

RESEARCH ARTICLE

Human energetic stress associated with upregulation of spatial cognition

Daniel P. Longman^{1,2}  | Jonathan C. K. Wells³  | Jay T. Stock⁴ 

¹School of Sport, Health and Exercise Sciences, Loughborough University, Loughborough, UK

²ISSUL, Institute of Sport Science, University of Lausanne, Lausanne, Vaud, Switzerland

³Childhood Nutrition Research Centre, UCL Institute of Child Health, London, UK

⁴Department of Anthropology, University of Western Ontario, London, Ontario, Canada

Correspondence

Daniel P. Longman, School of Sport, Health and Exercise Sciences, Loughborough University, Loughborough, LE11 3TU, UK. Email: d.longman@lboro.ac.uk

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Abstract

Objectives: Evolutionary life history theory has a unique potential to shed light on human adaptive capabilities. Ultra-endurance challenges are a valuable experimental model allowing the direct testing of phenotypic plasticity via physiological trade-offs in resource allocation. This enhances our understanding of how the body prioritizes different functions when energetically stressed. However, despite the central role played by the brain in both hominin evolution and metabolic budgeting, cognitive plasticity during energetic deficit remains unstudied.

Materials: We considered human cognitive plasticity under conditions of energetic deficit by evaluating variability in performance in three key cognitive domains. To achieve this, cognitive performance in a sample of 48 athletes ($m = 29$, $f = 19$) was assessed before and after competing in multiday ultramarathons.

Results: We demonstrate that under conditions of energetic deficit, performance in tasks of spatial working memory (which assessed ability to store location information, promoting landscape navigation and facilitating resource location and calorie acquisition) increased. In contrast, psychomotor speed (reaction time) remained unchanged and episodic memory performance (ability to recall information about specific events) decreased.

Discussion: We propose that prioritization of spatial working memory performance during conditions of negative energy balance represents an adaptive response due to its role in facilitating calorie acquisition. We discuss these results with reference to a human evolutionary trajectory centred around encephalisation. Encephalisation affords great plasticity, facilitating rapid responses tailored to specific environmental conditions, and allowing humans to increase their capabilities as a phenotypically plastic species.

KEYWORDS

cognition, energetics, evolution, life history, trade-offs

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1 | INTRODUCTION

1.1 | The energetics of life history theory

Life history theory describes the competitive allocation of resources between key physiological functions (Leonard, 2012; Stearns, 1989, 1992; Zera & Harshman, 2001). Under conditions of energetic stress, life history theory predicts the existence of trade-offs in allocation between competing functions relating to reproduction, maintenance, defense, growth and storage (Bronson, 1991; Reznick et al., 2000; Stearns, 1992). Selective pressures therefore encourage the development of phenotypically plastic mechanisms to effectively capture and appropriately distribute energy and resources between physiological functions (Angilletta et al., 2003; Kaplan & Gangestad, 2005; Lotka, 1922; McDade et al., 2008; Stearns, 1992).

Although the trade-offs predicted by life history theory are expected to result in a negative relationship between investment in two functions, negative covariation is frequently absent when phenotypic comparisons are made between individuals within a population (Cody, 1966; Glazier, 2000). This may be explained, at least in part, by inter-individual variation in resource acquisition exceeding variation in resource allocation (van Noordwijk & de Jong, 1986).

Recent work within the field of human athletic palaeobiology has identified ultramarathon competitions as a valuable experimental model for the detection of negative covariation in resource allocation (Longman et al., 2020). While it is not possible to control individual energy intake without compromising ecological validity, it is possible to nullify the effect of this variation in resource acquisition by studying humans under conditions of negative energy balance. This novel approach takes advantage of the energy deficits imposed by ultramarathons (Knechtle et al., 2005) to push physiological and cognitive systems to the limits of adaptive plasticity. The resultant negative energy balance negates the effect of inter-individual variation in resource acquisition, provoking and unmasking detectable life history trade-offs at the level of the individual. This model allows for the direct analysis of physiological trade-offs in internal resource allocation (Longman, Prall, et al., 2017). Subsequent determination of the physiological hierarchy of functional preservation during energetic stress will (a) provide a step-change in the understanding of human life history trade-offs, (b) contribute to knowledge underpinning recent advances in human energetics (Pontzer, 2015a; Pontzer, 2015b) and (c) shed new light on our adaptive capabilities as a phenotypically plastic species (Longman et al., 2020).

