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RESEARCH ARTICLE

Impaired distance perception and size constancy following bilateral occipitoparietal damage

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Abstract Accurate distance perception depends on the processing and integration of a variety of monocular and binocular cues. Dorsal stream lesions can impair this process, but details of this neurocognitive relationship remain unclear. Here, we tested a patient with bilateral occipitoparietal damage and severely impaired stereopsis. We addressed four related questions: (1) Can distance and size perception survive limitations in perceiving monocular and binocular cues? (2) Are egocentric (self-referential) and allocentric (object-referential) distance judgments similarly impaired? (3) Are distance measurements equally impaired in peripersonal and extrapersonal space? (4) Are size judgments possible when distance processing is impaired? The results demonstrate that the patient's lesions impaired both her distance and size perception, but not uniformly. Her performance when using an egocentric reference frame was more impaired than her performance when using an allocentric reference frame. Likewise, her distance judgments in peripersonal space were more impaired than those in extrapersonal space. The patient showed partial preservation in size processing of novel objects even when familiar size cues were removed.

Keywords Distance · Depth · Parietal · Stereopsis · Simultanagnosia · Balint's syndrome

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Introduction

A veridical representation of the three-dimensional world requires accurate perception of object distance and object size. Distance perception requires the integration of diverse cues; size perception is determined by size constancy, the scaling of an object's retinal subtense by estimated distance (Emmert 1881). The neural correlates of these processes have long been linked to dorsal stream function. Ninety years ago, Holmes and Horrax reported the case study of a soldier with bilateral parietal lobe lesions who exhibited extensive distance perception deficits (Holmes and Horrax 1919). This patient could not determine the closer of two objects even though he possessed normal visual acuity. He had also lost stereopsis, a binocular distance cue. Additional reports have linked distance perception deficits with dorsal stream damage (Critchley 1953; Holmes 1918; Riddoch 1917). Other reports have related dorsal stream damage to deficits in size constancy (Ferber and Danckert 2006; Rode et al. 2006; Wyke 1960). In such classic neuropsychological reports lesion location is roughly estimated and deficits are based on the bedside clinical evaluations.

More recently, a number of fMRI studies have investigated stereopsis and have identified a number of dorsal stream areas associated with stereopsis, such as retinotopic area V3A and caudal intraparietal sulcus (Backus et al. 2001; Brouwer et al. 2005; Inui et al. 2000; Iwami et al. 2002; Kwee et al. 1999; Naganuma et al. 2005; Neri et al. 2004; Nishida et al. 2001; Rutschmann and Greenlee 2004; Rutschmann et al. 2000; Tsao et al. 2003; see review in Parker and Cumming 2001). However, stereopsis is not the sole cue used to assess object distance. In fact, individuals who have lost the use of one eye and are restricted to monocular cues generally show little impairment in every day situations (reviewed in Steeves et al. 2008).

In the present study, we investigated aspects of distance perception in a single patient with bilateral occipitoparietal damage. This patient suffers from many of the neurological symptoms associated with Balint's syndrome: simultanagnosia, optic ataxia, and distance perception deficits (Balint 1909; Holmes and Horrax 1919; see discussion in Harvey and Milner 1995). Patient EE555 reports misjudging distances, bumping into objects, and accidentally poking people in the face. However, she reports no difficulty estimating object size. The following experiments were motivated by this apparent contradiction: inaccurate distance estimation accompanied by accurate size estimation, and also by the fact that newer research on the parietal lobes provides clues as to which variables that should modulate distance perception. In Part 1, we examined Patient EE555's ability to access several common monocular distance cues. In Part 2, we investigated EE555's ability to estimate distance according to egocentric or allocentric reference frames. In Part 3, we investigated EE555's ability to estimate the size of novel objects.

General methods

Patient EE555

Patient EE555 (female, age 39, 16 years education) experienced three parietal lobe infarcts in the watershed between the posterior and middle cerebral arteries between May and June 2004. MRI revealed symmetrical lesions in lateral inferior parietal regions, extending from the occipital lobe [superior middle occipital gyrus Brodmann areas (BA) 19] through the angular gyrus (BA 39) in and around inferior and middle portions of the IPS. Damage did not encroach into the precuneus or superior parietal lobe; see Fig. 1a. EE555 was tested in several sessions at least 30 months after her last stroke and her condition remains stable.

Table 1 summarizes EE555's behavioral testing. She shows two of the three cardinal symptoms of Balint's syndrome: simultanagnosia and moderate optic ataxia. Simultanagnosia is illustrated by her inability to perceive scenes or to perceive more than one object simultaneously. For example, she demonstrates complete local bias with Navon letters. Optic ataxia is illustrated by her aberrant reaching behavior: she reaches beyond objects with either hand and trawls for them with an open hand.

EE555 has normal visual acuity (20/20) and preserved color and shape perception as determined by ceiling performance on card-matching tasks (e.g., "Find the yellow square"). She has normal object recognition as shown by her ability to name common objects when shown line drawings or photographs. She can visually track slowly moving objects, and can maintain convergence on objects moving towards or away from her in the *z* plane. It is difficult to evaluate EE555's visual fields because she cannot simultaneously fixate centrally and perceive peripheral objects.

We tested stereopsis using the TNO test for stereoscopic vision (Lameris Ootech, Nieuwegein, The Netherlands). EE555 was able to perceive only the first two pre-screening

