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Cognitive adaptations for gathering-related navigation in humans

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Abstract

Current research increasingly suggests that spatial cognition in humans is accomplished by many specialized mechanisms, each designed to solve a particular adaptive problem. A major adaptive problem for our hominin ancestors, particularly females, was the need to efficiently gather immobile foods which could vary greatly in quality, quantity, spatial location and temporal availability. We propose a cognitive model of a navigational gathering adaptation in humans and test its predictions in samples from the US and Japan. Our results are uniformly supportive: the human mind appears equipped with a navigational gathering adaptation that encodes the location of gatherable foods into spatial memory. This mechanism appears to be chronically active in women and activated under explicit motivation in men.
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1. Introduction

Our experience of the world feels immediate, complete and effortless, but may be generated less impartially than we think. Increasing evidence suggests that our perceptual, cognitive and memory faculties preferentially process objects, events and relationships that have carried adaptive significance throughout our evolutionary history (New, Cosmides, & Tooby, 2007). Such "biases" may be implemented at the most fundamental, physiological level. For example, trichromatic color vision likely evolved in our primate ancestors because individuals sensitive to the red-green color spectrum could better distinguish more nutritious plant foods (Rowe, 2002). To the frustration of nutritionists, our taste preferences strongly reflect the priorities — and scarcities — of fats, salts, proteins and sugars in the ancestral world (Drewnowski & Greenwood, 1983). A number of adaptively relevant biases are also evidently engrained in our

attentional capacities, such as implicit prioritization of faces (Ro, Russell, & Lavie, 2001), eye-gaze (Friesen & Kingstone, 1998) and animate objects of all kinds (New, Cosmides et al., 2007). Similar evolved biases may also characterize memory; for example, recent studies suggest a retention bias for information processed for relevance to survival (Nairne & Pandeirada, 2008).

For every species, the acquisition of material and energetic resources is one of the most long-standing and fitness-relevant adaptive problems. Here we pursue the idea that, during human evolution, natural selection has built specialized cognitive adaptations to support efficient gathering of plant foods.

1.1. Sexually dimorphic specializations for harvesting of plant foods

Ancestral hominins made much of their living gathering a wide variety of immobile foods, but there is strong evidence that this foraging strategy was sexually differentiated (Murdock, 1936; Murdock, 1967; Tooby & DeVore, 1987). Based on ethnographically known hunter-gatherers,

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females adopt a relatively habitual gathering strategy (Murdock, 1967, Marlowe, 2007), gathering more often and more exclusively than males. In contrast, males gather more opportunistically, often in the course of pursuing their primary foraging activities, such as hunting animals (Marlowe, 2007). At least two lines of evidence suggest that this sex difference in foraging style has significant time depth in the human lineage. First, all described hunter-gatherers manifest this sex difference, including populations whose most recent common ancestor lived more than 100,000 years ago (Chen et al., 2000; Gonder, Mortensen, Reed, de Sousa, & Tishkoff, 2007); indeed, this set includes the most genetically divergent of all extant human populations (Knight et al., 2003) — San and Hadza — suggesting that a sexual division of foraging labor is the primitive (basal) condition for *Homo sapiens*. Second, although hunting provides only a small percentage of chimpanzee (Pan troglodytes) foods, there is nevertheless a conspicuous male bias in chimpanzee hunting (Mitani & Watts, 2001; Stanford, Wallis, Matama, & Goodall, 1994). This evidence helps to characterize the primitive condition for panids (the taxon that includes chimpanzees as well as all extinct and extant humans) and which thus prevailed at least 7 million years ago: a diet derived principally from plant food foraging but one where any hunting is primarily done by males.

The computational requirements of habitual and opportunistic gathering differ, so cognitive adaptations for gathering in women and men should differ in parallel. In order to optimize their foraging efforts, gatherers should register cues that predict the differential return rates of potentially gatherable foods (Schoener, 1971). A diverse body of results suggests that selection has more strongly favored such mechanisms in women: relative to men, women prefer colors associated with ripeness (Hurlbert & Ling, 2007), make finer taste discriminations (Jameson, Highnote, & Wasserman, 2001), have better taste memory (Baker, 1987) and are better at discriminating and remembering types of plants (Neave, Hamilton, Hutton, Tildesley, & Pickering, 2005). Recent ethnographic evidence suggests a sex difference in taste preferences, with women preferring fruit sources over meats while men exhibit the reverse preference (Berbesque & Marlowe, 2009). Here we evaluate whether humans have also evolved navigational specializations for gathering and whether aspects of this computational design differ predictably between the sexes.

