IMPOVERISHED DESCRIPTIONS OF FAMILIAR ROUTES IN THREE CASES OF HIPPOCAMPAL AMNESIA

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Abstract

Recent research has challenged classic theories of hippocampal function in spatial memory with findings that the hippocampus may be necessary for detailed representations of environments learned long ago, but not for remembering the gist or schematic aspects that are sufficient for navigating within those environments (Rosenbaum et al., 2000). We aimed to further probe distinctions between detailed and schematic representations of familiar environments with three hippocampal amnesic patients by testing them on a route description task and mental navigation tasks that assess the identity and location of landmarks, and distances and directions between them. The amnesic cases could describe basic directions along known, imagined routes, estimate distance and direction between well-known landmarks, and produce sketch maps with accurate layouts, suggestive of intact schematic representations. However, findings that patients' route descriptions lack richness of detail, along with impoverished sketch maps and poor landmark recognition, substantiates previous findings that detailed representations are hippocampus-dependent.

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Introduction

The hippocampus (HC) has long been implicated in learning and memory (Scoville & Milner, 1957), and in spatial memory in particular (O'Keefe & Nadel, 1978). It is well established that the HC is required for forming new spatial memories in animals (Morris, Garrud, Rawlins, & O'Keefe, 1982; Olton, Becker, & Handelmann, 1979) and humans (Kumaran et al., 2007; Maguire, Nannery, & Spiers, 2006; Rosenbaum et al., 2000; Teng & Squire, 1999) but remote spatial memory for places learned long ago had not been investigated until recently. Studies of remote spatial memory in humans suggest that the HC is needed for representing some, but not all, aspects of remote spatial memory. Specifically, individuals with compromised hippocampal function can make accurate decisions about spatial relations contained within remotely learned environments, such as the locations and identity of landmarks, and the distances and routes between them (e.g., Rosenbaum et al., 2000; Rosenbaum, Winocur, Binns, & Moscovitch, 2012; Teng & Squire, 1999). However, at least some of these individuals appear to have difficulty representing details contained within old environments, such as landmarks (Rosenbaum et al., 2000; Rosenbaum et al., 2005; Rosenbaum et al., 2012) and minor roads (Maguire et al., 2006). The current study further investigates possible dissociations between schematic, gist-like representations of spatial environments and representations of peripheral details that may be necessary for vivid re-experiencing of routes but that are not essential for navigation.

Classic theories of HC function make different predictions about the role of the HC in spatial memory. To account for findings of place cells in the HC of rats freely navigating a newly learned maze, O'Keefe and Nadel (1978) postulated that the HC supports the formation of a “cognitive map”, which contains allocentric spatial representations (flexible, viewer-independent knowledge of spatial relations among landmarks) of an environment. In extending the Cognitive Map Theory (CMT) to humans, they suggested that allocentric representations may provide the context in which episodic memories unfold. However, CMT does not differentiate between recent and remote cognitive maps and therefore it is not clear if hippocampal damage would lead to impaired spatial and episodic memory, regardless of when the memory was acquired.

A second influential theory of hippocampal function, the Standard Consolidation Theory (SCT), posits that declarative memories (whether episodic, semantic, or spatial in nature) initially rely on the HC, but gradually become established in the neocortex and thus, over time, no longer require the HC for the maintenance or retrieval of those memories (Scoville & Milner, 1957; Squire, 1992). Strong support for SCT is found in observations of temporally graded retrograde amnesia in individuals with hippocampal damage, which typically occurs together with anterograde amnesia (Winocur & Moscovitch, 2011).

Amnesic patients with hippocampal damage have extended findings of intact remote semantic memory to include spatial memory (K.C.: Rosenbaum et al., 2000; Rosenbaum et al., 2005; E.P.: Teng & Squire, 1999; T.T.: Maguire et al., 2006), but there is additional evidence to show that episodic memory of events that were experienced as long ago as childhood may be lost (e.g., K.C.: Rosenbaum, McKinnon, Levine, & Moscovitch, 2004; Rosenbaum et al., 2005; S.J.: Rosenbaum et al., 2008; H.M. and W.R.: Steinvorth, Levine, & Corkin, 2005). Moreover, although there is evidence suggesting that amnesic individuals are able to navigate familiar remote environments, representations of detailed features appear to be lost in at least some patients (Maguire et al., 2006; Rosenbaum et al., 2000; Rosenbaum et al., 2005). For instance, when Rosenbaum and colleagues (2000) tested K.C., an amnesic person with bilateral medial temporal lobe lesions caused by a motor vehicle accident, he retained the ability to negotiate his way in his premorbidly learned home neighbourhood and drew a sketch map of this neighbourhood with the general schematic layout intact; however, his sketch map contained noticeably fewer landmarks and streets compared to controls' sketch maps. In addition, K.C. performed poorly compared to controls on a landmark recognition task as a result of his inability to recognize individual houses and landmarks that were salient but unlikely to be critical for navigation (Rosenbaum et al., 2000).

Additional findings of impoverished detailed representations are suggested in Maguire and colleagues' (2006) report of the case T.T., a former London taxi driver with bilateral hippocampal damage due to viral encephalitis. T.T. performed normally on static mental navigation tests that involved recognition of landmarks from static photos and judgments of spatial relations in imagination, as well as dynamic tests that involved active navigation in a virtual reality rendering of downtown London. Although T.T. could rely on main artery roads to reach a destination, he had difficulty on those dynamic tests that required navigation along non-artery (minor) roads, which may require a more fine-grained, detailed spatial representation. In addition, T.T.'s floor plans of houses that he had lived in before and after the onset of his hippocampal damage were inaccurate relative to his wife's in terms of the placement of several key features, such as the staircase and balconies (Maguire et al., 2006). T.T.'s errors on this task appear to be consistent with the impoverished sketch maps drawn by K.C.

Findings of what appears to be impoverished detailed representations of large-scale environments may parallel the patients' episodic memory impairment, where narratives of personal events lack contextual details that would otherwise enable them to vividly re-experience their past (Rosenbaum et al., 2000; Rosenbaum et al., 2008). Neither SCT nor CMT predict this pattern of impaired and preserved function. An alternative account, the Multiple Trace Theory (MTT; Moscovitch et al., 2005; Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006), argues that some types of memory can exist independent of the HC. According to MTT, a new trace element is added each time a memory is retrieved, serving to strengthen the memory. Most often only the semantic (gist) information of a memory is reactivated, meaning that over time traces of gist-like representations of the memories become well represented neocortically and, as a result, are less vulnerable to disruption. This may be contrasted with episodic or detailed information, which is believed to always rely on the HC, regardless of the age of the memory (Nadel & Moscovitch, 1997; Moscovitch et al., 2006).

More recently, MTT was extended to accommodate findings of dissociations in spatial memory in amnesic patients with hippocampal damage. A "transformation hypothesis" was proposed to predict that all relational/declarative memories, including spatial, initially depend on the HC but with time and/or experience can exist independent of the HC within neocortical regions if they lose their detailed, contextual features (Winocur & Moscovitch, 2011; see also Rosenbaum, Winocur, & Moscovitch, 2001). Within spatial memory, this would include coarse, schematic, gist-like information, such as well-known landmarks and the approximate relations between them. Fine, detailed information about an environment, in contrast, would continue to rely on HC function, similar to detailed episodic representations, regardless of how long ago that information was acquired. An important addition to MTT is that the transformed memory is not believed to replace the initial, more detailed memory but, rather, the two representations can coexist and even interact when the situation requires it. The Transformation Hypothesis was built on findings that healthy older individuals and cases of hippocampal amnesia have difficulty representing detailed features of well-known environments that they can otherwise navigate in imagination and in the real world (Maguire et al., 2006; Rosenbaum et al., 2000; Rosenbaum et al., 2005; Rosenbaum et al., 2012).

The current study aims to determine if finer dissociations might be revealed between impaired and preserved aspects of remote spatial memory in a way that more closely parallels known dissociations between impaired re-experiencing of personal episodes but intact memory for personal facts. One way to do this is to assess participants' ability to describe the route that would be taken between a particular start and end point, with and without the requirement to provide vivid descriptions of details along the way. This was the approach taken in a study of healthy older adults by Hirshhorn, Newman, and Moscovitch (2011), which suggested that the HC is required for vivid re-experiencing of a route, but not for map-like knowledge of it (for related findings, see Ciaramelli, Rosenbaum, Solcz, Levine, & Moscovitch, 2010 and Rosenbaum et al., 2012).

To further elucidate the role of the HC in retrieving schematic and detailed representations of familiar environments, we extended Hirshhorn and colleagues' (2011) route description task, along with spatial memory measures of distance, direction, and landmark recognition (Ciaramelli et al., 2010), to amnesic patients with hippocampal damage and episodic memory impairment. If the hippocampus is needed for representing detailed spatial features to enable rich re-experiencing of an environment, but not for schematic representations of spatial relations, then amnesic patients with hippocampal damage would be expected to produce fewer details in sketch maps of well-known neighbourhoods, although the general configuration of the sketch maps would be intact. Another task that allows for assessment of both detailed and schematic representations within the same measure is the route description task, on which amnesic participants would be expected to show a similar pattern of fewer details (such as landmarks and sensory descriptions of perceptual features along the route) but intact directions to navigate from the start to end locations in their verbal descriptions of routes. To compensate for less vivid details within the descriptions, amnesic participants might rely to a greater extent than controls on spatial references that may be based on schematic representations. Finally, amnesic individuals would be expected to provide accurate judgments of distance and direction between well-known landmarks on a vector mapping task, which is thought to depend on a context-free survey representation of the environment conducive to allocentric representations. In contrast, recognition of the visual appearance of landmarks located in remotely learned environments, especially those that constitute perceptual details that are not essential to navigation, might be compromised in hippocampal amnesia.

Findings of impoverished detailed representations of environments and intact schematic representations sufficient for navigation in amnesic patients with clear evidence of hippocampal damage would provide more definitive support for alternate theories of hippocampal function, such as MTT and its derivative, the Transformation

Hypothesis, which view the role of the HC as involved in representing and binding of vivid details to enable the replay of routes for the purpose of re-experiencing.

Methods

Participants

Amnesic cases. Three previously studied amnesic individuals with extensive MTL damage (D.G., D.A., and K.C.) participated in the study. Detailed descriptions of all three cases, including the results of neuropsychological and neuroanatomical evaluation, have been documented previously (Kwan, Craver, Green, Myerson, & Rosenbaum, 2013; Rosenbaum et al., 2000; Rosenbaum et al., 2005; Rosenbaum et al., 2008). At the time of testing, D.G. was 47 years old, D.A. was 61, and K.C. was 62. All three cases were tested on the route description test in the current study. D.G. and D.A. were also administered several static navigation tasks for familiar, premorbidly learned environments, designed to assess remote spatial memory for distance, direction, and landmark appearance. As reviewed in the introduction, K.C.'s performance on tests of recent and remote spatial memory had been assessed previously at age 49 (13 years prior), and was not tested further in the current study (Rosenbaum et al., 2000; Rosenbaum, Winocur, Grady, Ziegler, & Moscovitch, 2007).