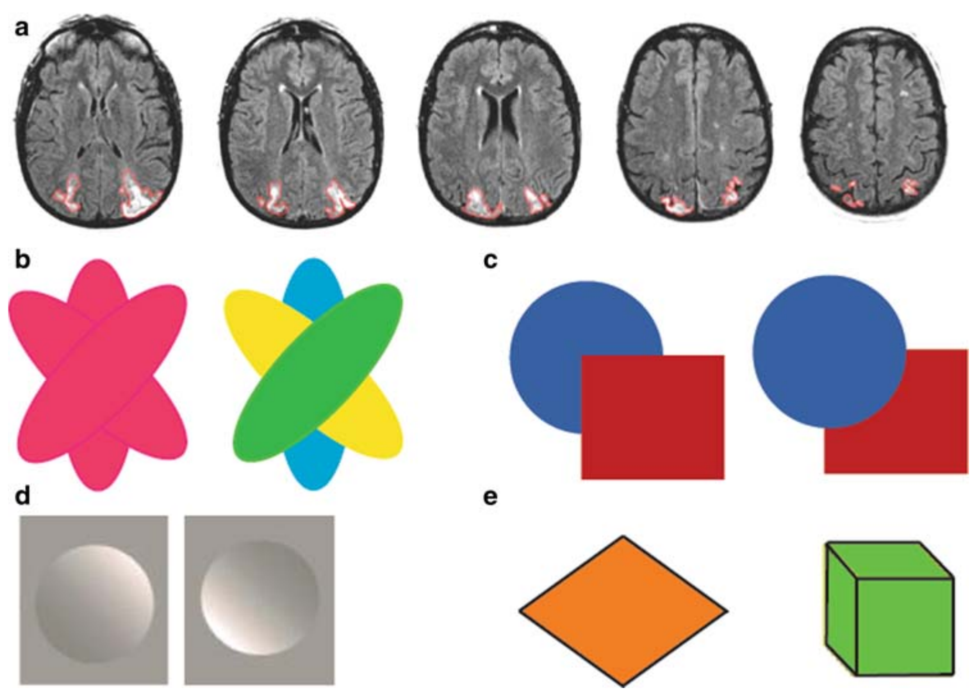

Fig. 1 **a** MRI brain images (T2 FLAIR) of Patient EE555. Hypodensities indicate lesion sites. **b** Example occlusion stimuli. To Patient EE555, the image on the *left* is a '*daisy*', whereas the figure on the *right* is a '*green oval*'. Due to her simultanagnosia, the underlying *yellow* and *blue* ellipses in the *right image* are not perceived. **c** Example stimuli used in Experiment 1. **d** Example stimuli used in Experiment 2. **e** Example of 2-D (*left*) and 3-D (*right*) stimuli used in Experiment 3

Table 1 Summary of Patient EE555's perceptual and motoric symptoms

Test	Performance
Color perception	+
Object identification	+
Sound identification	+
Illusory contour perception (Kanisza)	+
Optic ataxia: reach towards object	–
Optic apraxia	+
Eye movements: horizontal	+
Eye movements: rapid tracking	–
Left-right orientation	+
Up-down orientation	+
Finger identification	–
Scene perception: cookie theft	–
Local/global processing: navon letters	–
Line cancellation	–
Language: Western Aphasia Battery	+

A "+" indicates normal performance, a "–" indicates abnormal performance

images. This finding indicates that her stereopsis is less than 240 s of arc at best.

All experimental protocols were approved by the Internal Review Board of the University of Pennsylvania and Temple University. All participants signed informed consent documents and were compensated for their time.

Part 1: Perception of monocular distance cues

Patients with occipitoparietal damage can experience severely impaired distance perception (Holmes and Horrax 1919). It is not clear to what extent this type of brain damage disrupts perception of monocular distance cues, those cues perceived by a single eye. Our preliminary testing established that stereopsis, a primary binocular cue, is severely impaired in Patient EE555. In Part 1, we assessed Patient EE555's ability to utilize certain monocular distance cues under optimal viewing conditions. Most monocular cues are pictorial in that they are intrinsic to the monocular image and are present in two-dimensional renderings such as photographs. These include: interposition, familiar size, texture, shadow, linear perspective, and relative height. We conducted testing with a subset of these cues and excluded others because they are not relevant to processing near items (e.g., atmospheric haze), or because simultanagnosia made it impossible for Patient EE555 to observe the cue (e.g., the separate lines used to create linear perspective).

Experiment 1: Occlusion

Occlusion is a dominant monocular depth cue. Our preliminary phenomenological observations indicated that EE555's simultanagnosia limited her access to occlusion cues. For example, EE555 described three identical overlapping ellipses as a 'daisy'; see Fig. 1b. In contrast, when the ellipses were different colors, EE555 perceived only the unoccluded ellipse. In order to investigate this further, a series of simple overlapping images were presented.

Ten images of two overlapping geometric shapes (circle, square, triangle, diamond) were constructed and presented using ePrime software on a Dell laptop computer. In each image there was one red and one blue object. The patient was told that there were exactly two objects in each display and was instructed to make a two alternative forced choice judgment indicating which object was in front: red or blue (chance = 50%). In this and all experiments, viewing time was unlimited, responses were unspeeded and normal lighting conditions were used. Stimuli were randomized and each stimulus was presented twice. There were 20 trials.

EE555 provided the correct answer on 75% (15/20) of the trials. These findings show that EE555 has reduced access to occlusion cues.

Experiment 2: Perspective in 2D and 3D shapes

This experiment assessed Patient EE555's ability to integrate linear perspective cues. The task was to name the identity of two- and 3-D shapes. She was shown 20 images of two-dimensional (2-D: e.g., circle, square) and 3-D geometric shapes (e.g., sphere, cube); see Fig. 1c.

The results show that EE555 described all but one shape as 2-D. Cubes and rectangular boxes were described as squares or rectangles; cylinders as circles, and pyramids as triangles. The exception was the sphere, which she accurately identified. Overall, accuracy was 80% for the 2-D shapes (she called two diamonds triangles) and 10% for the 3-D shapes, leading to an overall accuracy level of 45% (9/20). These data suggest that EE555 is impaired at accessing perspective cues.

Experiment 3: Shadow

Circles can appear to be protruding bumps or sunken depressions depending on the position of shadows and shading (Ramachandran 1988), see Fig. 1d. Here, we examined EE555's ability to access shadow and shading cues. EE555 was pseudorandomly presented with 10 protruding and 10 sunken circles. EE555 correctly stated that the protruding circles 'puffed out' 100% of the time (10/10 trials) but incorrectly stated that the sunken circle appeared "flat" rather than sunken 100% of the time (10/10 trials). These data suggest that in addition to difficulty perceiving occlusion and linear perspective cues, she has difficulty interpreting shadow and shading cues. The findings of Part 1 show that EE555 has irregular access to several monocular distance cues.

Part 2: Reference frame and proximity

In Part 2, we asked whether the patient's performance differed as a function of reference frame: egocentric or allocentric. This comparison was prompted by studies suggesting that dissociable neural systems exist for egocentric and allocentric processing. Specifically, neurons in the monkey lateral intraparietal area—an area thought to be homologous to the human angular gyrus—respond to the egocentric distance between an object and a body part, such as the monkey's hand (Genovesio and Ferraina 2004; Sakata et al. 1997). In contrast, damage to the ventral visual stream extending into the medial temporal lobe, causes disproportionate deficits in allocentric spatial memory (Carey et al. 1998; Hartley et al. 2007; Holdstock et al. 1999, 2000; Murphy et al. 1998; but see Shrager et al. 2007). The well-known patient DF, who has bilateral ventral stream lesions, exhibits intact egocentric task performance, but impaired performance when forced to apply an allocentric reference frame (Carey et al. 1998; Carey et al. 2006; Murphy et al. 1998). These reports suggest that temporal lobe structures perform computations essential for processing objects in an allocentric reference frame (Murphy et al. 1998). These findings predict that Patient EE555 would have a greater impairment processing distance in an egocentric reference frame.