1.2. Two cognitive models of plant food foraging

1.2.1. Hunter-Gatherer Theory

Silverman and Eals (1992) were among the first to propose a female specialization in gathering-related spatial cognition. Analyzing the task of gathering, they argued that gatherers would require memory for the relative positions of edible plants in tangled banks of other vegetation. Consequently, they predicted a female advantage for what they called object location memory, defined as memory for the relative positions of objects within a constrained array. Their proposed mechanism operates by encoding the locations of objects relative to each other; because plant locations can be indexed relative to the location of non-food objects and landmarks, this mechanism would benefit from encoding the locations of any similarly scaled object that could reference the location of an immobile food source.

Numerous empirical studies have tested these predictions and shown a content-general female advantage on relational spatial memory in a diversity of cultures (McBurney, Gaulin, Devineni, & Adams, 1997; Montello, Lovelace, Golledge, & Self, 1999; Silverman, Choi, & Peters, 2007; for review, see Voyer, Postma, Brake, & Imperato-McGinley, 2007). In other words, as predicted by the Hunter-Gatherer model, women show better memory for the relative locations of objects across a broad range of object categories. Importantly, however, this female advantage is highly sensitive to the spatial integrity of the array; the sex difference either disappears or reverses when the task's relational component is removed. For example, swapping the location of two objects preserves both the relational integrity of the array and the female advantage; in contrast, moving objects to new (previously unoccupied) locations obliterates relational integrity and females do not outperform males in such conditions (James & Kimura, 1997; Postma, Jager, Kessels, Koppeschaar, & van Honk, 2004). In this second set of conditions the task becomes a test of absolute — not relative — spatial memory. As argued above, a collapse of the female advantage in such conditions can be seen as consistent with the Silverman and Eals' tangled-bank analysis.

1.2.2. Gathering Navigation Theory

The spatial demands of plant food gathering are not limited to the kind of "tangled-bank" memory measured by Silverman and Eals' (1992) object location task. Superior tangled-bank memory of the type predicted and shown by Silverman and Eals should enable a gatherer to efficiently locate resources within a local patch of vegetation. However, gatherers exploit resources over a large area, and object location memory does not facilitate navigation to, from or among resource patches at this scale. A successful gatherer must also be able to encode the location of immobile resources in a manner that supports navigation — that is, encoding absolute location within a represented environment, not just position relative to nearby objects. As discussed above, women have not been found to demonstrate superior performance on such absolute spatial memory tasks, at least with the wide range of stimulus categories that have been used in previous studies. But there is evidence that women do show superior absolute spatial memory when the stimulus set is restricted to the ecologically relevant class of gatherable food items (New, Krasnow, Truxaw, & Gaulin, 2007).

It seems plausible, then, that in addition to the mechanism that subserves tangled-bank memory, humans also have

Table 1
A comparison of two cognitive models of plant-food foraging

	Theory	
	Hunter-Gatherer	Gathering Navigation
Original reference	Silverman & Eals, 1992	New, Krasnow et al, 2007
Selected ability	Tangled-bank memory	Navigation to plant resources
Operationalization	Relative object location	Absolute plant location
Predicted female advantage	Relative location of objects within a spatially stable array	Absolute location of gatherable foods in a global environmental frame
Manipulation predicted to disrupt female advantage	Movement of neighboring items disrupting the relational array	Shift to non-gatherable content
Evidence for disruption	James & Kimura, 1997; Postma et al., 2004	Present study

navigational specializations for gathering. The mechanism predicted by this Gathering Navigation Theory should be preferentially activated by high-quality resources, encoding their locations better than the locations of low-quality resources. We tested this prediction in a large, complex, real-world environment — an outdoor farmer's market — and found that men and women demonstrated better absolute location memory (tested via direction estimation) for foods with higher caloric density. Because ancestral women gathered more often and more exclusively than ancestral men, we proposed that selection should have acted more strongly to hone and maintain these abilities in women. Consistent with this prediction — and despite using a test methodology (direction estimation) that typically advantages men — we observed a significant female advantage in location memory for gatherable foods (New, Krasnow, et al., 2007).