Healthy comparison controls. Thirty-eight healthy comparison controls (26 women), matched for age (*M* = 68.13, *SD* = 15.48) and education (*M* = 16.92, *SD* = 2.85), were tested on the route description task (Hirshhorn et al., 2011). Comparisons in performance on tests of mental navigation were made with a separate group of 6 controls; 2 women and 1 man with extensive experience navigating in the environment familiar to

D.G. (City S), matched for age (*M* = 46.67, SD = 0.58) and education (*M* = 17, SD = 3.61), and 3 women with extensive experience navigating in the environment familiar to D.A, (Neighbourhood M), also matched for age (*M* = 44.67, SD = 13.61) and education (*M* = 16.33, SD = 2.08).

Controls were recruited through the patients' family and friends, postings in community centres and at York University, and via online advertisements. Additional control route description transcripts were obtained from Hirshhorn and colleagues' (2011) previously collected data set and rescored by the same raters as in the current study. All participants were fluent in English and provided written informed consent in accordance with the Human Research Ethics Committees of Baycrest and York University. Each participant received monetary compensation for his or her time.

Materials and Procedure

A summary of experimental tasks and how they are believed to relate to allocentric (viewer-independent) and egocentric (viewer-dependent) representations, and schematic and detailed representations is presented in Table 1.

Route description task. All three amnesic cases and matched controls were asked to describe one to two familiar walking routes. Although participants described different routes based on their personal experiences, all participants were asked to describe routes that took approximately 10 minutes to walk, allowing us to compare performance on this task across participants. At first, participants were asked to provide the basic directions necessary to get from their start point to their end point. Then, they were asked to provide as much detail as possible, describing not only their surroundings but also where visual features of the environment were located in relation to each other and to the participant. Participants were instructed to continue with their descriptions until they came to a natural end. The examiner then probed participants for further details of three landmarks that were mentioned by the participant. Examiners refrained from introducing any new landmarks that had not already been mentioned by the participant.

Each route description was segmented into a set of statements by one of two independent, reliable scorers, blind to group membership, using a modified version of Hassabis, Kumaran, Vann, and Maguire's (2007) scoring procedure. Each segmented statement, or meaningful unit of information, was classified as belonging to one of 3 categories: 'entities', 'sensory descriptions', and 'spatial references'. The entities category included any distinct item mentioned (landmark, person, or object). The sensory descriptions category included any descriptive statement about an entity along the route, regardless of modality. Spatial references referred to statements about the participant's location in space, the relative position of entities along the route, or explicit measurements (see Hassabis et al., 2007 for more detail on scoring). Information provided by participants that fell outside of these categories (such as emotions, thoughts, or actions) was not included in the total output as it was considered extraneous to our primary objective of probing detailed spatial-perceptual representations of routes in remote spatial memory. The number of statements in each category was divided by the participant's total output, allowing us to examine the proportion of each individual's total output that was attributed to spatial references, entities, or sensory descriptions, while controlling for variations in total verbal output among participants.

Independent, blind scorers also provided a quality judgment score for each route, on a scale of 1-10, reflecting how well they could envision a detailed, vivid image of the route and features along the way in their own minds eye, after reading participants' transcribed route descriptions. Quality judgment scores were averaged for those participants who provided two familiar route descriptions.

Static mental navigation tasks. Amnesic cases D.G. and D.A., and six control participants were tested on static navigation tasks known to assess memory for familiar, remote environments for distance, direction, and landmark appearance (Ciaramelli et al., 2010; Rosenbaum et al., 2000, Rosenbaum et al., 2012).

Environments.

At the time of testing, D.A. had lived in Neighbourhood M for 29 years. Neighbourhood M is approximately $2km^2$, close in size to the one in which K.C. had lived and on which he was tested. Amnesic case D.A. lived in this area for nine years prior to the onset of his amnesia, and continues to reside there. The three age- and education-matched controls also currently reside in the neighbourhood; two controls had lived there for 25+ years, and one control had lived there for 11 years at the time of testing[1].

Case D.G. and matched controls were tested on "City S", a premorbid environment, approximately $50km^2$, that D.G. lived in for the first 25 years of his life. At the time of testing, D.G. had not lived in City S for 22 years and does not visit it often. Likewise, all controls matched to D.G. had lived in City S for 22-25 years and moved away from their neighbourhood 22 years ago.

[1] While it would have been ideal to also test controls who had moved away from Neighbourhood M at the time of D.A.'s onset of amnesia, attempts to recruit such controls were unsuccessful. Nevertheless, using only controls that currently reside in the neighbourhood would serve to make D.A.'s intact performance on static navigations tasks all the more remarkable.

Sketch Mapping.

Participants were first asked to reproduce the configuration of spatial elements of their environment in a sketch map. The maps were analyzed for the amount of detailed information provided (number of landmarks and street segments, defined as the total number of named or unnamed streets, roads, walkways and lanes drawn on a map that are bound by segments on at least one side), and accuracy in the placement of those details. The overall gestalt, scale, and relative relationships between landmarks and street segments were commented on qualitatively.

D.G. and matched controls were given the boundaries of smaller regions, measuring approximately $2km^2$, located within the larger City S, to make the environment comparable to the one on which D.A. and matched controls were tested and to encourage the production of a more detailed map. To control for familiarity, we opted to have all participants draw the $2km^2$ region with which they were most familiar. D.G. and Control 101 provided a sketch map of an identical region, however controls 103 and 104 drew distinct regions in City S that were similar in size and complexity to D.G.'s region.

Vector Mapping.

For each of 10 pairs[2] of landmarks, participants were given an outline map that included only the boundary roads of the environment. The position of one of the landmarks from the pair was indicated on the map, and participants were asked to draw a vector representing the distance and direction from that landmark to an unmarked landmark. Deviation in estimates from actual directions in degrees and distances in

[2] One control for D.A.'s Neighbourhood M was tested on 9 pairs of landmarks.

centimeters was calculated for each trial and averaged to derive absolute error scores. The performance of each patient was independently analyzed using Crawford and Garthwaite's (2002) modified t-test procedure, which allows comparison of single cases to small control samples. All analyses were tested at a significance level of $p < .05$.

Landmark recognition.

Participants were shown photographs of landmarks, located within the target environment, as well as photographs of unknown 'foil' landmarks, located outside of the target environment. Foils were matched to each target landmark in terms of building category, architectural style, and contextual features. For each photograph, participants were asked whether or not the landmark was within the target environment and, if so, to provide some additional identifying information (name, location, type of building, etc.). The proportion of hits was calculated, with one point given for each landmark correctly recognized and identified, and a half point given for each landmark correctly endorsed as a target but not identified. In addition, the proportion of false alarms (foil landmarks erroneously identified as within the target environment) was calculated. Each individual amnesic case was compared to controls on two dependent variables, hits and false alarms, using Crawford and Garthwaite's (2002) modified t-test procedure.

Results

Route Description Task

As predicted, all patients were able to provide the basic directions for their route. Analysis of the route description task revealed that the total output for D.G. and K.C. was comprised of significantly fewer sensory description segments (t = -1.734, p = 0.046 and t = -2.013, p = 0.026, respectively; see Figure 1), whereas the total output for D.A. approached significance (t = -1.604, p = 0.059; see Figure 1)[3]. This suggests that patient route descriptions lacked detail about what things looked like along the route compared to controls.

Surprisingly, neither D.G., D.A., nor K.C. differed significantly from control participants in terms of the proportion of entities provided (D.G.: t = -0.387, p = 0.351; D.A.: t = -0.365, p = 0.359; K.C.: t = -0.119, p = 0.453; see Figure 1)[3].

Nonetheless, as predicted, spatial references comprised a significantly larger proportion of amnesic participants' output compared to that of controls (D.G.: t = 2.703, p = 0.005; D.A.: t = 2.512, p = 0.008; and K.C.: t = 2.739, p = 0.005; see Figure 1). While patients' total output consisted of proportionally more spatial references compared to controls' output, it is unclear if the actual number of spatial references (as opposed to proportion) provided by patients differed from controls. Post-hoc analyses using Crawford and Garthwaite's (2002) modified t-test procedure were used and showed that each patient's actual number of spatial references did not differ significantly from that of controls (D.G.: t = -0.923, p = 0.181; D.A.: t = 0.970, p = 0.169; K.C.: t = -0.487, p = 0.315).

In line with our hypotheses, we found that the quality of D.G.'s and K.C.'s route descriptions was rated as significantly lower compared to the quality of controls' descriptions (t = -2.196, p = 0.017, and t = -2.433, p = 0.010, respectively; see Figure 2), indicating that scorers had greater difficulty envisioning for the visual appearance of routes described by patients than routes described by controls. Contrary to our

[3] Withholding an outlier did not change the results.

predictions, the quality of D.A.'s route descriptions was not rated differently than the quality of controls' descriptions ($t = -0.537$, $p = 0.297$; see Figure 2).

Static Mental Navigation Tasks

Results of the vector mapping and landmark recognition tasks are presented in Table 2 for D.G. and D.A. K.C.'s data, originally reported in Rosenbaum et al. (2000), are included in the table for comparison. The sketch maps were qualitatively analyzed and described below.

Sketch mapping.

Amnesic case D.G. retrieved fewer landmarks and street segments (5 landmarks and 19 street segments; Figure 3) compared to control 101 (17 landmarks, 21 street segments; Figure 4), control 103 (18 landmarks, 33 street segments; Figure 5), and control 104 (43 landmarks, 52 street segments; Figure 6).

While D.G.'s sketch map contained considerably fewer streets and landmarks than the sketch maps of controls, landmarks and street segments that were included were properly placed and did not deviate from the scale more than those included by controls. Interestingly, unlike controls, some of the street segments included by D.G. were detached at both ends, which may reflect D.G.'s fine motor difficulties. However, D.G.'s sketch map shows a basic schematic representation of his home environment, limited to major streets and landmarks, and minor streets that would have been pertinent for navigating to his home.

D.A.'s sketch map, presented in Figure 7, included 7 landmarks and 28 street segments, which, like that of D.G., is impoverished in comparison to control 301 (41 landmarks, 76 street segments; Figure 8), control 302 (25 landmarks, 32 street segments; Figure 9), and control 304 (43 landmarks, 42 street segments; Figure 10). Also similar to D.G., D.A. correctly placed landmarks and street segments and maintained an accurate overall layout and scale.

Vector mapping.

In line with previous research with K.C. (Rosenbaum et al., 2000), amnesic case D.G. did not differ significantly from controls on the vector mapping task in terms of the mean deviation from the correct direction in degrees (t = -0.178, p = 0.438; see Figure 11) or distance in centimeters (t = 0.703, p = 0.277; see Figure 12). Amnesic case D.A. performed similarly to controls in terms of distance (t = 1.197, p = 0.177, Figure 12), but showed worse performance than controls for direction, a result that approached statistical significance (t = 2.443, p = 0.067). Careful inspection of the results revealed that D.A.'s worse performance was due to a single error in which he confused two gas stations in his neighbourhood, resulting in a deviation of 173° from the correct direction on one trial. When this trial was removed from the analysis, D.A.'s estimates of direction were indistinguishable from controls' estimates (t = 0.739, p = 0.269, Figure 11).

