Spatial adaptations for plant foraging: women excel and calories count

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We present evidence for an evolved sexually dimorphic adaptation that activates spatial memory and navigation skills in response to fruits, vegetables and other traditionally gatherable sessile food resources. In spite of extensive evidence for a male advantage on a wide variety of navigational tasks, we demonstrate that a simple but ecologically important shift in content can reverse this sex difference. This effect is predicted by and consistent with the theory that a sexual division in ancestral foraging labour selected for gathering-specific spatial mechanisms, some of which are sexually differentiated. The hypothesis that gathering-specific spatial adaptations exist in the human mind is further supported by our finding that spatial memory is preferentially engaged for resources with higher nutritional quality (e.g. caloric density). This result strongly suggests that the underlying mechanisms evolved in part as adaptations for efficient foraging. Together, these results demonstrate that human spatial cognition is content sensitive, domain specific and designed by natural selection to mesh with important regularities of the ancestral world.

Keywords: foraging adaptations; sex differences; optimal foraging theory; spatial cognition; navigation

1. INTRODUCTION

Spatial cognition in humans is not a unitary faculty (Halpern 2000); rather, it seems to reflect the operation of a number of functionally distinct (and neurally dissociable) cognitive specializations, each designed for solving a different adaptive problem. The selection pressures shaping some of these specializations would have been similar for ancestral men and women, producing sexually monomorphic computational design. In certain cases, however, ancestral men and women would have faced distinct spatial demands; in these cases, we should find that the resultant cognitive mechanisms are sexually dimorphic.

Such sex differences are well documented in the existing literature on human spatial abilities. Spatial tasks exhibit some of the largest and most reliable sex differences in cognitive performance. On many spatial tasks, male advantage is typical (Linn & Petersen 1985; Voyer *et al.* 1995) and these findings have often been used to conclude that men have superior spatial ability (Linn & Petersen 1985). Using an evolution-minded approach, however, Silverman & Eals (1992) predicted and documented a specific female advantage. Their foraging adaptation theory argues that hunting mobile prey and gathering immobile resources have different computational requirements; to the extent that the universal sexual division of foraging labour among described hunter–gatherers (Murdock 1967) characterized our ancestral past, sexually dimorphic foraging-related cognitive specializations should be observable in the minds of modern men and women.

According to this foraging adaptation theory, many of the spatial tasks that presently show a male advantage engage cognitive mechanisms designed by natural selection for successful hunting. In hunting, mobile prey are pursued over erratic and unpredictable courses often through unfamiliar environments; given the energetic costs of transport, the spoils should be carried home via a more direct route, a task that can be accomplished by vector integration (Gallistel 1990) or from vector computation within a survey representation of the environment. Past tests of navigating and wayfinding (Moffat *et al.* 1998; Sandstrom *et al.* 1998; Lawton & Morrin 1999; Silverman *et al.* 2000; Malinowski 2001), as well as some laboratory tasks such as mental rotation (Linn & Petersen 1985; Voyer *et al.* 1995), may elicit a male advantage by engaging spatial mechanisms that evolved for this kind of navigation while hunting.

The spatial problems posed by gathering are quite different. Gathered resources are stationary and vary in quality and availability with time—a fig tree may have nothing valuable now but be laden with fruit in the near future. To relocate diverse resources as they become valuable requires a mechanism that registers and stores the locations of many stationary food resources within a survey map of a more constrained and well-known environment. A well-designed adaptive specialization for gathering would accumulate such information automatically, without special attention, during daily activities. Silverman & Eals (1992) argued that, if a sexually dimorphic spatial adaptation for gathering exists, women should excel at remembering the locations of items within a complex spatial array, especially in incidental learning tasks.

Silverman and Eals operationalized these skills as 'object-location memory' and devised a number of pencil-and-paper and desktop tasks to assess it. The predicted female advantage has sometimes been demonstrated on these tasks, but the effect is sensitive to details of task presentation, sometimes appearing robustly and sometimes disappearing entirely (Eals & Silverman 1994; James & Kimura 1997; Dabbs *et al.* 1998; see Postma *et al.* 2004 for a review). Arguably, some of these

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effects are theory relevant (e.g. larger female advantage in incidental than directed learning tasks), but others are more difficult to interpret (e.g. no female advantage for difficult-to-name objects), leaving their experimental demonstration vulnerable to alternative interpretations.