In Part 2, we also examined distance perception as a function of peripersonal space (within arm's reach) and extrapersonal space (beyond reaching distance). In humans, peripersonal and extrapersonal space are thought to be processed by separable neural systems: peripersonal space relies on inferior parietal regions including the supramarginal and post-central gyri, whereas extrapersonal space processing is thought to rely on ventral premotor, middle frontal and superior temporal areas (Committeri et al. 2007). Further evidence comes from the neuropsychology literature reporting patients with hemispatial neglect limited to peripersonal space (Berti and Frassinetti 2000; Guariglia and Antonucci 1992), or restricted to extrapersonal space (Bisiach et al. 1986). Given the location of Patient EE555's occipitoparietal lesions, these studies predict that she would show greater deficits in peripersonal space.

Experiment 4: Egocentric distance judgments in the Z plane

Methods

Control subjects: Performance was compared to that of two normal control subjects (both female; 56 and 44 years old; 14 and 12 years of education, respectively).

Stimuli: Two types of stimuli were used (1) an unfamiliar object stimuli, a 5 cm^3 white cube and (2) a familiar object stimuli, a 20-ounce plastic bottle.

Procedure: The experimenter placed one object at one of four possible distances: 6, 12, 24, or 36 in. The task was to verbally estimate the distance of the object. Throughout Part 2, trials with the familiar and unfamiliar objects were randomized, as were the distances and ten measurements for each object at each distance were taken. There were a total of 80 trials.

Analysis: Experiments in Part 2 compared the performance of EE555 with age- and education-matched female control subjects. Because the tasks were trivially easy, control subjects' performance in many cases showed minimal variability, making statistical comparisons using *z* scores impossible. Instead, we report the difference score (DS) between each group estimate and the correct response. We also provide a "spatial index" (SI) that shows judged distances normalized by the correct distance to facilitate comparisons across conditions:

Spatial index (SI) = (performance mean − actual distance)/actual distance.

With this measure, an SI score of 0 reflects perfect performance, distance underestimations fall below 0, and overestimations above 0. The absolute value of the SI indicates the magnitude of distance judgment errors as a proportion of the actual distance being judged. For the purposes of this paper, we consider SI absolute values greater than 0.5 to represent a significant difference. This arbitrary cutoff value provides a conservative assessment of function that allows for considerable measurement errors. For example an SI of 0.5 corresponds to an error of plus or minus 3 in. when the object was placed at 6 in. or an error of 18 in. when the object was placed at 36 in.

Results and discussion

The control subjects estimated the distances of familiar and unfamiliar objects with high accuracy and estimation errors were small (all DS < 1.5 in.); see Fig. 2 and Table 2. Likewise, Patient EE555 accurately estimated the distance of familiar objects (all SI < 0.1). However, she inaccurately estimated the distance of unfamiliar objects. She overestimated the distance of unfamiliar objects by more than 15.0 in. at every location. EE555's SI scores for the unfamiliar object met our criteria for significance at each distance

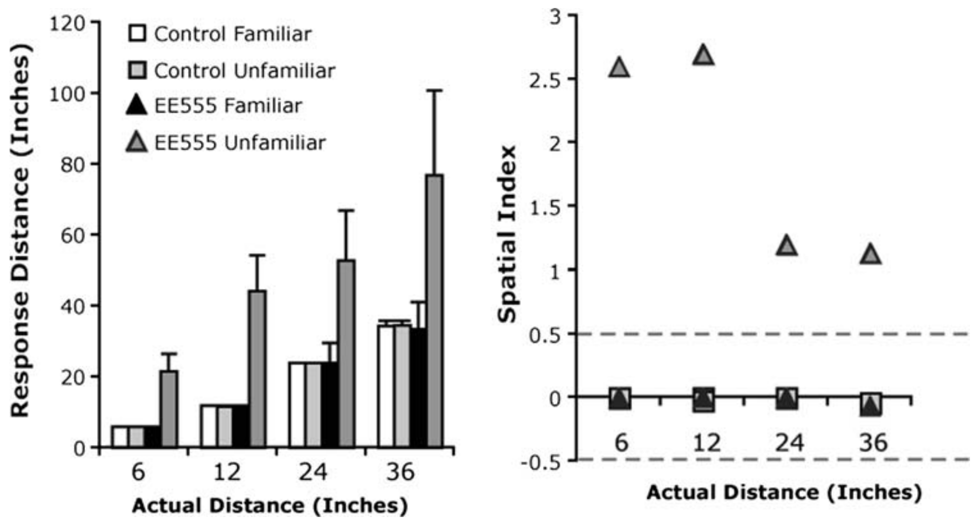

Fig. 2 Results of Experiment 4. *Left*: Estimated distance as a function of actual object placement. *Bars* indicate object distance estimation in inches. The *patient's error bars* reflect the within-subject variance. The *control subjects' error bars* reflect the standard error of the mean. *Right*: The spatial indices (SI) are plotted as a function of actual distance. Performance outside the two *dashed lines* is considered significantly abnormal

Table 2 Summary of performance for Patient EE555 and control subjects for Experiments 4–7

	Familiar object				Unfamiliar object			
	6 in.	12 in.	24 in.	36 in.	6 in.	12 in.	24 in.	36 in.
Exp 4								
EE555	6.0 (0)	12.0 (0)	24.0 (5.7)	33.6 (7.6)	21.6 (5.1)	44.4 (9.9)	52.8 (14.1)	76.8 (24.1)
Control	6.0 (0)	12.0 (0)	24.0 (0)	34.5 (1.5)	6.0 (0)	11.75 (.25)	24.0 (0)	34.7 (1.4)
Exp 5								
EE555	16.6 (4.2)	20.2 (5.9)	27.8 (5.8)	–	19.6 (5.7)	25.2 (4.8)	32.0 (5.4)	–
Control	5.8 (1.1)	12.1 (1.1)	22.7 (.8)	–	5.95 (.9)	13.3 (1.8)	23.1 (.07)	–
Exp 6								
EE555	6.6 (1.6)	12.7 (2.5)	18.9 (3.3)	24.8 (2.7)	9.7 (9.7)	17.7 (5.3)	26.6 (4.6)	36.7 (2.0)
Control	5.7 (.6)	13.2 (.3)	22.4 (.28)	39.7 (3.4)	6.1 (.02)	12.8 (.01)	23.1 (.1)	40.9 (4.1)
Exp 7								
EE555	5.2 (1.8)	8.1 (2.1)	17.5 (4.2)	30.2 (2.5)	6.5 (1.3)	13.8 (3.7)	25.7 (6.1)	37.0 (3.9)
Control	6.6 (.6)	13.0 (1.1)	21.4 (2.0)	34.8 (4.8)	7.2 (.8)	13.1 (.6)	22.7 (.6)	36.3 (3.2)