1.2 | The energetics of encephalisation

The development of an enlarged and elaborated brain is considered a defining characteristic of human evolution (Foley & Lee, 1991; Lee & Wolpoff, 2003). The pronounced encephalization accompanying the evolution of the Homo clade has brought a plethora of benefits and enhanced individual fitness (Barrickman et al., 2008; Parker & McKinney, 1999). Although the specific selective pressures leading to

hominin encephalization are debated, recent evidence reporting that Net Primary Productivity was inversely correlated with brain size among hominins over the past one million years suggests that resource availability exerted selective pressure on brain size in the hominin lineage (Will et al., 2021).

Encephalization imposes a significant energetic burden (Elia, 1991; Isler & van Schaik, 2006; Shirley et al., 2019). The brain's high energetic turnover reflects the metabolically demanding nature of intense neuronal activity, and accounts for 20%–25% of adult resting metabolic rate — a figure 2–3 times higher than for chimpanzees (Judaš et al., 2013; Peters et al., 2004). The issue of how an enlarged and elaborated brain can be metabolically afforded is a prominent and persistent question within human evolution (Aiello & Dunbar, 1993). Life history theory suggests that energy savings in other organs or tissues could allow for energetic diversion to the brain, without the need to increase overall metabolic expenditure (Isler & van Schaik, 2006; McNab & Eisenberg, 1989). Trade-offs at an evolutionary timescale have been proposed between brain size and digestive tract development (Aiello & Wheeler, 1995), adiposity (Navarrete et al., 2011) and skeletal musculature (Leonard et al., 2003).

In addition to being both fitness-enhancing (Barrickman et al., 2008; Parker & McKinney, 1999) and metabolically demanding (Peters et al., 2004), cognition mirrors other physiological traits in that it too is functionally plastic in nature (Dukas, 1998; Jones et al., 2006; Mercado, 2008). As with other physiological functions, trade-offs involving cognitive function are not restricted to evolutionary timescales and may arise from short-term adaptive phenotypic plasticity. For example, the conceptual framework provided by life history theory has recently been used to develop the “cognitive costs of reproduction hypothesis,” which suggests that the high energetic costs of human female reproduction may cause a decline in cognitive function during pregnancy (Ziomkiewicz et al., 2019). At an even more acute level, we experimentally observed a trade-off between a measure of cognitive function (a free recall test of memory) and muscular activity when simultaneously challenged, with relative preservation of cognition (Longman, Stock, & Wells, 2017). These results indicate an evolved response granting the brain preferential access to glucose; a well-fuelled brain may provide better chances of survival when confronting an environmental challenge than well-fuelled muscles (Beedie & Lane, 2012).

1.3 | Do trade-offs exist between cognitive processes in humans?

Functional trade-offs between cognitive domains have been observed in a range of species at the inter-individual level. For example, the trade-off between decision speed and accuracy has attracted research interest (Chittka et al., 2009). When the penalty of an error is high, such as when scanning an environment for hidden predators, it may be preferable to spend more time to increase accuracy (Ings & Chittka, 2008). In contrast, when the cost of poor accuracy is low it might be advantageous to perform a quick and rough analysis

(Kay et al., 2006). Fast and inaccurate bees, for instance, can forage for nectar more effectively than slower, more accurate bees (Burns, 2005). However, trade-offs between cognitive processes at the intra-individual level remain understudied in humans.

The current study sought to assess human cognitive plasticity under conditions of energetic deficit. This was done by considering variability in performance in three key cognitive domains. As negative energy balance has previously been found to provoke detectable trade-offs between physiological processes (Longman, Prall, et al., 2017), and the brain is highly energetically demanding (Peters et al., 2004), trade-offs between cognitive processes during energetic deficit were anticipated.

The cognitive domains considered were spatial working memory (SWM), episodic memory (EM), and psychomotor speed (PS). Memory is central to cognitive evolution, serving as an information repository allowing us to think, reason and plan for the future (Dukas, 2004; McGaugh, 2013). SWM, a subdivision of memory, temporarily stores information related specifically to locations. The navigational abilities facilitated by SWM may be particularly useful when finding the way home following foraging or long-distance hunting trips. SWM may also play a role in directly facilitating food acquisition by allowing recollection of the location and quality of previously visited feeding sites (Henry & Stoner, 2011).