The results of New, Krasnow et al. (2007) support Gathering Navigation Theory, but they left some key predictions untested. At least partially distinct from mechanisms that may subserve relational tangled-bank memory, Gathering Navigation Theory predicts a gathering-related specialization within an absolute memory system. Absolute memory encodes object locations relative to an environmental frame. This encoding can be categorical (i.e., northwest quadrant) or metric (Kosslyn et al., 1989) or utilize the two modes in combination (Huttenlocher, Hedges, & Duncan, 1991); importantly, though, this encoding is relative to the environment rather than relative to other objects. An absolute memory system designed for gathering, because it encodes environment-relative locations rather than object-relative locations, would have little use for information about the locations of non-food items. Thus, our hypothesized absolute spatial mechanism should operate preferentially for gatherable content. Therefore, Gathering Navigation Theory predicts a sexually differentiated mechanism that specifically supports absolute spatial memory for gatherable resources. If the female advantage either arises from a non-spatial processing advantage or reliably generalizes to gathering-irrelevant categories, Gathering Navigation Theory would not be supported. In light of the Postma et al. (2004)

results (no female advantage on content-general, absolute spatial memory), a gatherable-specific female advantage for absolute spatial memory, if found, would be striking.

Table 1 outlines the differences between Silverman and Eals' (1992) Hunter-Gatherer Theory and Navigational Gathering Theory described here. It should be clear that these are not mutually exclusive theories; tangled-bank memory and absolute plant location memory solve different spatial problems for gatherers. To date, the predictions of the Hunter-Gatherer Theory have been generally supported, including the definitive disruption by perturbations of the relational array. At present, some ecologically relevant evidence supports Gathering Navigation Theory's prediction of superior absolute spatial memory for plant foods (New, Krasnow et al., 2007; Pacheco-Cobos, Rosetti, Cuatianquiz, & Hudson, 2010), but the definitive disruption by non-food content has yet to be tested. A central goal of this study was to test for that disruption.

Further predictions of Gathering Navigation Theory can be generated. Differences between female and male performance should reflect the different attentional protocols of habitual vs. opportunistic gathering. Because ancestral women were habitual gatherers, this navigational mechanism should operate more spontaneously in women. In their daily collecting rounds, gatherers encounter large numbers of plants, some of which are potential future resources. A cognitive mechanism that processes information about the location of potential future resources automatically — without competing for volitional attention with other concurrent activities, such as resource transport, child care and predator avoidance — would improve habitual gathering efficiency. The attentional signature of such a habitual gathering mechanism would consist of relatively consistent location memory accuracy across items despite variance in visual attention. In contrast, given the computational requirements of opportunistic gathering (as practiced by hunters), it is expected that the male navigational gathering mechanism would not operate automatically, but could nevertheless be activated by situations of explicit or exogenous motivation. This motivation could be item specific (e.g., when encountering particularly good gatherable items such as honey) or situation specific (e.g., when preferable hunting options are absent). The attentional

signature of such an opportunistic gathering mechanism would consist of (i) improved location memory accuracy with increasing amounts of visual attention given the absence of situational motivation and (ii) consistent location memory accuracy despite variance in visual attention given adequate situational motivation.

1.2.3. Why sexual differentiation?

If sexually monomorphic gathering was the ancestral state, then it is not necessarily the case that male specialization in hunting would result in sexually differentiated gathering mechanisms. For example, male spatial adaptations for hunting could simply be added onto those that served the needs of both sexes prior to a significant male specialization on hunting. In such a scenario, males might have hunting-related spatial advantages but females would have no distinct abilities. In other words, a female spatial advantage for plant-food foraging would evolve only if there were a cost to males of maintaining this phylogenetically older ability. Thus, the predicted sex differences assume that certain aspects of foraging-related cognition have been reduced in males but retained in females. Such a prediction is justified if plant-related and animal-related foraging adaptations differ (as argued above) and are costly to maintain unused. Such is likely the case, as neural mechanisms are both materially and energetically costly (see Lassek & Gaulin, 2008). If males engaged less in habitual gathering than did females, then the mechanisms that support habitual gathering in males would be under less selection against entropic mutation and under greater selection to spend fewer material and energetic resources in their construction and maintenance. For at least these reasons, Gathering Navigation Theory predicts sexual differentiation.