Landmark Recognition

D.G. recognized 68% of the landmarks from City S, which approaches significant impairment (t = -2.448, p = 0.065) compared to controls (M = 91%, SD = 0.08%; see Figure 13). The proportion of false alarms produced by D.G. (18%) did not differ significantly from the proportion of false alarms produced by controls (M = 27%, SD = 16%; t = -0.459, p = 0.346).

D.A. correctly identified 100% of the target landmarks from his neighbourhood and did not differ significantly from controls who recognized an average of 95.6%, SD = 3.8% (t = 1.003, p = 0.211; see Figure 13). However, D.A. also exhibited a significantly higher proportion of false alarms (93%) compared to controls (M = 2%, SD = 3.8%; t = 20.494, p = 0.001), indicating that DA mistakenly identified landmarks as located within his home neighbourhood. Although D.G. is much more conservative in his responding than D.A., results indicate that both have difficulty recognizing landmarks.

Discussion

Previous research has pointed towards a possible dissociation between schematic and detailed representations of space, with the HC required to support the latter but not the former. The purpose of the current study was to examine the role of the HC in schematic and detailed spatial representations, and possible interactions with episodic re-experiencing, in a more direct way by assessing three cases of hippocampal amnesia on tests of route descriptions, judgments of spatial relations, and landmark recognition based on remotely learned environments that had been navigated extensively by patients and controls.

Intact Schematic Representations of Space in Hippocampal Amnesia

All three amnesic cases were found to have intact schematic representations of their respective environments, as reported in Rosenbaum et al. (2000) for K.C. and in the current paper for D.A. and D.G. This conclusion is based on the patients' intact performance on a vector mapping task and correct configuration and layout of familiar home environments on sketch maps. These tasks are believed to require flexible use of allocentric representations of the familiar environment (Ciaramelli et al., 2010). Intact performance on a route description task also speaks to the integrity of the three cases' schematic spatial representations, though here participants may have relied to a greater extent on egocentric representations (Rosenbaum et al., 2004; Rosenbaum et al., 2012). Further corroborating the claim that the HC is not required for navigating familiar environments, D.G., D.A. and K.C. were able to provide basic directions from the start to end point of premorbidly familiar walking routes. In addition, the total output of the route descriptions provided by each case consisted of a significantly greater proportion of spatial references than perceptual details in comparison to controls. However, post-hoc analyses comparing patients' actual number of spatial references to that of controls suggests that this finding may be more indicative of the patients' paucity of detail than an over-provision of spatial references.

The current results substantiate previous research claims that at least some aspects of spatial memory that are schematic in nature, whether allocentric or egocentric, can be preserved following hippocampal damage (Rosenbaum et al., 2000). The current study only allows for speculation about the brain structures that are required for maintaining schematic representations of environments. Nevertheless, a recent fMRI study of remote spatial memory in K.C. provides some clues. K.C. and controls familiar with the neighbourhood in which K.C. lived were tested on static mental navigation tasks, including landmark recognition and navigation tasks used in the current study (Rosenbaum et al., 2007). The tasks engaged several common regions, including: middle-superior frontal gyrus, which has been implicated in spatial working memory; medial-superior parietal lobule, known for its role in egocentric processing and imagery; retrosplenial/posterior cingulate cortex, involved in heading direction; and parahippocampal cortex, required for acquisition of new landmarks (for reviews, see Aguirre & D'Esposito, 1999; Epstein, 2008; Maguire, 2001; Weniger, Ruhleder, Wolf, Lange, & Irle, 2009). K.C. showed activation in these regions in the right hemisphere in relation to intact performance on the various mental navigation tasks, whereas controls recruited these regions in both hemispheres (Rosenbaum et al., 2007). In K.C. and D.A., for whom detailed volumetric data are available, medial-superior frontal gyrus and superior parietal cortex appear to be intact. Posterior cingulate cortex is slightly reduced in volume in D.A. and parahippocampal cortex is structurally compromised in both patients, though activation in these regions in K.C. appears to be functionally relevant (Rosenbaum et al., 2007), and the same may be true of D.A.

Impaired Detailed Representations of Space in Hippocampal Amnesia

As hypothesized, our results implicate the HC as necessary for recollecting detailed representations of space. Similar to K.C. (Rosenbaum et al., 2000), amnesic cases D.G. and D.A. produced sketch maps that, while accurate in their overall configuration and layout, had fewer landmarks and fewer streets than controls, suggestive of an intact schematic representation but difficulty with accessing a detailed representation of neighbourhoods learned long ago.

Performance of the amnesic cases on the route description task may also shed light on the necessity of the HC for retrieving detailed representations of space. The proportion of entities named did not differ between patients and controls, contrary to our hypothesis that control participants would name more entities along the route. This may be due to a natural inclination for both patients and controls to mention mostly those landmarks or entities along the route that are pertinent to navigation, or those that are especially salient, in that they are useful in differentiating a route from any other. It is possible that entities incidental to navigation may have been accessible to control participants, but not divulged in this task as expected.

What is of note is that although patients and controls provide a similar proportion of entities, only the controls seem to be able to describe them in detail. As hypothesized, both D.G.'s and K.C.'s total output was comprised of significantly fewer sensory description segments compared to healthy controls, and D.A. showed a trend towards significance. Even when probed for additional information, the three cases had difficulty describing landmarks. Their descriptions were often vague, whereas control participants would often describe several additional, more detailed, aspects of the probed landmarks, such as colour and size (see Figure 14 for sample descriptions from a patient and control).

Both D.G. and K.C. received significantly worse quality judgment ratings compared to controls, suggesting that, unlike controls, neither patient was able to evoke vivid images in independent scorers' minds based on the route descriptions that they provided. Unlike D.G. and K.C., D.A. did not differ significantly from controls in terms of quality judgment ratings. It is possible that the high quality judgment score might be a reflection of D.A.'s very particular descriptions of the schematic aspects of space. For example, D.A. would describe the route down to the meter, and was much more specific when describing the distance from one part of the route to the next compared to the majority of controls. It is possible that raters felt this amount of spatial detail evoked a sense of vividness comparable to that achieved by the descriptive details proffered by controls, and may have been factored into his quality judgment score. This may reflect a strategy that D.A. has adopted to compensate for areas of deficit in episodic re-experiencing and spatial detail memory. Indeed, we have shown previously that D.A. has, at times, demonstrated performance that is indistinguishable from or better than controls on tasks that have been otherwise shown in amnesic cases and in lesioned animals to depend on hippocampal function (Ryan, Moses, Barense, & Rosenbaum, 2013).

Amnesic cases D.G. and D.A. both had difficulty recognizing landmarks, results that are in line with previous findings in K.C. (Rosenbaum et al., 2000; but see Maguire et al., 2006). Their impaired performance on the landmark recognition task further implicates the HC in retrieving a detailed visual perceptual representation of space. The results from the current study are also consistent with findings that the HC plays a non-mnemonic role in the discrimination of spatial scenes and binding of information into a unified percept (Erez, Lee, & Barense, 2013; Graham, Barense, & Lee, 2010; Lee et al., 2005). The results are also consistent with recent research by Barker and Warburton (2011) showing that the HC plays a role in recognition memory specifically when a stimulus must be remembered to occur in a particular place. Our landmark recognition task explicitly examined this type of memory, as we asked participants to decide whether each landmark presented could be found in their pre-experimentally familiar environment.

The current study found impaired detailed and intact schematic representations in the route description task, thought to rely on egocentric representations, and the sketch mapping task, thought to predominantly rely on allocentric representations. Although some work has shown that an allocentric framework is often adopted for sketch mapping

(Ciaramelli et al., 2010), it is possible that using an egocentric approach could lead to similar results (Pick, 1993). As such, future studies should investigate how detailed and schematic representations relate to allocentric and egocentric representations, using a more purely allocentric task.

Our findings of intact schematic representations and impoverished detailed representations of familiar environments in amnesic patients with clear evidence of hippocampal damage provide support for the recently developed Transformation Hypothesis (Winocur, Moscovitch, & Sekeres, 2007; Winocur & Moscovitch, 2011), which proposes that the HC plays a key role in the binding of information from multiple modalities into vivid recollections. Perceptually rich representations, both visual (Erez et al., 2013; Graham et al., 2010; Lee et al., 2005) and in visual imagery (as in the current study), are impoverished following hippocampal damage. Findings of impaired landmark recognition in S.B. and house recognition in K.C., two individuals with compromised hippocampi, have been found alongside impaired autobiographical memory for details about personal events (Rosenbaum et al., 2005; Rosenbaum et al., 2000), linking episodic memory and perceptual details. It is possible that impoverished detailed representations of environments may not just parallel episodic memory impairment found in hippocampal amnesia, but may interact with or contribute to it. A paucity of perceptual details may contribute to impoverished episodic memory, as context-specific perceptual details are required to form a rich episode and engage in vivid re-experiencing (Robin & Moscovitch, 2014). St-Laurent, Moscovitch, Jadd, and McAndrews (2014) had individuals with unilateral medial temporal lobe epilepsy and healthy controls describe the perceptual features and story lines for film clips, written narratives, and personal autobiographical memories. They found that patients showed a deficit in perceptual details, especially in the autobiographical memory and film clip conditions, suggesting that a paucity of perceptual episodic memory details may impair re-experiencing of the past (St-Laurent et al., 2014). These findings are consistent with neuroimaging work that shows that the HC seems to be driven by the vividness of episodic memories or future imaginings (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Rabin, Gilboa, Stuss, Mar, & Rosenbaum, 2010; Bergouignan, Nyberg, & Ehrsson, 2014). Findings of impoverished detailed representations that lack perceptual richness suggest that the hippocampus may play an important role in binding details from multiple modalities into vivid recollections, as predicted by the Transformation Hypothesis.

Conclusions

Prior to the current study, conclusions regarding dissociations between detailed and schematic representations of space were largely inferred from performance of amnesic patients on separate tasks. The current study included two measures, a route description task and a sketch mapping task, that allow for both detailed and schematic representations to be assessed within the same measure. Use of the route description task in a previous study by Hirshhorn and colleagues' (2011) demonstrated impoverished perceptual details of routes retrieved by healthy older adults. The authors concluded that age-related changes to HC function likely accounted for these results, but it was not possible to rule out the contribution of other brain structures that also undergo age-related changes as responsible for the poor performance in the older adults.