Consistent with the role of SWM in food acquisition, food biases in SWM have recently been identified in which the locations calorierich and savory-tasting foods were recalled more accurately than the locations of calorie-poor or sweet-tasting foods (de Vries et al., 2020). This suggests that cognitive processes relating to memory prioritize the extraction of preferred sources of nutrition from the environment. While the benefits of targeting calorie-rich foods are clear, the prioritization of savory over sweet foods (regardless of calorie content) may reflect human prioritization of protein consumption over other macronutrients when nutritional intake targets are not met (Simpson & Raubenheimer, 2005), and the subsequent challenge of ingesting sufficient protein.

EM, in contrast, describes the ability to recall information about specific events over a longer period. A key feature of episodic memory is the ability to bind separate pieces of information together, which allows the building of social networks, and may be linked to language, empathy, and the sense of self (Allen & Fortin, 2013).

Finally, psychomotor abilities link cognitive functions with physical movements. The speed of execution reflects the ability to process and respond to environmental information quickly and accurately. Reaction time, a core measure of PS, was measured here (Jakobsen et al., 2011).

We have previously observed that physiological functions providing the greatest immediate survival value are preserved at the expense of other functions during conditions of energetic stress (Longman, Prall, et al., 2017; Longman, Stock, & Wells, 2017). Due to its role in facilitating calorie-acquisition, we hypothesized that SWM would be prioritized over EM and PS in participants experiencing ultramarathon-induced energetic deficit.

2 | MATERIALS AND METHODS

Male and female athletes were recruited from the 2018 Jordan Ultra and the 2019 Sri Lanka Ultra (both organised by Ultra X). All athletes were informed of the opportunity to participate prior to the event, and those willing to participate were included in the study. Both events were competitive, 250 km 5-day footraces. The air temperature and humidity were similar for all stages within each race (Jordan 28–35°C and 10%–20% humidity; Sri Lanka 24–33°C and 60%–80% humidity). The races attracted a high caliber of athlete (the winner of each race was a former champion of the prestigious Marathon des Sables). Baseline measurements were taken the day before the beginning of each race and were repeated 4-days later following the third stage (cumulative distance covered = 150–160 km). Repeat measures were collected at this point due to the logistical constraints imposed by the race locations.

2.1 | Assessment of cognitive function

Performance in the cognitive domains of SWM, EM and PS was assessed using validated tablet-based tests selected from the Cambridge Neuropsychological Test Battery (CANTAB; Cambridge Cognition, Cambridge, UK).

SWM performance was assessed using the CANTAB SWM Test. This test analyzed ability to store and subsequently use spatial information relating to the location of hidden tokens to guide decision-making in a foraging task. Specifically, the participant was challenged to search for tokens hidden within boxes and was instructed to avoid revisiting boxes that had previously been found to contain a token. The number of boxes, and therefore the difficulty of the task, gradually increased to a maximum of 12 (Arai et al., 2016; Barnett et al., 2010; Henry & Stoner, 2011; Rock et al., 2014). Two outcome variables were reported:

- SWM-1—the number of errors made. This is the number of times the participant selects a box previously found to contain a token.
- SWM-2—the degree of strategy used when conducting a search. This is the number of times the participant begins a new search by selecting a new box.

EM was assessed using the CANTAB PAL (paired associates learning) Test. This test quantified ability to learn an association between a visual stimulus and a location. Boxes were displayed on the screen and opened in a randomized order to reveal a pattern in one or more of the boxes. Once the boxes closed, the participants were presented with a pattern and challenged to remember which closed box contains that specific pattern (Barnett et al., 2015; de Jager et al., 2002; Yurko-Mauro et al., 2010). As with SWM, two outcome variables were reported:

- EM-1—the number of first-time correct answers.
- EM-2—the number of errors made.

TABLE 1 Descriptive characteristics of the sample cohort.