For each experiment, the mean distance for each group is provided in inches

In parentheses is EE555's standard deviation, and for the controls, the standard error of the mean is given

These values provide an assessment of within-subject variability across tasks

with greater SI values at the closer distances (SI unfamiliar = 2.6, 2.7, 1.2, 1.1). These results demonstrate that EE555 was particularly inaccurate when making egocentric distance judgments for unfamiliar objects and that her performance was worse at closer distances. The present study required verbal distance estimates. In the following studies we asked subjects to place the object at a given distance. Our logic was that if the patient were permitted to use her sense of proprioception, she might achieve normal performance.

Experiment 5. Egocentric object placement in the *Z* plane

Methods

The same subjects, objects and general procedure were repeated from Experiment 4. The primary change was that subjects placed the object at a verbally instructed distance. The second difference was that the 36-inch condition was eliminated because it was beyond the reach of seated subjects.

Results and discussion

The control subjects performed with high accuracy; see Fig. 3 and Table 2. In contrast, Patient EE555 placed the familiar and unfamiliar object beyond the instructed distance across all conditions (DS familiar = 10.6, 8.2, 3.8 in.; DS unfamiliar = 13.6, 13.2, 8.0 in.). The SI scores show that the magnitude of EE555's impairment reached significance at the closer two distances (SI familiar = 1.8, .7; SI unfamiliar = 2.3, 1.1). At the 24-inch distance, her SI score was within the normal range. These findings are consistent

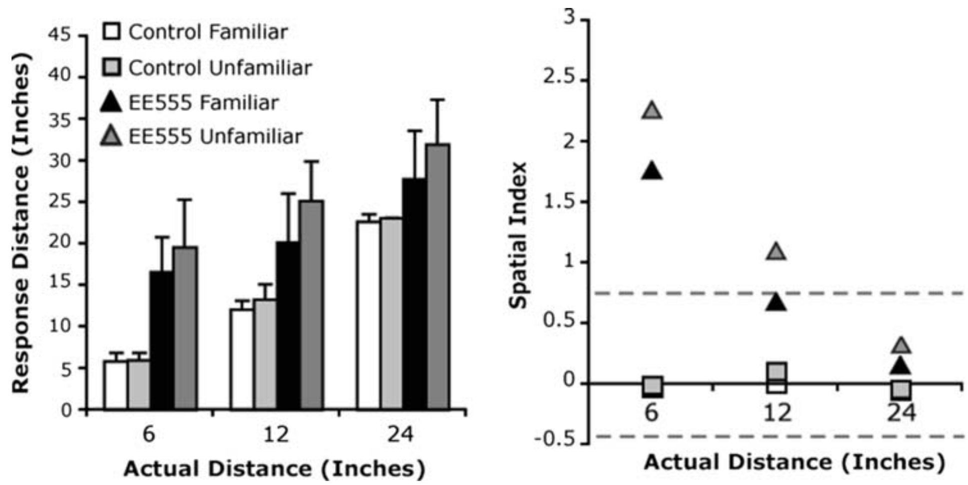

Fig. 3 Results of Experiment 5. *Left*: Object distance placements in an egocentric reference frame. EE555 placed both the familiar and unfamiliar object at greater distances than control subjects. *Error bars* for EE555 represent the standard deviation of her responses; *error bars* for the control subjects represent the standard error of the mean. *Right*: The spatial indices are plotted as a function of actual distance. Performance outside the two *dashed lines* is considered significantly abnormal

with the findings of Experiment 4 in which performance was more impaired at closer distances, but here, her performance was poor for both the familiar and unfamiliar object. These data suggest that the object placement task reduced the benefit of familiar object size, which she could use to estimate distance in Experiment 4. In the next experiment, we tested whether distance estimates were equally impaired when using an allocentric reference frame.

Experiment 6: Allocentric object placement in the *Z* plane

Methods

One previously tested and one new control subject participated (both female; 56, 53 years old; 14, 15 years of education). The procedure was modified from the previous experiment in several respects. Four distances were tested (6-, 12-, 24-, 36- in.). Two objects were used during each trial, either two unfamiliar cubes (5 cm^3) or two familiar plastic bottles. One item served as a reference object placed approximately 8 in. in front of the subject and remained stationary during the trial. Subjects were verbally instructed to place an object a designated distance behind a reference object thereby employing an allocentric reference frame.

Results and discussion

Control subjects performed with high accuracy when placing the object using an allocentric reference frame; see Fig. 3 and Table 2. Patient EE555 performed accurately when placing the familiar object. For the unfamiliar object, she tended to overestimate the placement of objects at the two closer points (6 and 12 in.; SI = 0.6, 0.5) but performed normally when placing objects at the two farther distances (SI < 0.5). These data indicate that the patient was less impaired when using an allocentric reference frame. However, performance at the closest locations remained less accurate than performance at farther locations. These data suggest that allocentric performance in the depth plane remains generally intact.

Whether these findings should generalize to the frontoparallel, or *x*–*y* plane, is unclear. Hemispatial neglect caused by unilateral right parietal damage is frequently associated with deficits in the *x*–*y* plane (reviewed in Mesulam 1999). In contrast there is a report of a patient with bilateral parietal damage performing a reaching task with better performance in the *x*–*y* plane as compared to the depth plane (Baylis and Baylis 2001). For this reason, we investigated allocentric distance performance in the *x*–*y* plane.

Experiment 7: Allocentric object placement in the *x*–*y* plane

Methods

The subjects, stimuli and procedure were identical to those used in Experiment 6. The only difference was that subjects were instructed to place the familiar or unfamiliar object to the right of the reference object in the frontoparallel or *x*–*y* plane (Fig. 4).