In the current study, we aimed to extend previous findings of intact schematic representations and hints of impoverished detailed representations by testing three individuals with hippocampal amnesia on static mental navigation tasks and a route description task. Individuals with amnesia were able to provide basic directions along a route, draw sketch maps that were schematically intact, and perform similarly to controls on a vector mapping task, indicative of intact schematic representations of familiar environments. However, the low proportion of sensory descriptions about features along the route, sketch maps that lacked detail, and poor landmark recognition performance by the patients provides converging evidence that the HC is necessary for representing details of environments. More definitive support comes from dissociations between intact descriptions of the spatial properties of routes but impoverished descriptions of sensory features along those routes on a single measure. On the surface, the current results accommodate recent theoretical claims by the Transformation Hypothesis that the HC is needed for generating and binding details into vivid representations, but not for recollecting schematic, gist-like representations of environments that are sufficient for navigation.

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Appendix A: Tables

Table 1.

Experimental tasks and how they are expected to relate to allocentric and egocentric representations, and schematic and detailed representations of space.

Experimental Task	Brief description	Prominent Reference Frame[a]	Specific Aspects of Task	Expected to provide insight about integrity of _____ representations
Route Description	*Provide basic directions for walking route and describe walking route in as much detail as possible, providing information about the appearance of landmarks and where they are located in relation to each other and yourself.*	E	Ability to provide basic directions	schematic
			Proportion of Spatial References	schematic
			Proportion of Entities	detailed
			Proportion of Sensory Descriptions	detailed
			Quality Judgment Rating	detailed
Sketch Mapping	*Draw a map of specified environment, including as many details as possible.*	A	Overall configuration	schematic
			# of landmarks, street segments	detailed
Vector Mapping	*Draw a line indicating distance and direction from specified landmark to unspecified landmark*	A	Deviation in distance (cm)	schematic
			Deviation in direction (°)	schematic
Landmark Recognition	*Recognize and identify landmarks from target neighbourhood amidst foil landmarks*	NA	Ability to discriminate between Hits and False Alarms	detailed

Note: H, hits; FA, false alarm; A, allocentric; E, egocentric; NA, not applicable.

[a]As reported in Ciaramelli et al., 2010; Rosenbaum et al., 2004; Rosenbaum et al., 2007.

Table 2.

Performance of amnesic cases and matched controls on static mental navigation tasks.

Experimental Task		Environment: City S. D.G.	Control Mean (SD) (n=3)	Modified *t*-test, one-tailed	Neighbourhood M. D.A.	Control Mean (SD) (n=3)	Modified *t*-test, one-tailed	Neighbourhood E. K.C.	Control Mean (SD) (n=4)	Modified *t*-test, one-tailed
MENTAL NAVIGATION										
Vector Mapping	deviation (km)	1.695	1.273(0.520)	*t* = 0.703, *p* = 0.277	1.620	1.020(0.434)	*t* = 1.197, *p* = 0.177	3.400	3.300(0.316)	*t* = 0.283, *p* = 0.398
	deviation (°)	16.000	19.050(14.876)	*t* = -0.178, *p* = 0.438	39.250	17.950(7.552)	*t* = 2.443, *p* = 0.067	11.000	19.075(18.117)	*t* = -0.399, *p* = 0.358
					24.390*	17.950(7.552)	*t* = 0.739, *p* = 0.269			
LANDMARK APPEARANCE										
Recognition	Proportion of H	0.682	0.909(0.079)	*t* = -2.488, *p* = 0.065	1.000	0.956(0.038)	*t* = 1.003, *p* = 0.211	0.229	0.914(0.034)	***t* = -17.808, *p* < 0.001**
	Proportion of FA	0.182	0.268(0.162)	*t* = -0.459, *p* = 0.346	0.933	0.022(0.038)	***t* = 20.494, *p* = 0.001**	0.688	0.052(0.027)	***t* = 21.127, *p* < 0.001**

Note: H, hits; FA, false alarm; SD, standard deviation.
* Influential observation withheld
Bold text indicates a significant difference in performance.
Amnesic case K.C.'s data reprinted from Rosenbaum et al., (2000). Note that unlike D.G. and D.A., K.C. was tested on a forced-choice landmark recognition task.

Appendix B: Figures

Figure Captions

Figure 1. Proportion of total output attributed to spatial references, entities and sensory descriptions on Route Description Task for amnesic cases and controls matched for age and education. All amnesic cases provided a significantly higher proportion of spatial references and approximately equal amount of entities compared to controls. Amnesic cases D.G. and K.C. provided significantly less sensory descriptions compared to controls, while D.A. was trending towards significance on this measure. Standard error is represented in the figure by the error bars attached to each column. Note: * and ** indicate statistical significance ($p < 0.05$, $p < 0.01$, respectively).

Figure 2. Quality judgment ratings representing scorers' judgments about how vivid a mental representation they could conjure based on participants' transcribed route descriptions. Amnesic cases D.G. and K.C. earned significantly lower quality ratings compared to matched controls, indicating that their route descriptions evoked a less vivid and detailed representation of the route and features along the way in scorers. Amnesic case D.A. did not differ significantly from controls on this measure. Standard error is represented in the figure by the error bars attached to each column. Note: * and ** indicate statistical significance ($p < 0.05$, $p < 0.01$, respectively).

Figure 3. D.G.'s sketch map of home neighbourhood in City S, showing an intact basic schematic representation of his home environment, but fewer landmarks compared to controls.

Figure 4. Control 101's sketch map of home neighbourhood in City S (same neighbourhood as D.G.)

Figure 5. Control 103's sketch map of home neighbourhood in City S.

Figure 6. Control 104's sketch map of home neighbourhood in City S.

Figure 7. Amnesic Case D.A.'s sketch map of home neighbourhood M, showing intact layout of environment, but fewer landmarks and street segments compared to controls.

Figure 8. Control 301's sketch map of home neighbourhood M.

Figure 9. Control 302's sketch map of home neighbourhood M.

Figure 10. Control 304's sketch map of home neighbourhood M.

Figure 11. Deviation in degrees for amnesic cases and their individually matched controls on the Vector Mapping task. Note influential observation withheld from amnesic case D.A.'s overall performance. None of the three amnesic cases differed significantly from their controls, matched for age, education, and environment. Standard error is represented in the figure by the error bars attached to each column. K.C.'s data reproduced with permission from Rosenbaum et al., 2000.

Figure 12. Deviation in distance (cm) for amnesic cases and their individually matched controls on the Vector Mapping task. None of the three amnesic cases differed significantly from their controls, matched for age, education, and environment. Standard error is represented in the figure by the error bars attached to each column. K.C.'s data reproduced with permission from Rosenbaum et al., 2000.

Figure 13. Proportion of hits and false alarms (FA) for amnesic cases and matched controls on the landmark recognition task. Amnesic case D.G. recognized fewer target landmarks than controls, but demonstrated a similar number of false alarms. D.A. showed a less conservative response style, identifying every target landmark, but also incorrectly identifying significantly more foil landmarks. Amnesic case K.C. also seems to have difficulty recognizing landmarks, with significantly less hits and more false alarms compared to his matched controls (forced-choice data from Rosenbaum et al., 2000). Standard error is represented in the figure by the error bars attached to each column. Note: ** indicates statistical significance ($p < 0.01$).

Figure 14. Sample transcript of patient and control probes from route description task. The sample patient probe (from K.C.'s route description) lacks in detail compared to the control probe, which includes intricate details about the structure being described, including colour and size.

Figure 1.

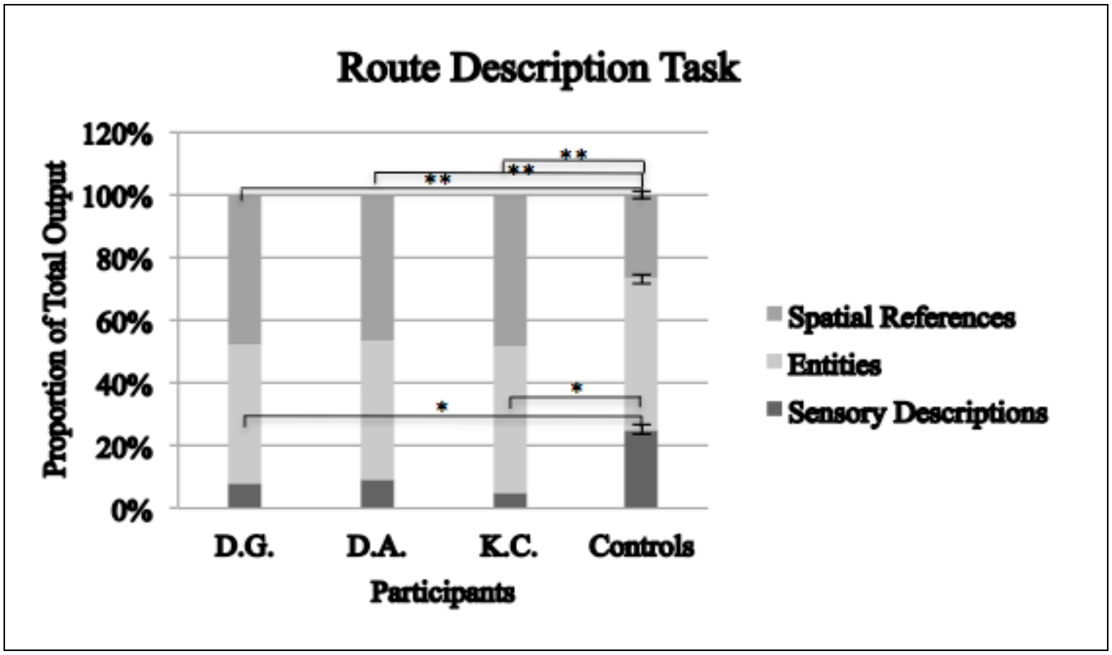

Route Description Task
120%
100%
80%
60%
40%
20%
0%
Proportion of Total Output
**
**
**
*
*
Spatial References
Entities
Sensory Descriptions
D.G.
D.A.
K.C.
Controls
Participants

Figure 2.