1.2.4. Is a male spatial advantage predicted for animal content?

Does this perspective on the ancestral sexual division of foraging labor (Marlowe, 2007) predict male-biased adaptations designed for hunting animals? Yes, but not in strict cognitive isometry to the hypothesized female navigational gathering adaptation. First, plants are immobile such that present location is strongly predictive of future location; this is not so for mobile animals, thus encoding their present locations is less helpful for future hunting. (For relocating animals, information about microhabitat or habitual ranging patterns may be more useful than content-free location information.) Moreover, animals present immediate risks of predation or injury that impinge similarly on both sexes; both sexes would benefit from an attentional system that continually monitored the location and state of nearby animals. For these reasons, we would expect an enhancement in spatial processing of animals compared to less active — and perhaps less immediately fitness-relevant — categories such as plants (e.g., New, Cosmides et al, 2007), but one that manifests similarly in both sexes. Gathering Navigation

Theory therefore does not predict a male advantage for animal content on the present task. Such considerations help to emphasize the design specificity of the hypothesized navigational-gathering adaptations.

1.3. Predictions

Testing the predictions of Gathering Navigation Theory requires an experimental task with four elements: (1) subjects must see multiple objects, only some of which are gathering relevant; (2) visual attention to these objects must be measured; (3) absolute memory for the locations of these objects must be tested; and (4) non-spatial aspects of object memory must be measured and controlled. These experimental elements allow testing of the following hypotheses:

H_1: Women have better absolute spatial memory than men for immobile food resources, such as fruiting trees.

H_2: This female advantage over men is specific to spatial memory and is not caused by a more general, non-spatial advantage.

H_3: This female advantage over men is specific to immobile food resources and does not generalize to other classes of content.

H_4: The navigational-gathering mechanism operates more automatically in women than in men.

Because the proposed mechanism should be a component of a universal human nature, Gathering Navigation Theory predicts that it will be reliably observed in populations around the world. Of course, cognitive mechanisms are often designed to be sensitive to environmental input, both in the course of their development and during their operation. We do not predict that this mechanism will operate identically in all populations or test conditions; rather that:

H_5: The performance signature of the navigational gathering adaptation (H_1 through H_4) should be reliably observed across cultures.

A growing literature suggests differences in spatial perception and cognition between Eastern and Western cultural groups (for review, see Nisbett, Peng, Choi, & Norenzayan, 2001) such as the US and Japan. Of particular relevance to the present theory, differences have been observed between Eastern and Western cultural groups in holistic processing of visual displays (Kitayama, Duffy, Kawamura, & Larsen, 2003) that could reasonably influence performance on the type of task we employ here. Therefore, we chose these two groups to test the robustness of the above predictions of Gathering Navigation Theory.

Our initial test of Gathering Navigation Theory utilized a test methodology with relatively high ecological validity — real-world orientation to actual gatherable resources (New, Krasnow et al, 2007); however, the above hypotheses are difficult to test with such methods. As performance on small-scale spatial memory tasks have been shown to correlate with

performance on real-world navigation tasks (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006), and as small-scale methods allow much finer experimental control, the present experiments use a small-scale, computerized test method.

2. Methods

2.1. Subjects

These predictions were tested in four undergraduate samples from the US and Japan. Each study consisted of a learning phase and a two-task test phase. Method parameters related to memory performance (presentation duration, image number, etc.) were varied across studies in order to sample for the predicted sex difference at a range of overall task difficulties (see Table 2 for individual study parameters and descriptive statistics).

2.2. Learning phase

In each learning phase, subjects viewed sets of six to nine images on a computer screen for several seconds (Fig. 1A, see Appendix A for sample images and set configurations). The images were drawn from several categories: fruit on the tree, tools on a workbench, animals in the wild, suburban buildings, jewelry and electronic devices. For a subset of subjects (n=74, 40 females) from Study 3 a Tobii x50 eye-tracker was used to record the amount of overt attention (visual fixation) that these subjects allotted to each image in the set during the learning phase.

Image sets were organized into blocks and each study consisted of multiple learning-phase blocks. Test-phase tasks followed each learning-phase block and tested only those previous images. Studies 1 through 3 each contained two learning-phase blocks, one occurring in an incidental learning condition and one in a directed learning condition. In the incidental learning condition, subjects were not aware

of the upcoming test phase. Subjects were therefore given a distracter task: they were instructed to count the number of images of buildings and to respond with this number after each set. During the directed learning condition, subjects were explicitly instructed to attend to all of the images during the learning phase to achieve the best performance on both identity and location components of the test phase. While performance for both sexes was generally higher in the directed learning condition, learning condition did not interact with sex in predicting either location or identity memory performance, so data from these two conditions were combined for testing the main hypotheses. Study 4 contained five learning-phase blocks, each with directed learning task instructions.