Results and discussion

All study participants performed with similarly high accuracy across all conditions; see Fig. 5 and Table 2. EE555 tended to underestimate distances when using familiar objects, but none of the SI scores reached significance (all SI < 0.35). These data suggest that the patient can assess distance according to an allocentric reference frame and is less impaired when interacting in the *x*–*y* plane than when performing in the *Z* plane. These data provide additional support for the view that EE555's performance when using an allocentric reference frame is generally intact.

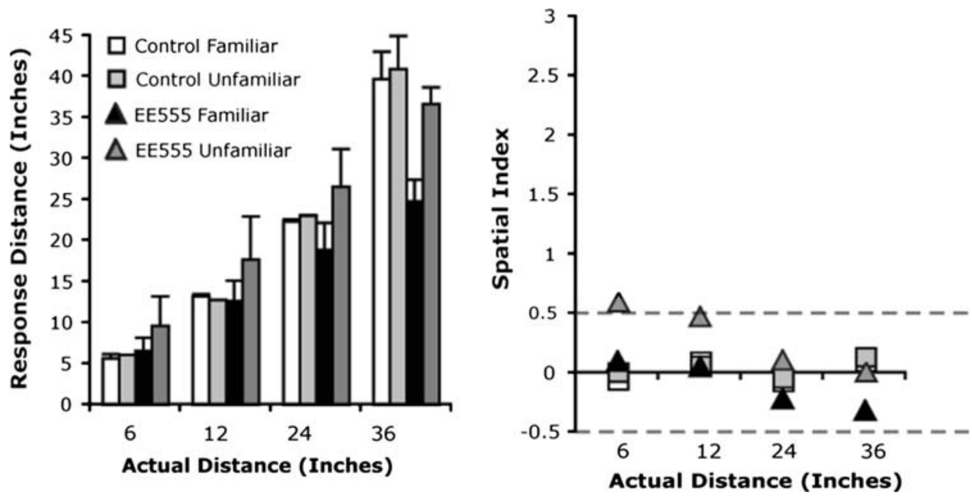

Fig. 4 Experiment 6 results. *Left*: Performance in the allocentric object placement task in the Z, or depth plane. *Error bars* on *EE555's bars* reflect the standard deviation of her performance; *error bars* on the *control subject bars* reflect the standard error of the mean. *Right*: Spatial indices (SI) are plotted as a function of the actual distance. Performance outside the two *dashed lines* is considered significantly abnormal

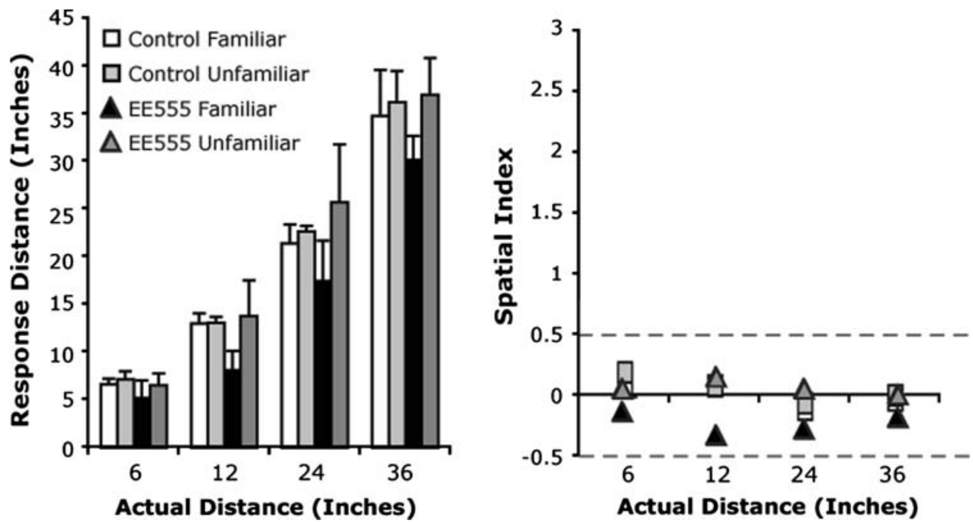

Fig. 5 Experiment 7 results. *Left*: Allocentric object placement in the frontoparallel plane. *Error bars* on *EE555's bars* reflect standard deviation; *error bars* on the *control subject bars* represent the standard error of the mean. *Right*: The spatial indices are plotted as a function of the actual distance of the object. Performance outside the *two dashed lines* is considered significantly abnormal

Part 3: Estimation of size and distance in the absence of stimulus familiarity

In Part 3, we examined whether EE555 experiences comparable disruptions in distance and size perception. Although dissociations of size and distance perception can occur (Gruber 1954), such a dissociation would be surprising since size estimates are linked to distance estimates via size constancy. We examined whether EE555 was impaired at estimating the size of novel objects and if so, whether performance relied on binocular (Experiment 8) or monocular (Experiment 9) vision. We predicted that in contrast to her self-reports of normal size perception, she would be impaired at estimating object size.

Experiment 8: Binocular size and distance judgments with unfamiliar objects

Methods

EE555's performance was compared to one female age-(41 years), and education-(14 years) matched normal control subject. The experimenter first placed either the 5 or 10 cm^3 cube at one of three distances: 28.5, 57 and 114 cm; see Table 3. Subjects were instructed to close their eyes until permitted to view the first presentation. Subsequently, they closed their eyes while the cube was removed and opened them when the second presentation was ready. There were approximately 2 s between presentations. Subjects remained still to prevent them from employing motion parallax to aid their judgments. There were two tasks. In the size judgment task, subjects were asked which cube was larger. In the distance judgment task, subjects were asked which cube was farther. Both tasks were three-alternative forced-choice (chance = 33%) with the following possible verbal responses: '1st cube', '2nd cube' or 'same size/distance'.