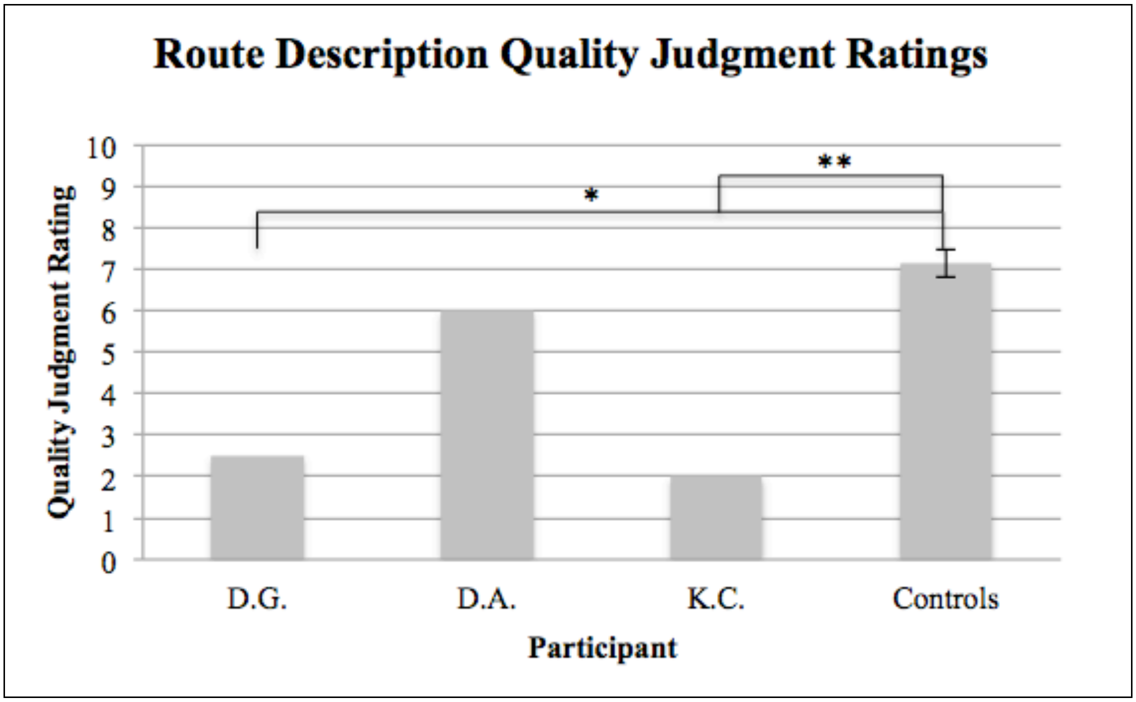

Route Description Quality Judgment Ratings
Quality Judgment Rating
10
9
8
7
6
5
4
3
2
1
0
*
**
D.G.
D.A.
K.C.
Controls
Participant

Figure 3.

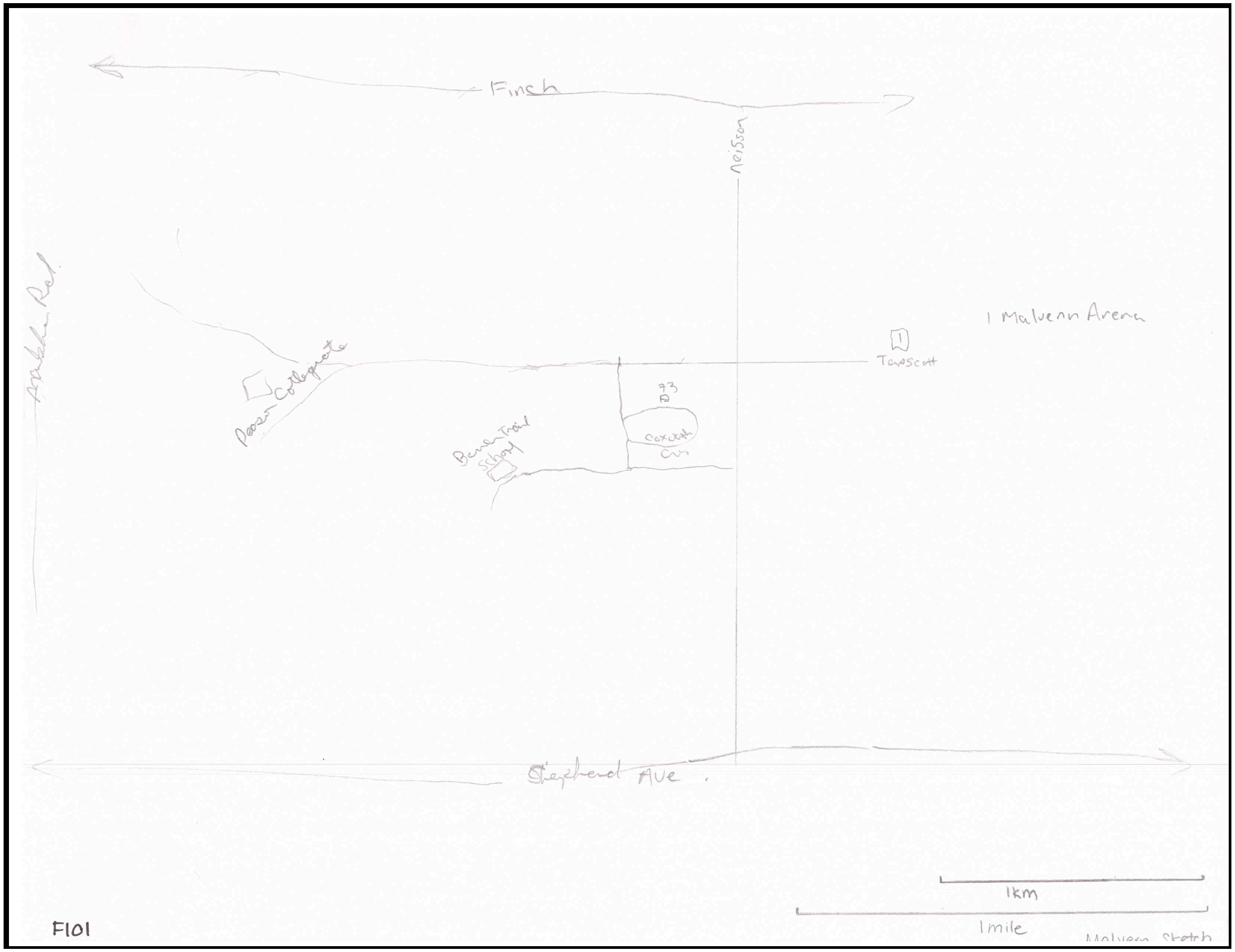

Finch
Neilson
1 Malvern Arena
Tapscott
Collegiate
73
Shepherd Ave
1km
1mile
Malvern Sketch
F101

Figure 4.

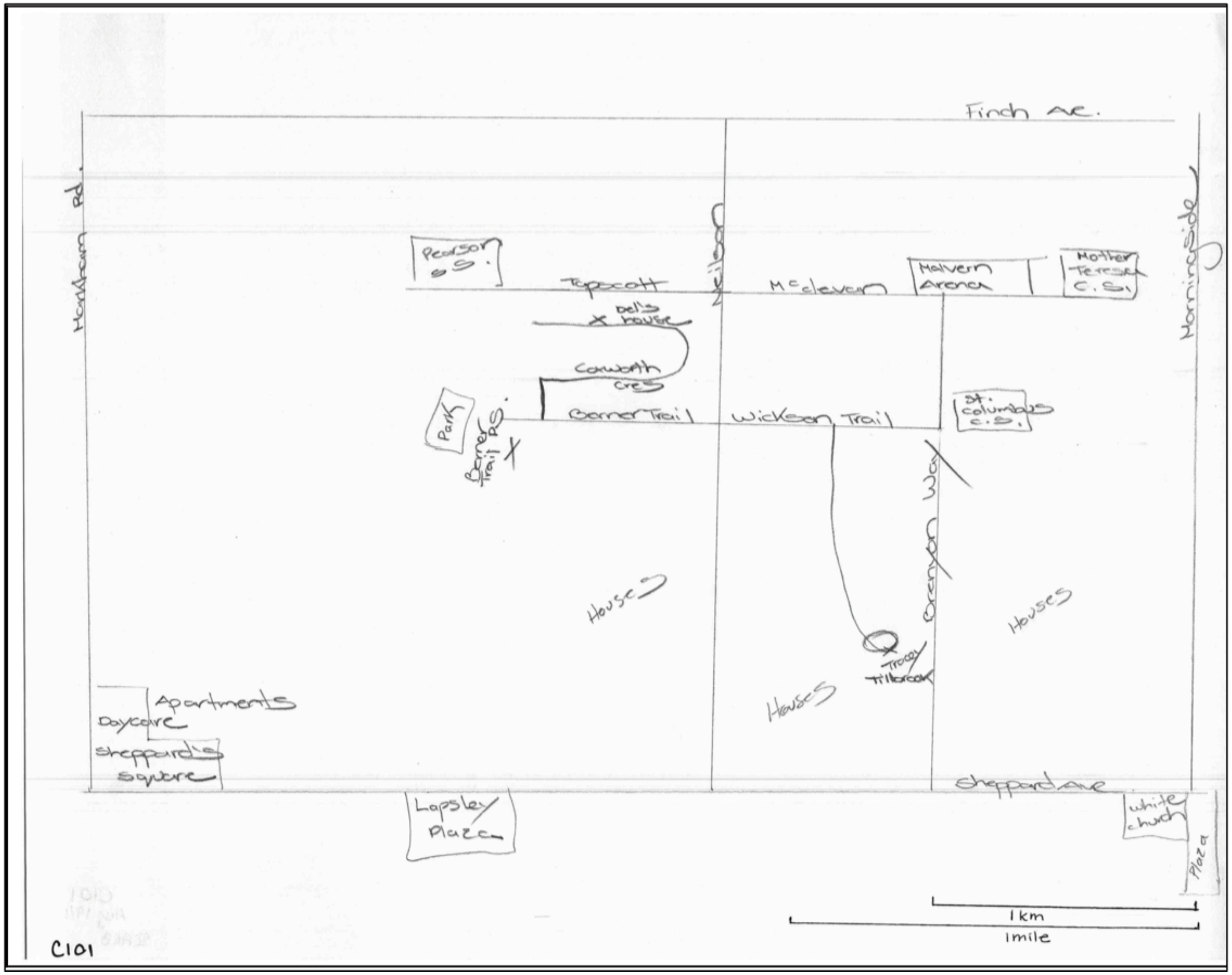

Finch Av.
Markham Rd.
Morningside
Pearson S.S.
Tapscott
Neilson
McLevin
Malvern Arena
Mother Teresa C.S.
Dell's house
Cornwath Cres
Berner Trail
Wickson Trail
Park
Berner Trail P.S.
St. Columbus C.S.
Brenyon Way
Houses
Houses
Houses
Tilbrook
Apartments
Daycare
Sheppard's Square
Sheppard Ave
Lapsley Plaza
White church
Plaza
1km
1mile
C101

Figure 5.