2.3. Test phase

The test phase of each study consisted of a non-spatial identity memory task and a spatial location memory task. For the identity memory task (Fig. 1B), subjects were shown a randomized sequence of individual images — some new and some repeated from the previous learning phase. Subjects were instructed to categorize the images as new or old. For the location memory task (Fig. 1C), subjects were shown a randomized sequence of individual images from the previous learning phase and a response array consisting of blank images in the configuration of the learning-phase array. Subjects were instructed to indicate the learning-phase location of each image. As no reference content was available at test (see Fig. 1), this location memory task should target absolute — rather than relational — spatial memory.

The studies differed in sequence of task presentation. For Studies 1 and 2, the test-phase tasks were interleaved such that subjects completed an identity memory question for each image, followed by an immediate location memory question whenever they responded that the image was "old." During the location memory question,

Table 2
Individual study attributes and descriptive statistics

Study no.	1	2	3	4
Population	UCSB	UCSB	UCSB	Kyoto and Waseda Universities
Total N (female n)	94 (49)	133 (70)	209 (110)	96 (48)
No. of blocks	2	2	2	5
No. of sets per block	5	5	6	3
No. of images per category	30	30	18	30
No. of images per set	9	9	6	8
Set duration on screen	5s	5s	5s	10s
Image category	Identity Memory accuracy±S.D., Location Memory accuracy±S.D.			
Animals	0.64±0.07, 0.18±0.11	–	0.91±0.10, 0.38±0.14	0.75±0.10, 0.43±0.14
Buildings	0.58±0.07, 0.10±0.07	0.58±0.06, 0.17±0.12	0.76±0.12, 0.26±0.10	–
Electronics	–	–	–	0.78±0.08, 0.50±0.14
Fruit	0.58±0.05, 0.09±0.07	0.58±0.06, 0.18±0.15	0.83±0.11, 0.28±0.11	0.77±0.09, 0.44±0.15
Jewelry	–	–	–	0.78±0.11, 0.49±0.18
Tools	–	0.54±0.08, 0.29±0.23	0.84±0.11, 0.30±0.12	–

Fig. 1. (A) Sample learning array, (B) identity probe and (C) location probe.

the image was not visible, as the center of the screen was a candidate location for the location memory question. For Study 3, the test-phase tasks were blocked such that subjects completed a location memory task on the old image set, followed by an identity memory task on the full set of images (new and old). For Study 4, the tasks were interleaved, but subjects received feedback on each identity memory response and were then prompted for a location memory response for each old image.

2.4. Data analysis

Subject responses were coded for accuracy and averaged within each category to compute an identity memory score and a location memory score for each image category for each subject. These data were analyzed using hierarchical linear regression, with sex as a first-step predictor of location memory for each image category and category-specific identity memory as a second-step control predictor. (Note that because sex is a dichotomous predictor, a regression analysis is identical to a t test.) This analytic approach offers two advantages: (i) the standardized regression coefficients (β) provide a common metric of effect size which can be compared across categories and studies, and (ii) the coefficient from the second-step analysis isolates the sex difference in location memory after individual differences in identity memory — as well as any processes the two types of memory share — have been controlled.

3. Results

Gathering Navigation Theory predicts a female spatial memory advantage for gathering-relevant content (H_1). In
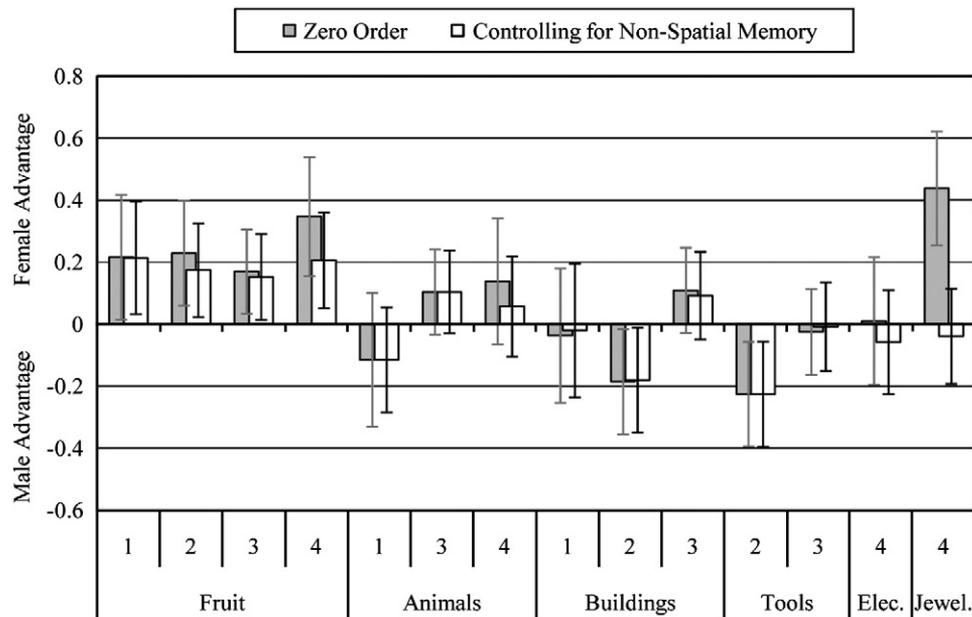