Such fragile effects may be a consequence of using experimental tasks that only weakly engage spatial adaptations for plant foraging. Put another way, the division-of-labour model has not been effectively tested because the scale ($8.5''$ by $11''$ or desktop), content (e.g. household items or machine parts) and task (did the item move?) do not match the scale (walking), content (immobile foods) and task (which way to the mongongo nut grove?) of real-world plant foraging. Thus, a stronger female advantage should be observed on a spatial task that better approximates the ancestral conditions of plant foraging: specifically, a task that provides both the cues appropriate to engage the hypothesized mechanism and the kind of information it is designed to process (i.e. the content and location of nutritional resource patches). No prior investigation has tested whether women demonstrate superior spatial memory for food resource locations at a real-world scale.

In this study, we employed the scale, spatial complexity and item diversity of a large farmers' market to assess memory for the location of immobile food resources such as leaves, fruits, nuts, roots and honey. If the Silverman and Eals' hypothesis is correct, then

H_1: Females will remember the locations of such food resources more accurately than men.

In general, women prefer to navigate by landmarks and routes, rather than by vectoring (Halpern 2000), and a methodology that emphasized route- and landmark-based strategies might well have produced a female advantage. However, our intention was not to replicate these well-known sex differences, but to test for a predicted content effect: females more accurately recalling the location of immobile foods. Thus, in order to most effectively jeopardize this hypothesis, we designed our study to favour *men's* established wayfinding strengths. To this end, participants were tested in a newly learned and directly experienced environment (Montello *et al.* 1999), were not explicitly oriented to any landmarks during exposure (Baenninger 1997) and were tested via pointing to the non-visible resource locations (Hegarty *et al.* 2006)—a vectoring measure that advantages the orientation strategy favoured by men and disadvantages the route strategy typically favoured by women (Lawton 1994). It is possible that such a design might obscure any actual female advantage. However, effective plant foragers would require the ability to flexibly integrate various navigation strategies as dictated by their nutritional needs and patterns of resource availability. Thus, we predict that women will also be able to form survey representations and estimate vectors to resource locations. To test for this ability, participants were tested at a central off-route location via pointing, a measure that minimizes the possible employment of route- and landmark-based strategies for responding. A female advantage on such a task would be strong evidence for a foraging-related adaptation.

The suite of cognitive skills labelled 'spatial abilities' most likely arose from selection pressures in a number of domains (e.g. searching for nutrients, searching for mates; Hewlett *et al.* 1986; Gaulin & FitzGerald 1989) and subdomains (e.g. searching for food versus searching for water; Petrinovich & Bolles 1954). Thus, although we predict a female advantage on resource location memory, some foraging-related selection pressures may have impinged similarly on ancestral males and females. For example, optimal foraging theory (Schoener 1971) addresses the mechanisms that underlie dietary choice. Such theories assume that foragers are capable of assessing the 'profitability' of potential food items as a basis for eating or rejecting them and have been validated on human foragers (Winterhalder & Smith 2000). This assumption justifies a collateral prediction:

H_2: The locations of more nutritionally valuable resources will be more accurately remembered than less nutritionally valuable resources.

Such a bias would support the argument that the mechanisms underlying resource location memory are adaptations for foraging.

2. MATERIAL AND METHODS
Data were collected during the spring and summer of 2004 at six separate meetings of the Saturday morning farmers' market in Santa Barbara, California. The market comprises 10 orderly rows of vendors laid out in a rectangular 0.6 ha area. There were typically approximately 90 food stalls.

(a) *Participants*
Eighty-six adults (41 females; mean age, 35 years) participated in this experiment. Data from 18 additional participants were discarded due to participant attrition, food running out at a target location or experimenter error during the task.

Participants were recruited near an entrance to the farmers' market and told that they could earn $10 (or $5 and a UCSB tote bag) by participating in 'farmers' market research'. This cover story—which does not refer to any spatial task—was used to ensure that the encoding of resource locations would be strictly incidental. All participants were given a consent form on which they were asked to indicate food allergies. Participants were then asked their age and how frequently they visited this farmers' market. The answers to these questions were recorded by the experimenter, who also made note of each participant's sex.

(b) *Materials and procedures*
Participants were led by a circuitous route to each of six food stalls, where they were given a food item to eat. The precise food items, stalls and routes were fixed on any given day of data collection but varied over the 6 days. Within each day, subjects were assigned equally to the 'forward' and 'reversed' versions of the fixed route (table 1 for food items and orders).

At each stall, participants were asked a set list of questions which served in part to promote the cover story and were also analysed as possible predictors of pointing accuracy:

(i) 'On a scale of 1–7, how much do you like the taste of this?'
(ii) 'On a scale of 1–7, how often do you eat this?'
(iii) 'On a scale of 1–7, how attractive do you think this stall is?'
(iv) 'How many times have you purchased from this stall?'