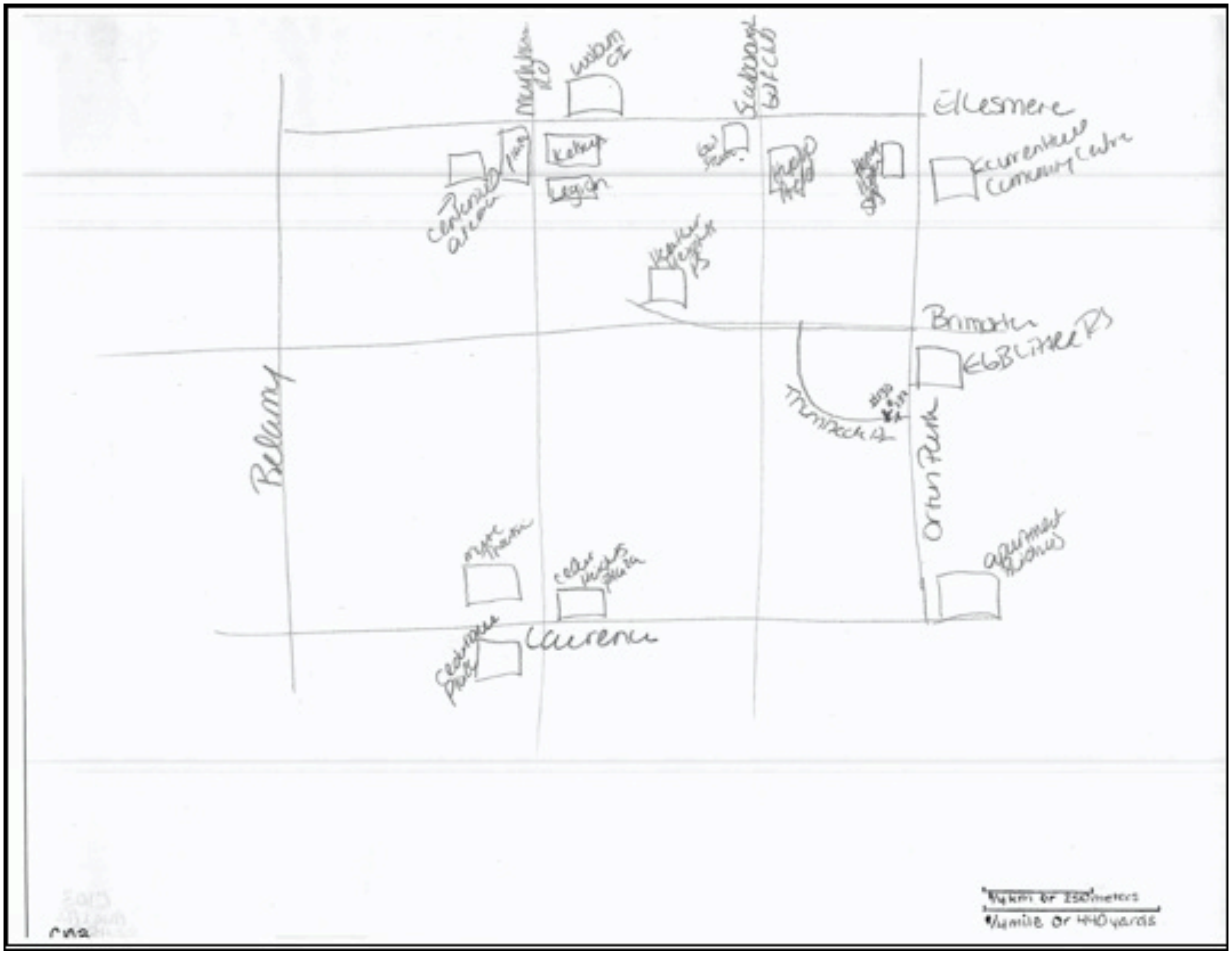

Ellesmere
Lawrence
Bellamy
Orton Park
1/4 km or 250 meters
1/4 mile or 440 yards

Figure 6.

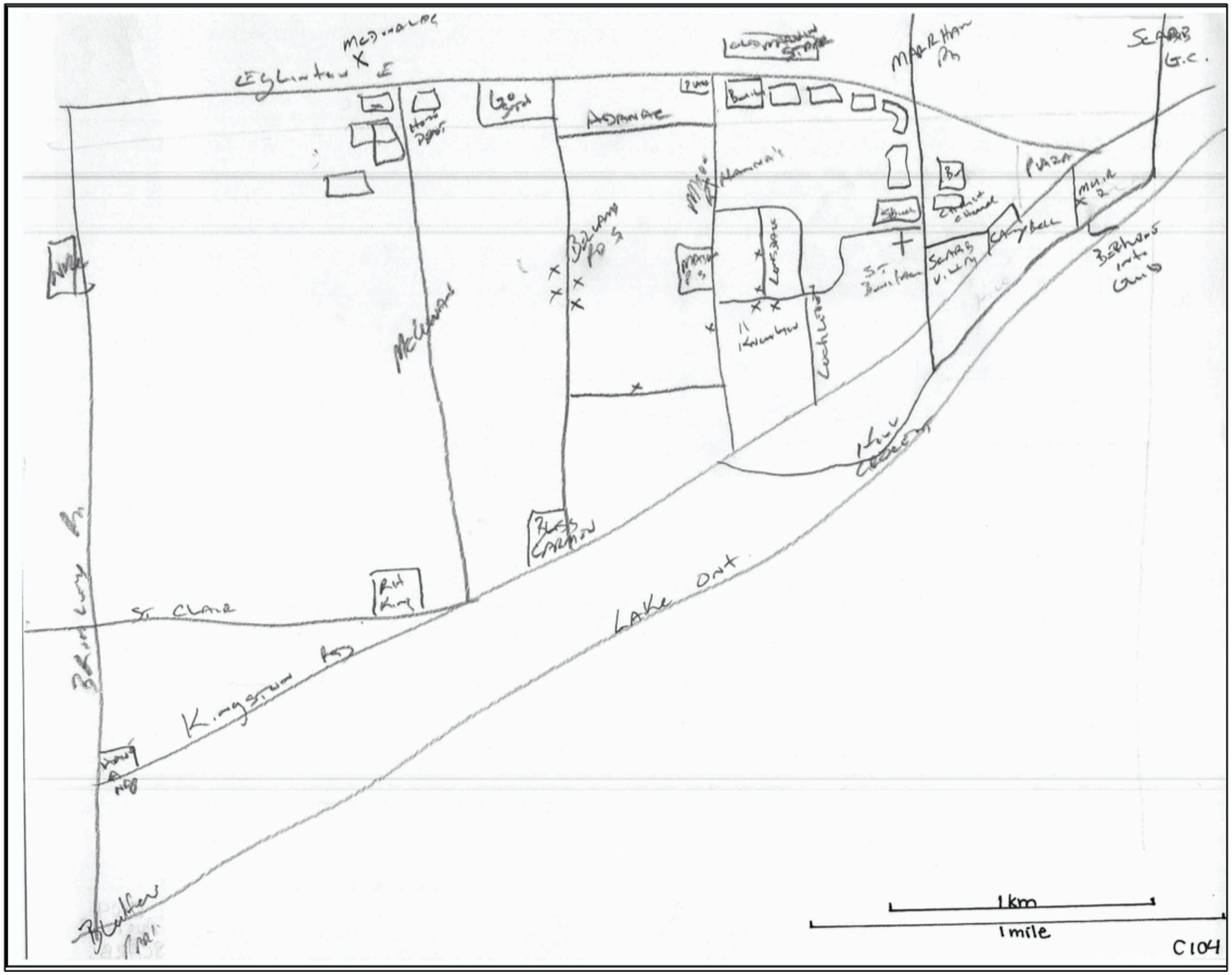
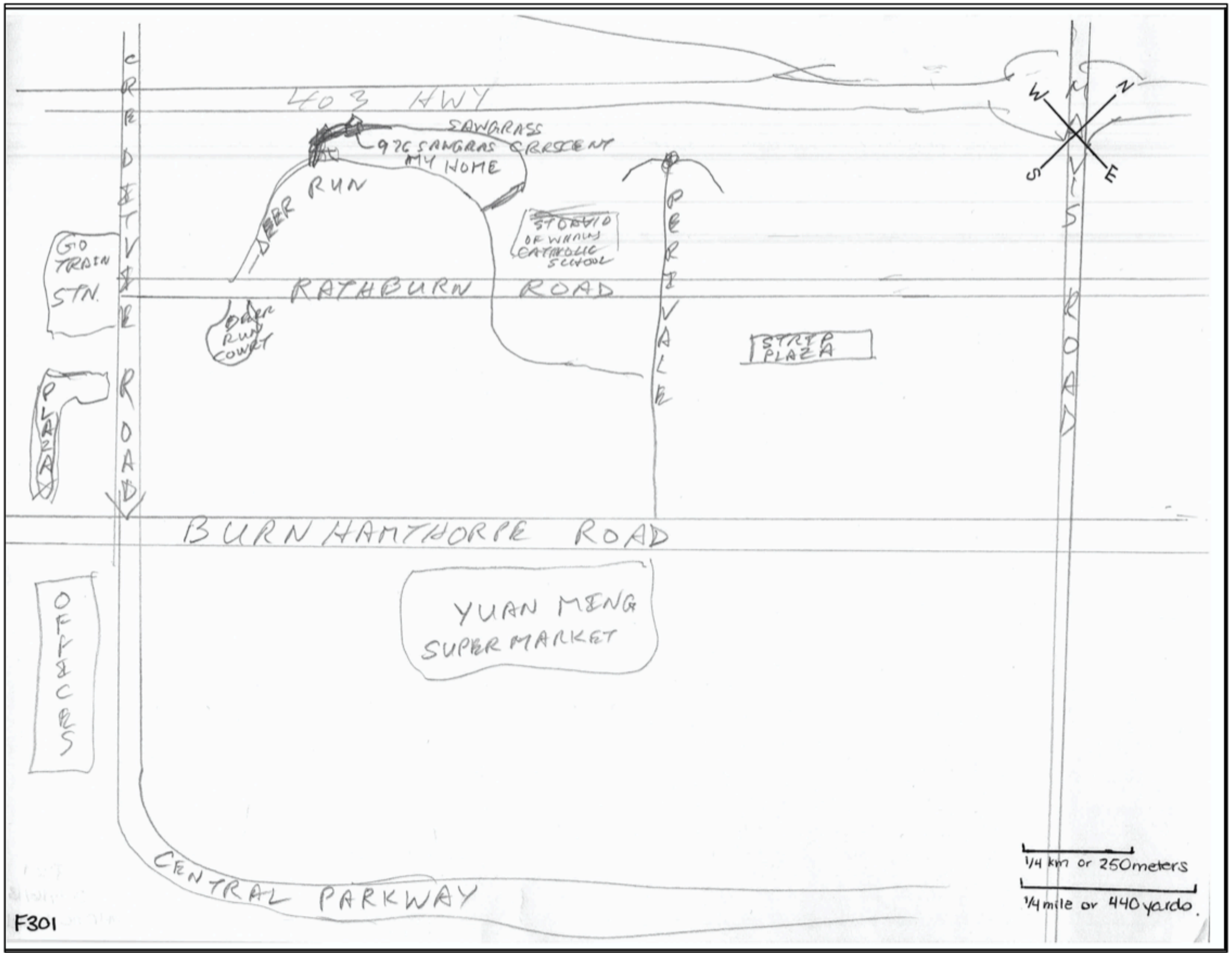
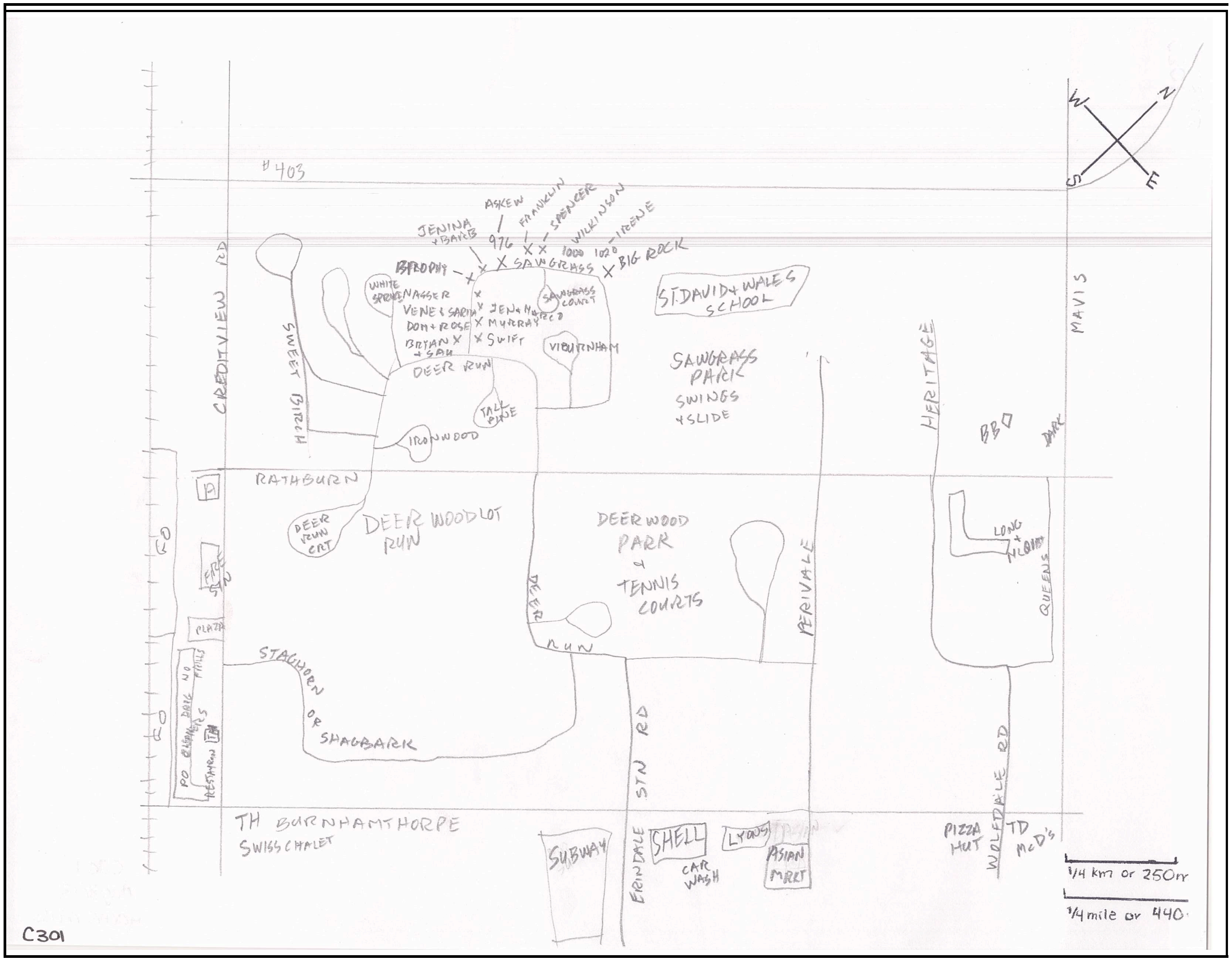