Fig. 2. Sex differences in location memory by category. This graph plots standardized regression coefficients (β) representing the sex difference in location memory for each image category presented in each study. Bars represent 95% confidence intervals to denote statistical significance. Positive values indicate a female advantage; negative values indicate a male advantage.

all four studies, women outperformed men on location memory for the "fruit on the tree" category (β's>.17, p's<.04). Furthermore, we can test whether this sex difference was truly spatial in origin (H_2) by controlling for non-spatial aspects of object memory (note that non-spatial sex differences in mechanisms of object perception — e.g., sexually differentiated color sensitivity — should similarly impact identity and location memory). As predicted, in all four studies this spatial sex difference for gathering-relevant content remained significant even when controlling for subjects' category-specific identity memory (β's>.14, p's<.03). This female advantage was limited to the "fruit on the tree" category: No other image content produced a sex difference in location memory once identity memory was controlled (H_3; see Fig. 2). Thus, as predicted by Gathering Navigation Theory, across all four studies including samples from both the US and Japan, we observe a female advantage that is spatial in nature and limited to gathering-relevant content (H_5).

Gathering Navigation Theory additionally makes predictions about the relationship between motivated attention and gathering-relevant location memory (H_4). For females, the gathering mechanism should operate relatively automatically, meaning that visual attention above some minimal encoding threshold should not improve location memory. As predicted, in females the amount of visual attention was not correlated with location memory performance in either the incidental or directed learning conditions (r's<.22, ns). For males, Gathering Navigation Theory predicts that the gathering mechanism does not operate automatically but can be activated in cases of cued or exogenous motivation. Two

features of the procedure allow testing of this prediction. First, in the incidental learning condition, cueing could be provided by individual items (emulating the case where an opportunistic gatherer encounters a particularly valuable item). Consistent with this prediction, the more a male is motivated to attend to a gathering-relevant item (as measured by looking time), the better his location memory (r=.41, p=.02). Second, in the directed learning condition, motivation is provided by the task instructions (emulating the case where an opportunistic gatherer must employ the more habitual gathering strategy due to environmental conditions). In this condition the gathering mechanism should be similarly — i.e., automatically — active in men and women. As predicted, in the directed learning condition, differential motivation to attend to gatherable items did not predict differential location memory in men (r=.02, ns). That is, when women and men are situationally motivated to remember the locations of immobile resources, both seem to perform spatial encoding automatically, though women still perform it better.

To test for sex differences in identity memory, identity memory scores were regressed hierarchically first on sex and then on sex- and category-specific location memory, in strict parallel to our primary tests for sex differences in location memory. A sex difference in gathering-relevant identity memory was observed in two of four studies (Fig. 3). A similar female identity advantage was observed for buildings in one of three studies and for jewelry in the single study where such stimuli were used. These female advantages generally remained significant when controlling for category-specific location memory, suggesting they may represent
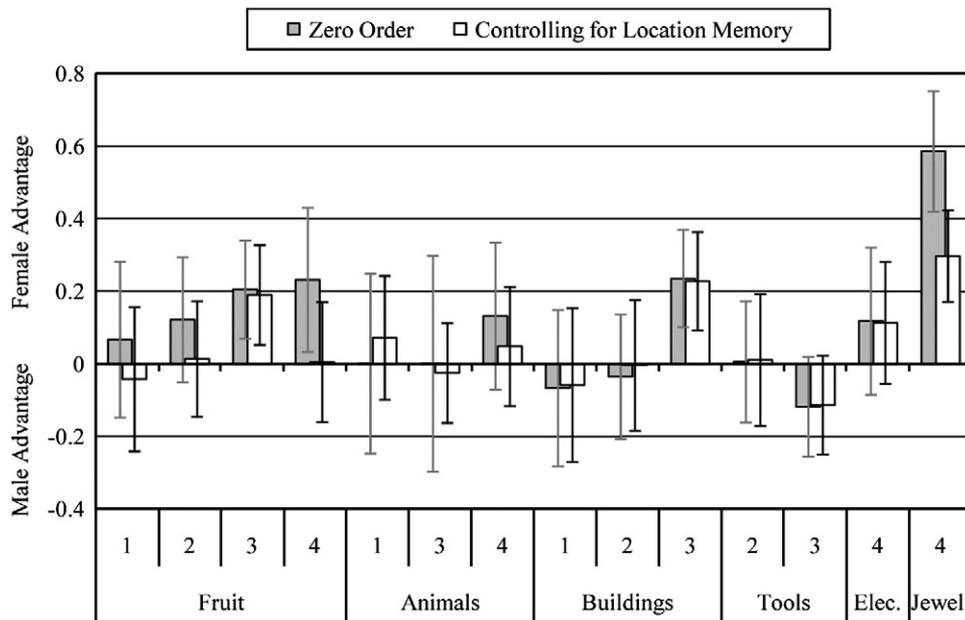