Table 1. Weekly items, routes and descriptive statistics. (Food items used over the course of the 6 day experiment are listed below. Item number indicates the order in which participants were led to each food item. Half of the participants were led around in the 'forward' direction, as indicated by the first number listed. The other half of the participants were led around in the 'backward' direction, as indicated by the second number, listed in parentheses.)

item number	day					
	1	2	3	4	5	6
1 (6)	cherries	oranges	olive oil	fennel	basil	strawberries
2 (5)	sugar peas	cherimoya	peaches	blueberries	peaches	plums
3 (4)	honey	almonds	radish sprts	apples	tangerines	carrots
4 (3)	tomatoes	basil	cauliflower	peaches	strawberries	cucumbers
5 (2)	almonds	rd lf lettuce	cherries	zucchini	peppers	green onion
6 (1)	cherimoya	avocado	zucchini	olive oil	zucchini	tangerines
n(F : M)	9(5 : 4)	15(7 : 8)	17(8 : 9)	17(6 : 11)	6(4 : 2)	22(11 : 11)
raw error (s.d.)	28.97° (13.91)	27.90° (19.36)	30.78° (13.93)	25.17° (12.72)	22.95° (7.58)	48.31° (17.71)

Table 2. Pointing error: hierarchical linear model (with robust standard errors).

effect	coefficient	s.e.	t	d.f.	p
between-subjects effects					
intercept	32.891	1.786	18.414	80	1.68×10^{-30}
sex	−8.917	3.634	−2.454	80	0.017
sense of direction	−3.737	1.276	−2.928	80	0.005
week rank	2.699	1.389	1.943	80	0.055
experience	−0.952	1.129	−0.843	80	0.402
within-subjects effects					
log(kcal)	−14.309	3.030	−4.722	478	3.07×10^{-6}
food liking	−0.275	0.794	−0.347	478	0.729
food eat often	1.380	0.790	1.747	478	0.081
stall liking	−0.903	1.105	−0.817	478	0.415
stall shop often	0.018	0.175	−0.104	478	0.918

Experimenters recorded participants' answers.

After visiting all six stalls, participants were taken to a pointing device in the centre of the market area. The pointing device was a flat, horizontal, circular board of 30 cm in diameter mounted on a camera tripod and located such that all of the visited stalls were obscured from view. The board was marked radially in 1° increments. A wooden pointer was fixed at the centre of the circle and could be spun freely. Participants were asked to aim the pointer at each of the six food items in one of two predetermined orders that differed from both presentation orders. The experimenter recorded the indicated bearing for each food item.

Participants then were asked to assess their general sense of direction on a 1–7 scale, a measure known to be correlated with field measures of navigational ability (Kozlowski & Bryant 1977; Sholl 1988; Montello & Pick 1993; Prestopnik & Roskos-Ewoldson 2000; Sholl *et al.* 2000). Participants were then offered information about the background and rationale of the study and were finally taken back to the farmers' market entrance to receive payment.

3. RESULTS

(a) Analytical methods

Pointing error, our inverse estimate of accuracy of food location memory, was measured in degrees as the smallest difference between each participant's estimate and the true bearing to each of the six food locations. Errors, therefore, ranged from 0° (perfect accuracy) to 180° (opposite from correct direction), with 90° indicating chance performance (Sholl *et al.* 2000). Smaller errors indicate greater accuracy.

To test our hypotheses, we modelled pointing error in a two-level hierarchical linear model (HLM) with individual pointing errors as first-level observations and participants as second-level observations (following the random coefficients method described in Raudenbush & Bryk 2002). As first-level predictors, we entered caloric density (kcal 100 g^{-1}, an estimate of nutritional value; USDA, no date http://www.nal.usda.gov/fnic/foodcomp/search/) which we log-transformed to correct for a strong negative skew, as well as the participants' four ratings of the pointed-to foods and stalls ((i)–(iv)). As second-level predictors we entered participant sex, as well as their number of weekly visits to the market, their self-rated sense of direction and a rank variable reflecting differences among weeks in the difficulty of the test environment. (Stalls and routes differed from week to week, leading to differences in weekly average error; including this variable allowed us to separate these theory-irrelevant differences from the effects of interest.)

(b) H_1: Are women more accurate than men at pointing to newly learned food locations?

Yes. Women were, on average, 9° more accurate in their pointing estimates than men ($\gamma = -8.917$, $t(80) = 2.454$, $p = 0.017$). This corresponds to a 27% improvement in performance compared with men.