Eglinton E
Home Depot
Markham Rd
Scarb G.C.
Plaza
Muir Dr
Bellamy Rd S
McCowan
St. Clair
Kingston Rd
Lake Ont
1km
1mile
C104

Figure 7.



403 HWY
SAWGRASS
MY HOME
RUN
GO TRAIN STN.
RATHBURN ROAD
STRIP PLAZA
PLAZA
BURNHAMTHORPE ROAD
YUAN MING SUPERMARKET
OFFICES
CENTRAL PARKWAY
W
N
S
E
1/4 km or 250meters
1/4 mile or 440 yardo.
F301

Figure 8.



#403
CREDITVIEW RD
MAVIS
RATHBURN
BURNHAMTHORPE
ERINDALE STN RD
DEERWOOD PARK + TENNIS COURTS
SAWGRASS PARK SWINGS + SLIDE
ST. DAVID + WALES SCHOOL
DEER WOODLOT RUN
SUBWAY
SHELL
CAR WASH
ASIAN MRKT
PIZZA HUT
TD
McD's
SWISS CHALET
1/4 km or 250m
1/4 mile or 440
C301

Figure 9.

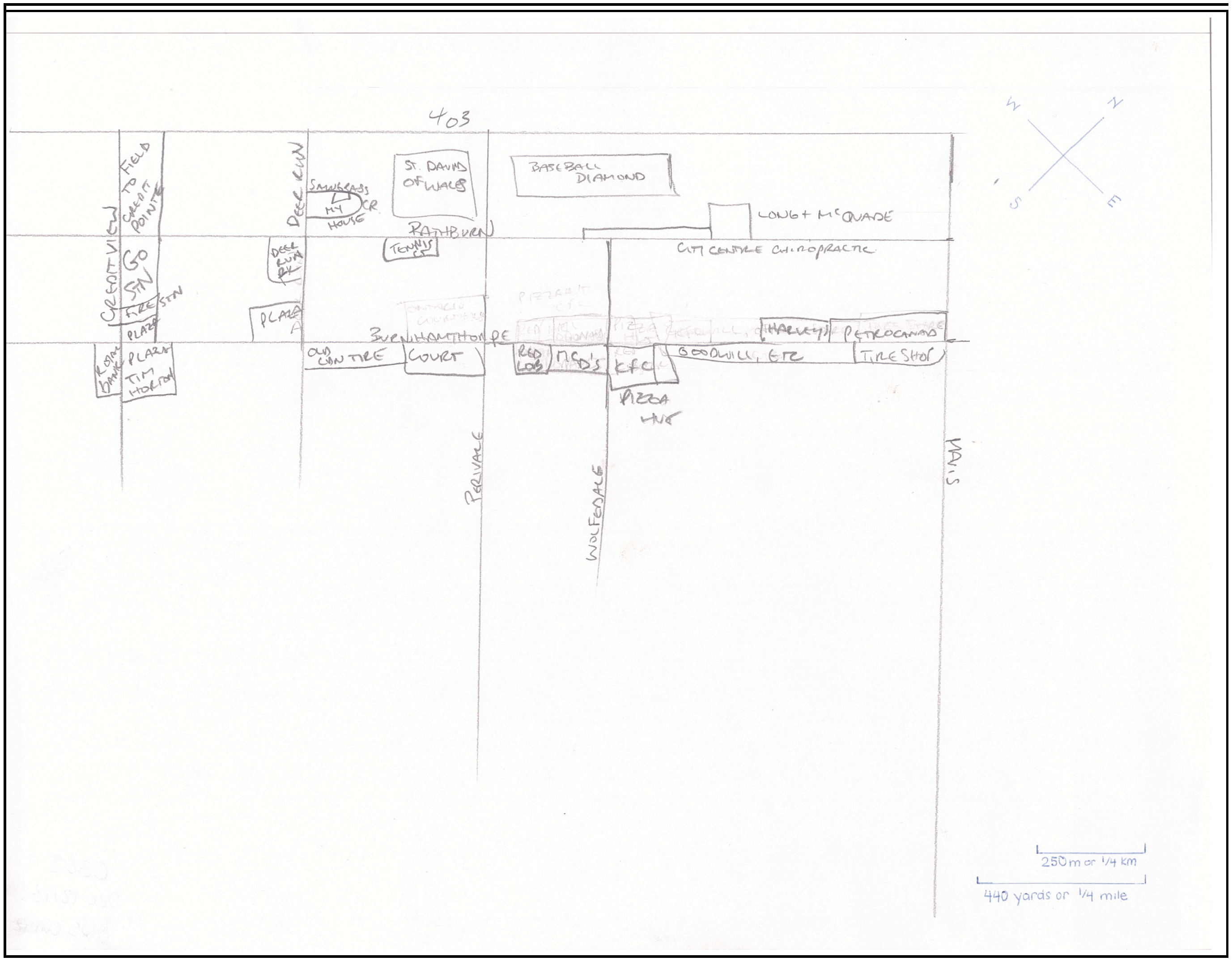

403
ST. DAVID OF WALES
BASEBALL DIAMOND
LONG + McQUADE
CITY CENTRE CHIROPRACTIC
RATHBURN
TENNIS CT
MY HOUSE
GO STN
PLAZA
OLD CDN TIRE
COURT
RED LOB
McD'S
KFC
PIZZA HUT
GOODWILL, ETC
HARVEYS
PETROCANADA
TIRE SHOP
TIM HORTON
PERIVALE
WOLFEDALE
HWY 5
250m or 1/4 km
440 yards or 1/4 mile

Figure 10.