Fig. 3. Sex differences in identity memory. This graph plots standardized regression coefficients (β) representing the sex difference in identity memory for each image category presented in each study. Bars represent 95% confidence intervals to denote statistical significance. Positive values indicate a female advantage; negative values indicate a male advantage.

an underlying non-spatial processing difference between men and women. However, as the female spatial gathering advantage replicated even when controlling for identity memory (see above), this sex difference in identity memory cannot account for the female spatial gathering advantage.

4. Discussion

4.1. Alternative explanations for the female spatial gathering advantage

Several other candidate explanations for the observed female advantage for gathering-relevant spatial memory can be ruled out by the present data. First, if women merely attend to immobile foods more than do men, a sex difference in location memory could emerge without any sex difference in the underlying spatial mechanisms. This hypothesis can be ruled out with the eye-tracker data from Study 3: women did not attend to the "fruit on the tree" category (mean=543 ms per image) more than men (mean=586 ms per image) (t_{72}=1.53, ns). This behavioral similarity suggests that the female advantage must reside downstream of visual attention.

Second, some may argue that the gathering-relevant content in these studies is female gender typed in current society (Brumfiel et al., 2007) and that this cultural effect explains the observed female advantage. Were this theory correct, a similar female advantage should be observed for any similarly gender-typed content, such as the "jewelry" images used in Study 4. Women did show better identity memory for jewelry, but they showed no advantage for location memory once this superior identity memory was controlled (see Fig. 2). This finding is inconsistent with any theory that attributes the sex difference in location memory for immobile foods to a more general gender-typed content effect.

A third possibility is that the observed female advantage might be due to male distraction or differential memory for the other image categories rather than to a female spatial specialization for gathering-relevant content. This hypothesis can similarly be ruled out because for no image category did men attend more than women (t_{72}'s<1.61, ns), nor did they demonstrate any replicable tendency to outperform women on location memory for any category (see Fig. 2).

A fourth concerns possible roles for ontogenetic plasticity in the mechanisms under study and how this plasticity may affect the observed sex difference. This class of reasoning is premised on the logic that every mechanism, psychological or otherwise, must be the result of some ontogenetic process and that environmental variability can potentially influence the course of this development. For example, while the societies we sampled are not characterized by subsistence gathering, there is an observable sex difference in the rate of a gathering-like behavior — shopping (International Mass Retail Association, 1993). A reasonable concern therefore is that, while the sex difference in spatial gathering memory

appears robust and replicable, it may be predicated by or dependent on particular histories of developmental experience. Evidence suggests, however, that this effect is likely minor: our initial study (New, Krasnow et al, 2007) found no effect of shopping experience on fruit location memory and the sex difference survived controlling for any variance the two variables shared. Furthermore, the jewelry control tested in the present study rules out the influence of a domain-general plasticity effect because a female spatial advantage for jewelry was not observed.

Finally, the results do not appear to be an artifact of idiosyncrasies in task detail or of overall task difficulty. While the four studies presented here varied enough to drive memory accuracy through a wide range of performance (Table 1) — from very low, occasionally chance levels in Study 1 to very high, occasionally near ceiling levels in Studies 3 and 4 — a female advantage for gathering-specific location memory was observed across all four studies and at surprisingly consistent effect size (Fig. 2). This pattern attests to the robustness of the predicted effects.