There were two experimental conditions and a control condition. In the constant physical size condition the same cube was presented at different distances (e.g., the 5 cm^3 cube at 57 and 114 cm), so that retinal size differed. In the constant retinal size condition the large cube was presented at double the distance of the small cube (e.g., the 5 cm^3 cube at 57 cm and the 10 cm^3 cube at 114 cm), so that

Table 3 Summary of testing conditions for Experiments 8 and 9

Cube 1 (cm^3)	Distance (cm)	Visual angle°	Cube 2 (cm^3)	Distance (cm)	Visual angle°
Testing conditions					
Constant physical size					
5	28.5	10.0	5	57.0	5.0
5	28.5	10.0	5	114.0	2.5
5	57.0	5.0	5	114.0	2.5
10	57.0	10.0	10	114.0	5.0
Constant retinal size					
5	28.5	10.0	10	57.0	10.0
5	57.0	5.0	10	114.0	5.0

retinal size remained constant. In the control condition the same cube was presented twice at the same distance. The trial types were randomized. The patient was tested in two binocular sessions; the control subject was tested in one binocular session. Sessions were separated by at least 2 months. EE555 performed a total of 63 size judgment trials: 18 control, 23 constant physical size and 22 constant retinal size trials. She performed 54 distance judgment trials: 10 control trials, 22 constant physical and 22 constant retinal trials.

Analysis: Because the task was 3-alternative forced choice and there were no distance estimations, we could not use the SI measurement. Instead, performance was evaluated using Fisher's exact probability test (Preacher and Briggs 2001). We compared patient and control performance and also EE555's performance to chance (33%). This test evaluates 2 × 2 contingency tables describing mutually exclusive outcome counts for two groups, and provides the probability (*P*) of skewed results as great or greater than that observed. For each comparison, the percentage of correct answers and Fisher *P* values are reported. Values below 0.05 were considered significant. Because control performance was at ceiling (100% consistent with size constancy) in both Experiments 8 and 9, we report one-tailed significance values.

Results and discussion

Control trials: When the same cube was presented twice at the same distance, EE555 performed no differently from the control subject when making size judgments (94.4%, $P = 0.64$, see Fig. 6; Table 4) or distance judgments (90.0%, $P = 0.52$). These data suggest that EE555 was compliant and able to perform the tasks. These data also indicate that poor performance was not due to memory demands imposed by the experimental paradigm.

Size judgment task: When *retinal size* was held constant and physical size differed, EE555 was impaired relative to the control subject (63.6%, $P = 0.05$) but her performance was significantly better than chance ($P = 0.03$). When physical size was constant and retinal sizes differed, EE555 selected the cube with larger retinal size, leading to extremely poor performance (8.7%, $P < 0.0001$) that was significantly below chance ($P = 0.0001$). These data indicate that EE555 relies heavily on retinal size cues when making size judgments. These data also suggest that when retinal size was held constant she accessed some unknown cue to make her decision and perform at above-chance accuracy.

Distance judgment task: When retinal size *or* physical size was constant, EE555 was significantly impaired at distance judgments (retinal constant: 27.2%, $P = 0.0005$; physical constant: 54.4%, $P = 0.001$). Performance was no different from chance for both conditions (P's > 0.11). These data support the view that she relies on retinal size when making distance judgments; objects with smaller retinal sizes were judged as farther. When retinal size was constant, EE555's distance judgments fell to chance performance.

Between task comparison: EE555's performance shows that she was better at making size judgments than distance judgments when retinal size remained constant ($P = 0.03$, two-tailed). When physical size was constant the reverse pattern was observed; EE555 was better able to make distance judgments than size judgments ($P = 0.001$, two-tailed). This analysis suggests that size judgments were not as reliant on retinal size cues as distance judgments because she performed above chance when retinal size was constant. However, they also show that when there was any difference in retinal size, EE555 chose the smaller retinal size as farther (performing accurately) and as smaller (performing inaccurately).

Experiment 9: Monocular size and distance judgments with unfamiliar objects

Methods

EE555's performance was compared to two female age- (41, 38 years), and education- (14, 16 years) matched normal

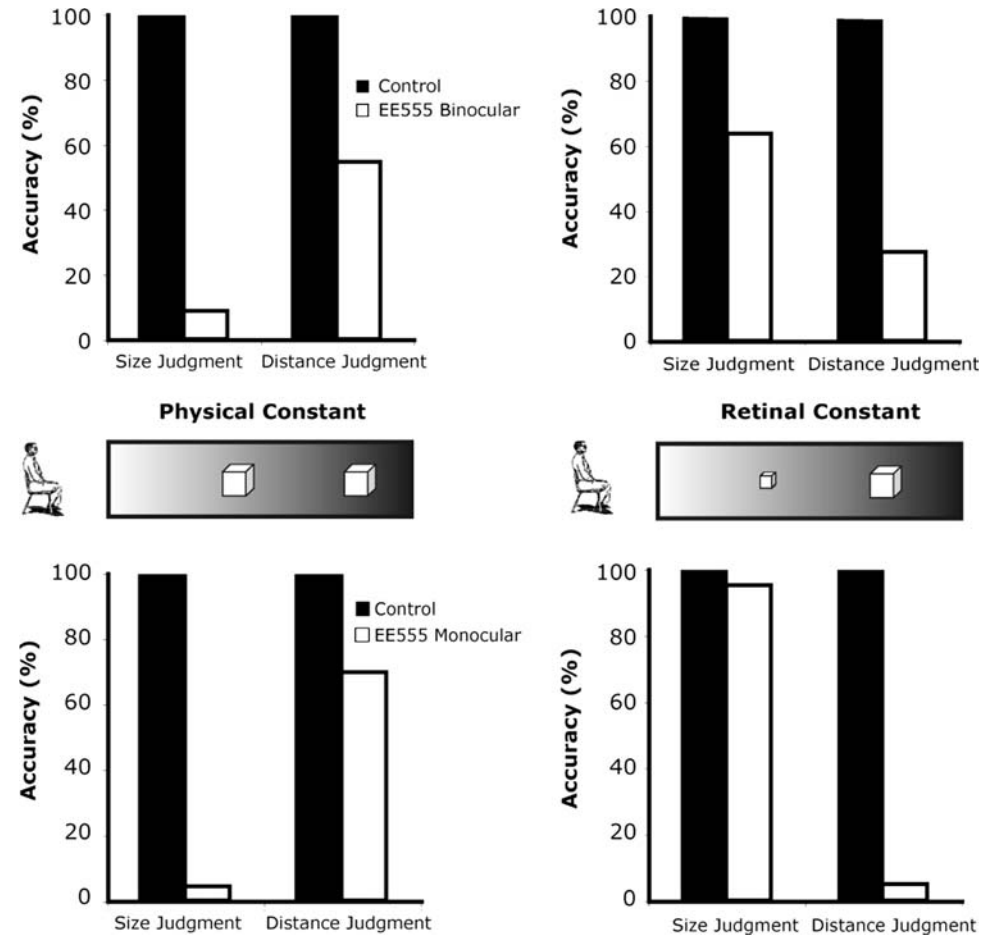

Fig. 6 *Top left*: Experiment 8 (binocular viewing) results for the size and distance tasks when the physical size of the object remains constant, but the retinal size varied. *Top right*: Experiment 8 results for the size and distance tasks when the retinal size remained constant, but the actual physical size of the two objects differs. The middle row provides a cartoon depiction of the physical constant and retinal constant conditions. *Bottom left*: Experiment 9 (monocular viewing) results for the size and distant tasks when the physical size was constant. *Bottom right*: Experiment 9 results for the size and distant tasks when the retinal size is constant

