquiry into this line of questioning and further analyses of the implicated neural areas are worthy of further pursuit.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Human subjects/informed consent The study protocol was approved by the Institutional Review Boards of the Minneapolis VA Medical Center and the University of Minnesota. The study was performed in accordance with the ethical standards outlined in the Declaration of Helsinki. All subjects provided written informed consent prior to participating in the study.

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