This female advantage in accuracy was not due to women having more experience at the farmers' market than men. Experience at the market did not predict performance, either as a zero-order effect or in the HLM model (table 2, between-subjects effects). The female
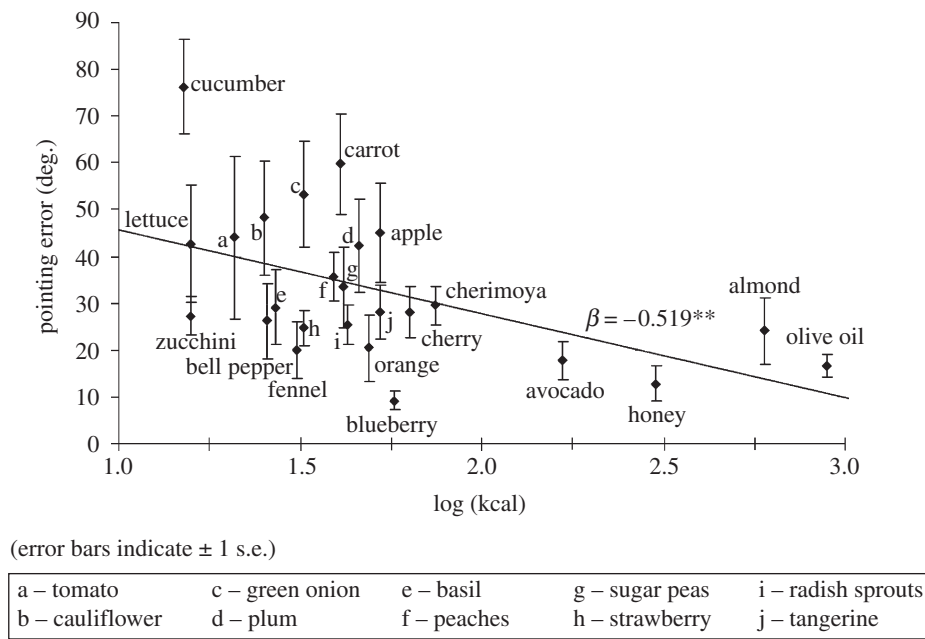
(error bars indicate ± 1 s.e.)

| a – tomato | c – green onion | e – basil | g – sugar peas | i – radish sprouts |
| b – cauliflower | d – plum | f – peaches | h – strawberry | j – tangerine |

Figure 1. Item-wise plot of mean error ($\pm$ s.e.) by (log) caloric density.

advantage is significant even after controlling for experience at the market.

Did this female advantage arise because our sample was composed of women who are unusually gifted at navigation? No. The sense of direction measure has been shown to be a good index of one's general ability to navigate and, as in prior research, there was a male advantage on this measure ($M_m = 5.37$, s.d.$_m = 1.26$; $M_f = 4.56$, s.d.$_f = 1.51$, $t(84) = 2.68$, $p = 0.009$, two-tailed, $d = 0.58$). Internal evidence confirms the ecological validity of this self-report measure: it predicted unique variance in pointing accuracy for both sexes ($\gamma = -3.737$, $t(80) = 2.928$, $p = 0.005$).

Clearly, a male advantage in general sense of direction cannot explain a female advantage in pointing accuracy on our task. Importantly, the female advantage in vectoring towards food items was independent of this general ability: it remains after controlling for sense of direction.

Weekly differences in the difficulty of test conditions did explain unique variance in pointing accuracy ($\gamma = 2.699$, $t(80) = 1.943$, $p = 0.055$), but the unique contribution of sex remains even after controlling for this and all other variables measured.

(c) H_2: Do people remember the locations of higher-quality foods more accurately?

Yes. Foods with higher caloric density were pointed to more accurately by both sexes ($\gamma = -14.309$, $t(478) = 4.722$, $p = 3.07 \times 10^{-6}$). Since small errors indicate greater accuracy, this relationship manifests as a negative correlation: high caloric density predicts low pointing errors.

This effect was not due to subjects preferring the taste of high over low caloric density foods. How much subjects *liked* the taste of each food did not correlate with pointing accuracy, even as a zero-level effect. In contrast, the effect of caloric density on pointing accuracy remained significant even after controlling for how much subjects liked the taste of each food, how often they eat each food, how attractive they found the stall selling the food, and how often they had purchased food from that stall. Indeed, none of these other variables made a zero-order or unique contribution to performance (table 2, within-subjects effects).