4.2. General discussion

From an evolutionary perspective, solutions to a diverse set of adaptive problems (such as finding food, avoiding predators, using tools, locating mates, etc.) are supported by spatial processing mechanisms. Where these ancestral problems required distinct solutions, we should expect that natural selection designed domain-specific spatial mechanisms to solve them. Where these problems impinged differently on ancestral men and women, we should suspect that the resulting mechanisms may be sexually differentiated. The present studies implicate a sexually dimorphic, domain-specific spatial processing mechanism. These results join a large literature documenting sex differences in spatial cognition (for review, see Voyer, Voyer, & Bryden, 1995). A number of these sex differences have begun to be explained as sexually differentiated solutions to different adaptive problems, such as finding mates (Gaulin & Fitzgerald, 1989), hunting game (Silverman et al., 2000), gathering plants from local patches (Silverman & Eals, 1992) and intrasexual aggression (Ecuyer-Dab & Robert, 2004). One profitable way forward would be to further parse the problems faced by our ancestors and the mechanisms that natural selection could have built to solve them. Whether these theories vie for explanation of a common phenomenon or propose distinct phenomena, they must yield testable predictions about the functional design features of the mechanisms they postulate.

Proceeding empirically, data can inform theories regarding the functional organization and scope of the hypothesized mechanisms. For example, a content-general tangled-bank spatial memory system is well documented, but data suggest the system is not activated unless fixed locations are identified (James & Kimura, 1997; Postma et al., 2004).

The tangled-bank system may also be limited to the spatial domain, as non-spatial memory tests designed to target gathering content show no sex difference in performance (Nairne et al., 2009). Finally, the present data suggest the tangled-bank and navigational-gathering selection pressures shaped at least two distinct sexually differentiated spatial gathering mechanisms.

Many aspects of human nature have been shaped by foraging selection pressures. The present evidence suggests that the human mind contains a gathering-specific navigational adaptation. This mechanism is activated by cues of gatherable foods and not by other categories of objects. Once a resource has been identified, this mechanism encodes its location into memory. This mechanism is more chronically active in women but can be activated in men with explicit motivation. Subjects from two cultures shown to be dissimilar in many aspects of spatial perception and cognition were effectively identical in their performance. Few people in the industrialized world — including the American and Japanese subjects in these experiments — engage in traditional foraging activities, instead deriving the bulk of their nutrition from supermarkets and restaurants. Despite current circumstances, human minds — especially female minds — seem to bear the marks of our evolutionary heritage of ceaseless searching for gatherable foods.
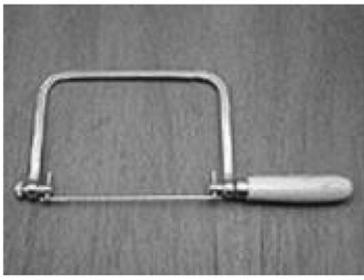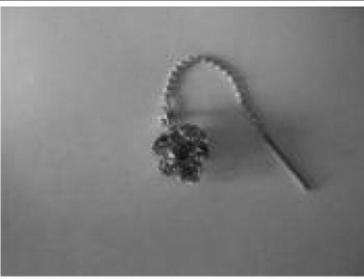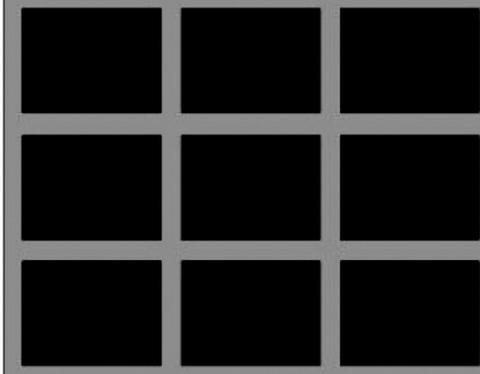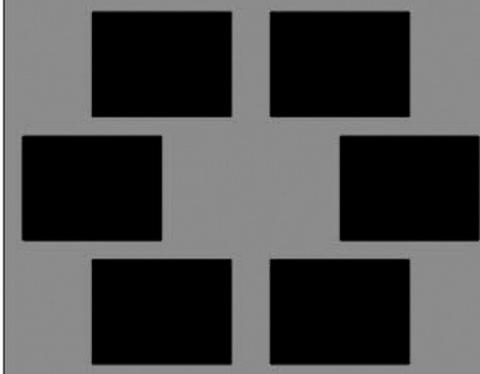
Acknowledgments

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Appendix A. Sample images

Appendix B. Learning phase image configurations