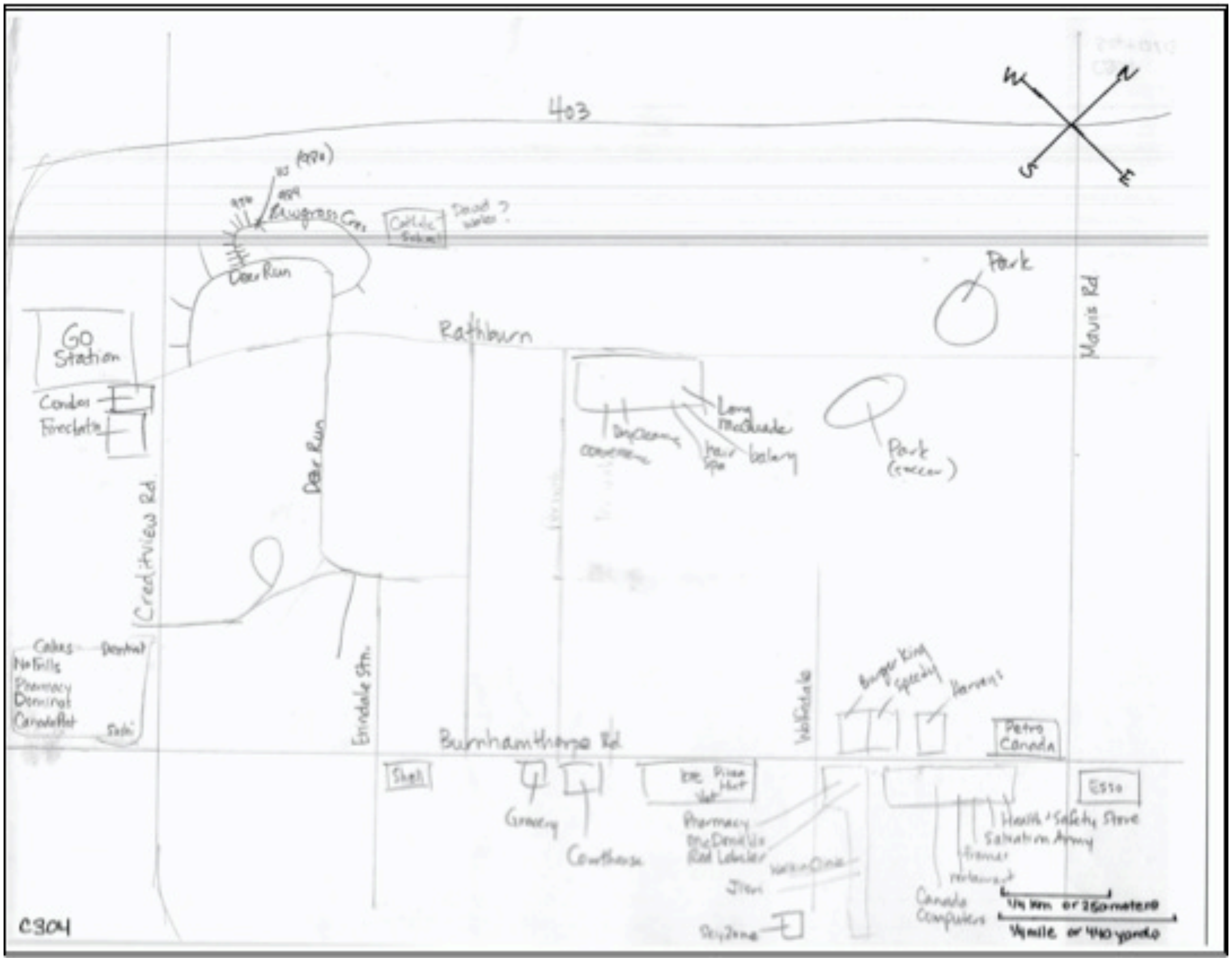

403
W
N
S
E
Park
Mavis Rd
Rathburn
Go Station
Condos
Deer Run
Credit view Rd
Park (soccer)
Erindale Stn.
Burnhamthorpe Rd
Shell
Grocery
Courthouse
Pizza Hut
Pharmacy
Burger King
Speedy
Harveys
Petro Canada
Esso
Health & Safety Store
Salvation Army
Canada Computers
1/4 km or 250 meters
1/4 mile or 440 yards
C304

Figure 11.

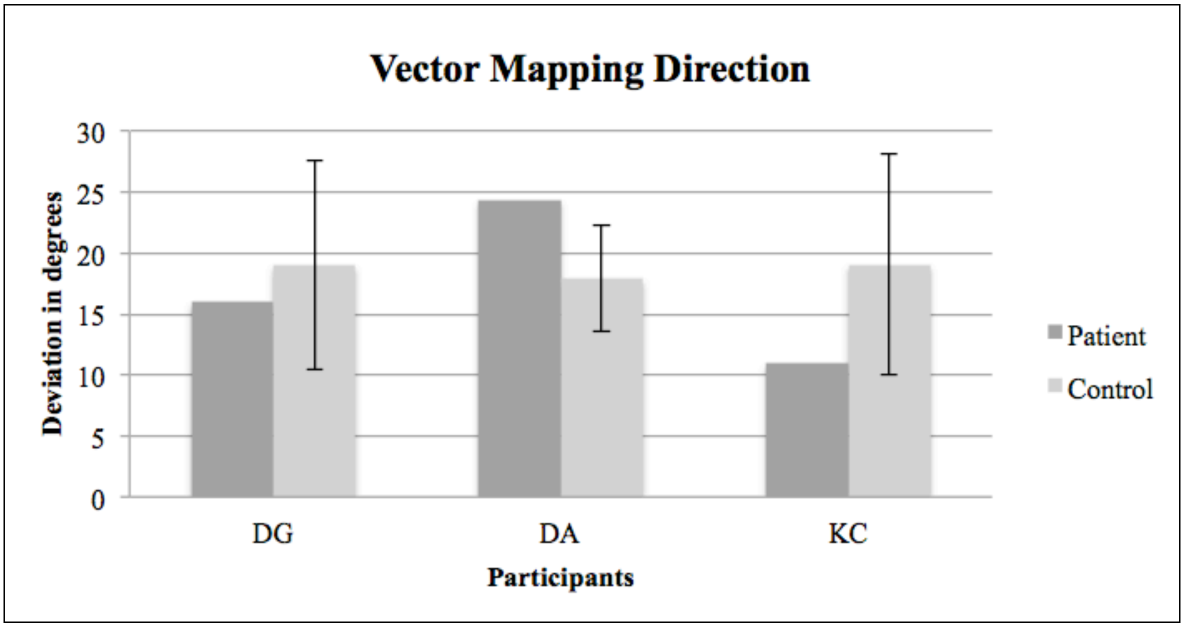

Vector Mapping Direction
Deviation in degrees
30
25
20
15
10
5
0
DG
DA
KC
Participants
Patient
Control

Figure 12.

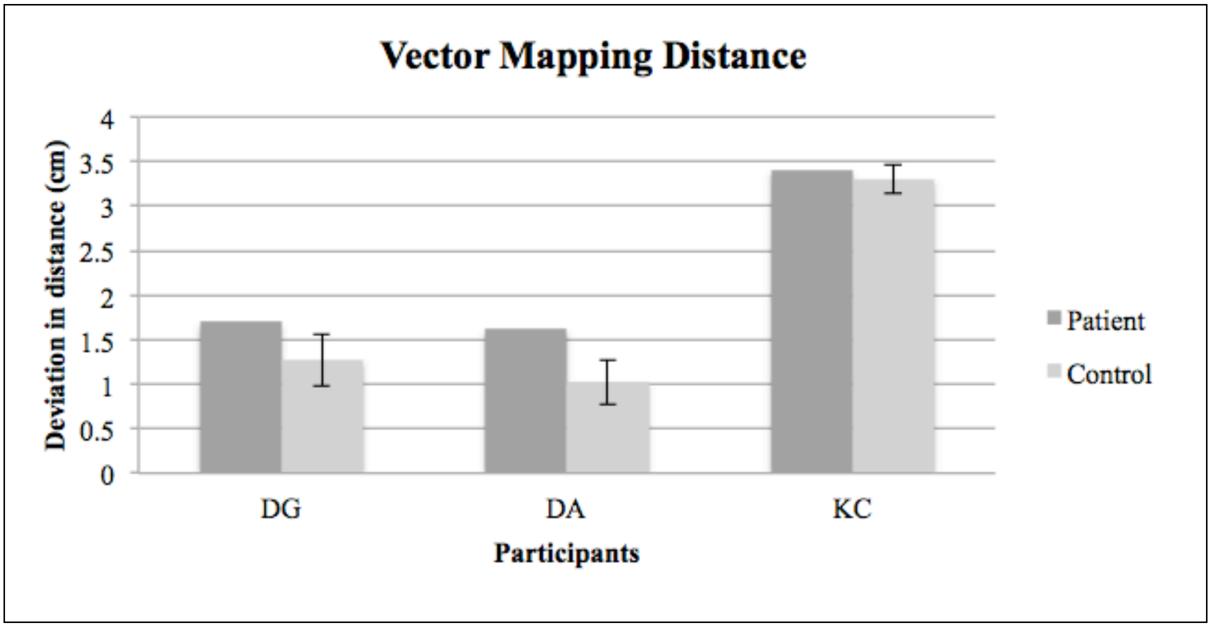

Vector Mapping Distance
Deviation in distance (cm)
4
3.5
3
2.5
2
1.5
1
0.5
0
DG
DA
KC
Participants
Patient
Control

Figure 13.

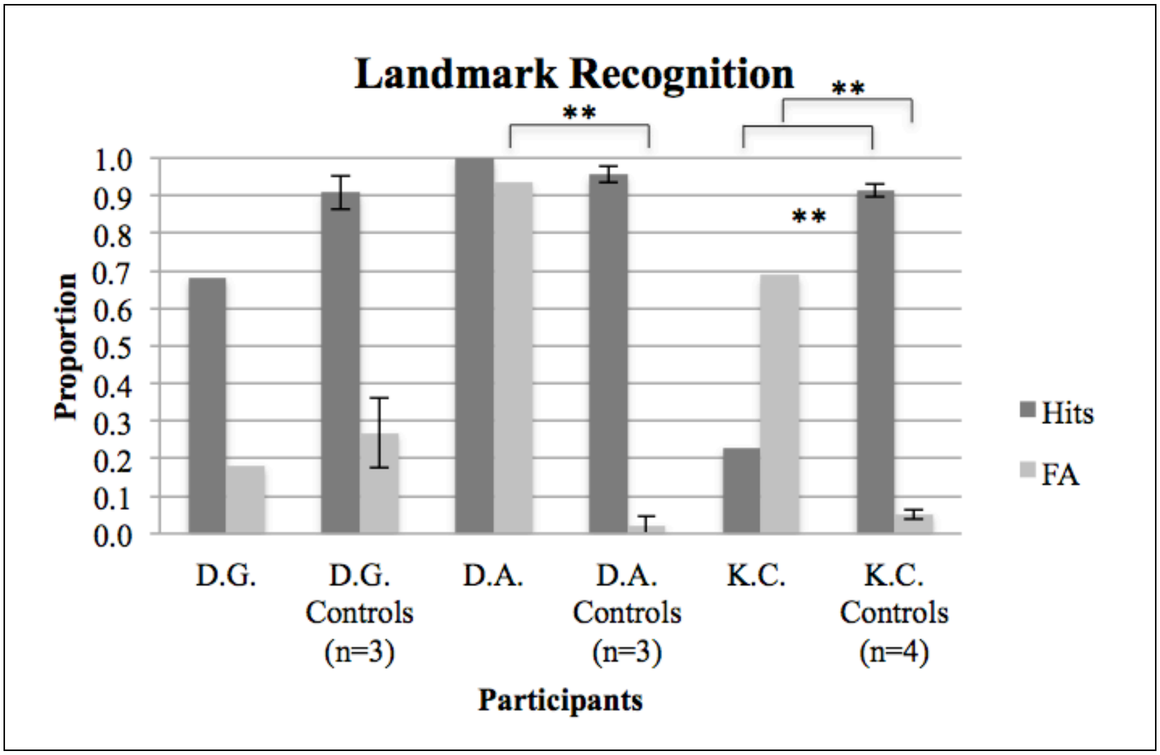

Landmark Recognition
**
**
**
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Proportion
Hits
FA
D.G.
D.G. Controls (n=3)
D.A.
D.A. Controls (n=3)
K.C.
K.C. Controls (n=4)
Participants

Figure 14.

<u>Sample Patient Probe (K.C.):</u>

Brother's House

" It's a bungalow, with a garage."

<u>Sample Control Probe:</u>

Splash pad

"The splash pad, uh, a couple of them are poles that are tall. If you press the button there are little spouts on the sides of it, so it just kind of sprays out over them. There are also, they look like pipes, they are arches and water comes down from the top of those ones. And basically it's just a… the arches are white, the poles I think are white. Um, the kids just run in and out all the time. What else can I think about… the walkway, uh, just between it and the boardwalk is now, it's a new kind of like a rubberized interlocking. So there's less chance of them slipping or falling on cement or that. Uh, because the, the ground part of the splash pad is kind of like that rusty reddish colour, it looks gravel-y, so it's got traction for them. But now they've got the other rubbery part from where they come out so that they don't fall."