The greater accuracy in locating high-calorie food items could conceivably have been driven by some other property confounded with caloric density in our sample of foods. For example, several of the highest calorie items might also be considered non-standard for other reasons (people rarely drink olive oil; olive oil and honey are liquids whereas the other items are countable objects, etc.). To account for this general class of alternative hypotheses, we replicated the HLM analysis after omitting data for the four highest calorie items (olive oil, almonds, honey and avocados). An inspection of figure 1 indicates that the negative correlation between caloric density and pointing accuracy is actually stronger below 2 log(kcal) than above, and despite the loss in power due to a restricted sample, the calorie/accuracy relationship is still significant when these items are removed.

A different and simpler approach to analysing these data is to use food items as the unit of analysis, averaging across all participants' pointing errors to a given item. This allows one to test for a relationship between average pointing accuracy elicited by each food and predictor variables. In this case, log-transformed caloric density of the food item as well as the four average ratings of the foods and stalls were regressed on the average pointing errors. As in the HLM analysis, foods with higher caloric densities were pointed to more accurately ($\beta = -0.519$, $t(25) = 2.849$, $p < 0.01$; figure 1). This effect was constant across women and men in both the HLM and item-wise analyses (z's < 0.451, n.s.). As in the HLM, participants did not point more accurately to foods that were more liked or eaten more often, nor to stalls that were liked more or shopped at more often (β's > -0.180, t's$(25) < 0.914$, n.s.).

Thus, in accordance with the prediction that the farmers' market context would activate adaptations that evolved for foraging, foods higher in nutritional quality were pointed to more accurately. Importantly, nutritional quality was the *only* variable to independently predict

variance in pointing accuracy; indeed, liking, familiarity, experience and other variables were not significantly correlated with pointing accuracy.

4. DISCUSSION

Silverman & Eals (1992) argue that the female advantage on pencil-and-paper and desktop measures of object-location memory reflects a selective pressure on ancestral women for plant-foraging efficiency. But their measures did not involve foods, tested spatial memory on a very small scale, and included no measure of vectoring; as a result, a female advantage on their measures is open to many alternative interpretations. For this reason, we deemed it important to examine whether a female advantage could be demonstrated on a task that closely resembles foraging for plant foods. From this theory, we predicted that women should remember the locations where they have previously encountered immobile resources (e.g. plants, honey) more accurately than do men. This is a counter-intuitive hypothesis. Accurate performance on our pointing task requires vectoring relative to a survey representation of resource locations—the type of spatial representation more often (Lawton 1994) and more proficiently (Saucier *et al.* 2002) employed by men. Although prior research suggests that men are frequently better at pointing to the locations of landmarks and other non-food objects under such circumstances, we have shown that women are better than men at pointing to spatial locations that contain nutritional resources. That navigational tasks requiring vector integration (dead reckoning) show a male advantage when the 'landmarks' are not food makes the present finding of a female advantage all the more compelling and offers less ambiguous novel support for the idea that ancestral sex differences in foraging behaviour may have shaped sex-specific cognitive adaptations.

Given that females are often the primary shopper for household goods (Fram & Axelrod 1990), for example, constituting 73% of the food shopping respondents in a 1992 consumer research study (IMRA 1992), it is reasonable to question whether the general shopping environment or context, rather than the food items *per se*, provided the cues that enhanced female performance. However, past research indicates that females are no better than men at learning generic item locations in real-world shopping locations (Kirasic 2000), nor pointing to the locations of unseen vendors, even when they were more familiar with the shopping centre (Dogu & Erkip 2000). More recently, males were generally better in learning the spatial layout of a simulated shopping centre (Tlauka *et al.* 2005). This research suggests that females' greater experience with typical shopping layouts themselves, or other aspects of the shopping context, did not account for their more accurate performance in the present study. Against the background of prior research on spatial learning in shopping environments, the present results suggest that it was the food items that provided the cues which preferentially engaged female location memory.

The finding that nutritional quality enhances spatial memory further supports the idea that our task is engaging a foraging-related spatial adaptation. Interestingly, spatial memory performance was not explicable in terms of consciously mediated and articulated preferences for the food items or their presentation. From the perspective of current theory in behavioural ecology, the registration of potential foods' relative nutritional values is a central requirement for optimally gathering foods from dispersed and varying locations (Schoener 1971). Thus, the more accurate localization of high-calorie food items (and not those explicitly preferred) appears to reflect the priorities of a psychological mechanism which was adapted for the efficient exploitation of plant foods during the 99.7% of human evolution when our ancestors were foragers. This result strongly indicates a cognitive system with fine-tuned dimensions of valuation (e.g. caloric density) built into its architecture and should encourage the further development of models of cognition that incorporate ecologically valid valuation as a computational element (Tooby *et al.* 2005).

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