Table 4 Data from Part 3. Size constancy accuracy for constant retinal size and constant physical size conditions and for both viewing conditions

	Constant retinal size (%)			Constant physical size (%)		
	Larger	Smaller	Same	Larger	Smaller	**Same**
Size judgments						
EE555 Bi	63.6	31.8	4.6	91.3	0	8.7
EE555 Mono	95.0	5.0	0	78.3	17.4	4.3
	Constant retinal size (%)			Constant physical size (%)		
	Farther	Closer	Same	**Farther**	Closer	Same
Distance judgments						
EE555 Bi	27.3	63.6	9.1	54.5	4.5	41.0
EE555 Mono	5.0	90.0	5.0	69.6	8.7	21.7

The headers refer to the three possible answers; in the constant retinal size conditions the answer refers to cube size and in the constant physical condition the answer refers to retinal size—correct answers are indicated by bold headings

Across tasks, the control subject was 100% accurate

Bi binocular viewing, *Mono* monocular viewing

control subjects. The sole change from Experiment 8 is that viewing was monocular. Subjects wore eye patches over their non-dominant (left) eye. The patient was tested in three monocular sessions separated by at least 2 months; the control subjects were tested in one monocular session. EE555 performed a total of 63 monocular trials: 23 control trials, 23 constant physical size, and 20 constant retinal size. The control subjects performed a total of 49 trials per task.

Results and discussion

Control trials: EE555 performed normally in the size judgment (91.3%, $P = 0.74$) and distance judgment tasks (89.7%, $P = 0.74$). These data confirm that EE555 was able to perform the task under monocular conditions.

Size judgment task: When the *retinal size* was constant, performance was not statistically different from control performance (74.1%, $P = 0.13$). When physical size was held constant, EE555 incorrectly chose the object with larger retinal size, leading to impaired performance (3.3%, $P = 0.0000002$) that was significantly below chance ($P = 0.003$). This pattern is an enhanced version of what was observed under binocular conditions. There was a greater degree of preserved performance when retinal size was held constant. When retinal size differs, EE555 selected the item with greatest retinal size as the largest item.

Distance judgment task: When the *retinal size* was constant, EE555 was impaired (14.8%, $P = 0.00002$), and did not differ statistically from chance performance ($P = 0.10$). In contrast, when the physical size was constant, EE555's performance was not different from the control group (70.0%, $P = 0.09$). These data can also be explained by a retinal size account. EE555 was impaired when retinal size cues were constant, but when they differed she selected the item with smaller retinal size as the more distant item.

Between task comparison: when retinal size was held constant, EE555 was better able to make size judgments than distance judgments ($P = 0.00002$, two-tailed). When physical size was held constant, she was better able to make distance than size judgments ($P = 0.000008$, two-tailed). These results were similar to the results described above and can be explained by a reliance on retinal size cues when the physical size was constant. The most surprising finding was that when retinal size was constant, EE555 was able to make size judgments but not distance judgments. This dissociation in task performance suggests that the mechanisms underlying size and distance judgments are partially dissociable.

General discussion

Neuroimaging findings indicate that a region of the dorsal visual stream around the junction of the occipital and parietal lobes is consistently activated when processing stereoscopic depth (Backus et al. 2001; Brouwer et al. 2005; Kwee et al. 1999; Neri et al. 2004; Nishida et al. 2001; Quinlan and Culham 2007; Tsao et al. 2003). Here we investigated whether this region is critically involved in monocular as well as binocular distance perception, and how these functions interact with size perception. Based on a review of the literature, we predicted that a patient with bilateral occipitoparietal lesions would exhibit (1) greater deficits when computing distance in egocentric as compared to allocentric reference frames; (2) greater deficits when computing distance in peripersonal as compared to extrapersonal space; and (3) deficits estimating object size. In general, these predictions were supported.

The brain damage suffered by Patient EE555 has led to a nearly complete elimination of stereopsis and an inconsistent ability to utilize several common and potent monocular pictorial distance cues: occlusion, perspective, and shadow. When required to verbally estimate the distance between her and an unfamiliar object according to an egocentric reference frame or to place an object at a designated distance from her, EE555 performed abnormally. However, such deficits appear to be largely limited to the egocentric reference frame, as EE555 was less impaired when asked to place objects a given distance from an external reference, either in the depth or horizontal planes. When placing objects in depth, EE555 performed worse at near distances compared to far distances in either reference frame.

Under some conditions, EE555 can accurately estimate distance and size, indicating her ability to access some distance information is preserved. For example, she is adept at using familiar size cues. Such a reliance on familiar size cues has previously been observed when patients with ventral stream damage are forced to rely on monocular distance cues to perform visuomotor tasks (Marotta and Goodale 2001). It is logical that when the full canon of distance cues is unavailable, a strategy develops that depends on remaining cues such as familiar size. EE555 also makes use of retinal size to estimate size and distance. However, even when familiar size and retinal size cues could not be used, EE555 shows some residual ability to compute object size. This dissociation suggests that the only additional cues that could be reasonably expected to remain present, accommodation and vergence, were accessed when there were no other competing sources of size or distance information.

Accommodation, the process of focusing the lens, and vergence, the process of moving the eyes in opposite directions to focus an object, are often overlooked in discussions of distance processing. Vergence angle can serve as an effective distance cue at distances up to 8 m (McKee and Smallman 1998; Mon-Williams and Tresilian 1999). Moreover, vergence angle is known to strongly affect perceived size (Hermans 1937). Vergence manipulations can in fact generate dissociations of judged size and distance, producing the "size-distance paradox" (Hermans 1954) in which depth cues lead observers to see closer objects as smaller and consequently judge them as farther (Gruber 1954). Accommodation can serve as a cue to distance within a restricted range of 2 m. It has been shown that accommodation can modestly affect size perception (Fisher and Ciuffreda 1988; McLin et al. 1988; Wallach and Leggett 1972) in a manner that optical changes in the size of the retinal image cannot explain (Smith et al. 1992). Accommodation states are not altered by monocular pictorial cues (Busby and Ciuffreda 2005; Ittleson and Ames 1950), although they are yoked to convergence (Martens and Ogle 1959) so one would not expect the use of accommodation to be impaired by the loss of pictorial cue information.

EE555's normal use of familiar size cues is paralleled by normal mental imagery of common object size. She accurately estimates the length of known objects (e.g., "Show me the length of a pencil") and will select the larger of two objects (e.g., car vs. truck) from memory (Berryhill et al. 2007). She also accurately estimates the absolute distance between objects in familiar environments. Patient EE555 commented that she found all of the tasks extremely easy indicating that she is often not cognizant of her perceptual impairment. When asked if she thought the world looked flat, she remarked that it looked the way it always had.

Anatomy of distance perception

It is unlikely that the observed distance perception deficits are a consequence of the clinical symptoms of simultanagnosia because these symptoms can be dissociated. Recently, a patient with right occipitoparietal damage, lacking simultanagnosia, was reported to have impaired size constancy (Grimsen et al. 2008). Also, we tested a patient with somewhat more superior bilateral parietal lobe lesions and simultanagnosia. This patient has normal stereopsis, distance perception and size perception (patient TQ591, unpublished data).

Neuroimaging studies of stereoscopic distance processing show activation clusters in retinotopic areas in the superior occipital lobe: areas V3A (Backus et al. 2001; Tsao et al. 2003), V7 (Brouwer et al. 2005; Tsao et al. 2003), and V4d-topo (Brouwer et al. 2005; Tsao et al. 2003). These activations tend to extend superiorly into the caudal intraparietal sulcus (Rutschmann and Greenlee 2004). The activated regions tend to exhibit greater adaptation to egocentric depth as compared to allocentric depth (Neggers et al. 2006; Neri et al. 2004), suggesting that these areas are especially tuned to the relationship between the viewer and the perceived object. We recently found that a similar region in the superior occipital lobe (V3A) is activated by monocular distance cues (Berryhill et al. 2008). EE555's lesions overlap with the superior occipital activations reported in the reviewed fMRI studies.

EE555's preserved abilities to utilize familiar size information, her probable use of accommodation and vergence, and her ability to compute allocentric distance indicate that these functions rely on neural processing mechanisms that are distinct from those needed to compute distance based on binocular and most monocular pictorial cues. Ventral stream regions intact in EE555 are thought to compute familiar size (e.g., Marotta and Goodale 2001) and allocentric distance perception (Carey et al. 1998; Hartley et al. 2007; Holdstock et al. 1999, 2000; Murphy et al. 1998). One fMRI study has linked a small midline occipitoparietal region to convergence and accommodation (Quinlan and Culham 2007), a neural region that is also preserved in Patient EE555.

Egocentric and allocentric reference frames

There are few neuropsychological examinations of allocentric distance perception. However, several pieces of evidence have linked allocentric spatial memory to the hippocampus. Parietal lobe regions are thought to be essential for egocentric processing (reviewed in Burgess 2008). The present data are consistent with this view. Patient EE555 exhibited striking egocentric distance judgment impairments but performed relatively normally when using an allocentric reference frame.

EE555's relatively preserved performance when using an allocentric reference frame contrasts with findings from ventral form agnosic patient DF. In this comparison, results from DF and EE555 reveal a double-dissociation. DF is impaired when using an allocentric reference frame but not when using an egocentric reference frame (Carey et al. 2006; Murphy et al. 1998); EE555 is more impaired at using an egocentric reference frame than an allocentric reference frame. These data support the neuroimaging results that indicate independent processing for each of these reference frames (Committeri et al. 2004).

Parietal damage has not always produced deficits in egocentric processing as we observed in EE555. For instance, patients with unilateral parietal lesions and hemispatial neglect may exhibit both allocentric (e.g. line bisection) and egocentric (e.g., deviations of body midline) spatial deficits (reviewed in Kerkhoff 2001). Findings from patients with bilateral parietal lobe damage is also mixed. A prior study of reaching and distance perception in a patient (RM) with bilateral occipitoparietal damage reported that he was modestly impaired when acting within an egocentric reference frame, more impaired when acting within an allocentric reference frame (Baylis and Baylis 2001). The source of these mixed findings remains in need of clarification.

Peripersonal and extrapersonal space

Parietal patients with spatial neglect may be disproportionately affected in either peripersonal or extrapersonal space (Bisiach et al. 1986). This observation has led to further investigations of the neural correlates of space corroborating the view that dissociable neural networks process peripersonal and extrapersonal space in both humans (Committeri et al. 2007) and monkeys (Previc 1998). The regions implicated in processing peripersonal space, inferior parietal lobe areas, overlap with Patient EE555's lesions. As the present results demonstrate, distance judgments were proportionately worse for the closest distances.

Conclusions

The present data confirm that bilateral lesions to occipito-parietal regions are associated with striking distance and size perception deficits, bearing out the results of neuroimaging studies (Backus et al. 2001; Berryhill et al. 2008; Brouwer et al. 2005; Inui et al. 2000; Iwami et al. 2002; Kwee et al. 1999; Naganuma et al. 2005; Neri et al. 2004; Nishida et al. 2001; Rutschmann and Greenlee 2004; Rutschmann et al. 2000; Tsao et al. 2003; see review in Parker and Cumming 2001). Importantly, the human brain appears to rely on distinct processing regions for different aspects of distance perception. Both binocular and monocular cues appear to rely on similar processing regions in the dorsal stream, which are specialized for the processing of cues within egocentric and peripersonal frames of reference. In contrast, allocentric and extrapersonal cues appear to rely on computations performed by other cortical areas.

Testing more neuropsychological patients will be required to establish the generality of the current findings, and to map the cortical functional dependencies implied by this investigation. One interesting avenue of further inquiry would be to examine how the computations for egocentric and allocentric distance perception differ. Portions of the dorsal stream may code for or receive input encoding information about one's position in space. If disrupted, the loss of this information may give rise to egocentric spatial deficits. Another interesting question is how egocentric and allocentric maps interact to guide navigation (Whitlock et al. 2008). Last, we note that fMRI studies have reported that activity in the parietal lobe is modulated by numerical distance, spatial distance, and temporal distance (Walsh 2003) thus raising the possibility that distance, broadly defined, may serve as a common metric for dorsal stream processing.

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