		Races combined Male <i>n</i> = 29 Female <i>n</i> = 19 Mean (SD)	Jordan Male <i>n</i> = 14 Female <i>n</i> = 12 Mean (SD)	Sri Lanka Male <i>n</i> = 15 Female <i>n</i> = 7 Mean (SD)
Age (year)	Male	35.3 (11.1)	35.6 (10.8)	35.1 (11.7)
	Female	32.1 (6.9)	32.0 (7.4)	32.1 (6.5)
Height (cm)	Male	180.5 (7.0)	180.9 (7.6)	180.0 (6.7)
	Female	169.6 (7.2)	171.5 (5.5)	166.3 (8.9)
Weight (kg)	Male	78.8 (8.6)	78.4 (6.3)	79.3 (10.5)
	Female	64.6 (6.1)	65.1 (5.6)	63.8 (7.4)
BMI (kgm ⁻²)	Male	24.2 (2.2)	24.1 (2.2)	24.4 (2.3)
	Female	22.5 (2.0)	22.2 (2.4)	23.0 (0.8)
Weight change (kg)	Male	-1.1 (1.4)	-2.0 (1.2)	-0.2 (1.1)
	Female	-1.3 (1.3)	-1.9 (1.0)	-0.2 (1.0)

PS was measured using the CANTAB RTI (reaction time) Test. This test required participants to place their finger on a “home” button until a yellow spot (the stimulus) appeared on the screen, at which time they moved to touch the yellow spot as quickly as possible (Akter et al., 2015; Giedraitiene & Kaubrys, 2019; Talebi et al., 2021). Again, two outcome variables were reported:

- PS-1—the time taken to release the home button following the stimulus.
- PS-2—the time taken to move to touch the yellow spot.

A recent study identified a small potential learning effect for both SWM and EM in patients with mild cognitive impairment (Cacciamani et al., 2018). Consequently, participants in the current study completed a practice test in advance of their pre-race baseline measurements.

To aid interpretation of the results, changes in SWM-1, SWM-2, EM-2, PS-1, and PS-2 have been multiplied by -1, so that a score increase represents an increase in performance.

2.2 | Body mass

Body mass was measured the day before the race, and 3–4 h (to allow for rehydration) following completion of Stage 3. Scales accurate to 0.1 kg were used (Seca, Hamburg, Germany).

2.3 | Statistical analyses

All variables were checked for normality using the Shapiro–Wilk Test, which identified several variables that were not normally distributed. For normally distributed variables, paired samples *t*-tests were performed to compare prerace and midrace metrics, and independent samples *t*-tests were used to compare differences between male and female athletes. For non-normally distributed variables,

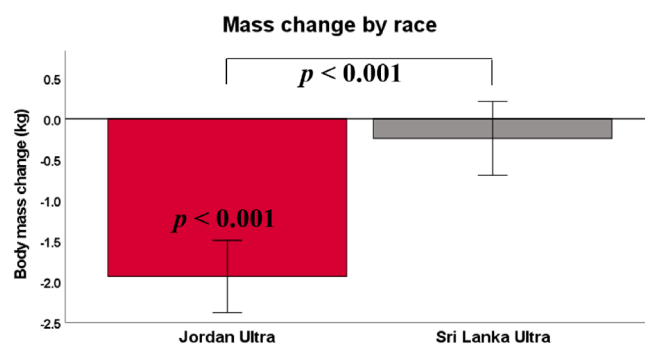


FIGURE 1 Bar chart showing a significantly greater mass loss during the Jordan Ultra than the Sri Lanka Ultra. Error bars represent a 95% confidence interval.

non-parametric equivalent tests were used (the Wilcoxon Signed-Rank Test and the Mann–Whitney Test). Analyses were conducted with the Statistical Package for the Social Sciences (SPSS) v.25, and significance set at <0.05.

This work was approved by the University of Cambridge Human Biology Research Ethics Committee (Application No: HBREC/2018.18). Informed consent was provided by each study participant. The data has been uploaded to Loughborough University's online Research Repository and can be accessed via the link <https://figshare.com/s/e693eddc61cfd1d97dc4>.

3 | RESULTS

Table 1 provides a description of the sample cohort across the two ultramarathons.

Athletes competing in the two races did not differ significantly in terms of baseline measures of age, height, mass, or BMI. However, the Jordan Ultra cohort lost mass (male $M = -2.0$ kg, $p < 0.001$; female $M = -1.9$ kg, $p < 0.001$), whereas the Sri Lanka Ultra cohort did not (male $M = -0.2$ kg, $p = 0.395$; female $M = -0.2$ kg,

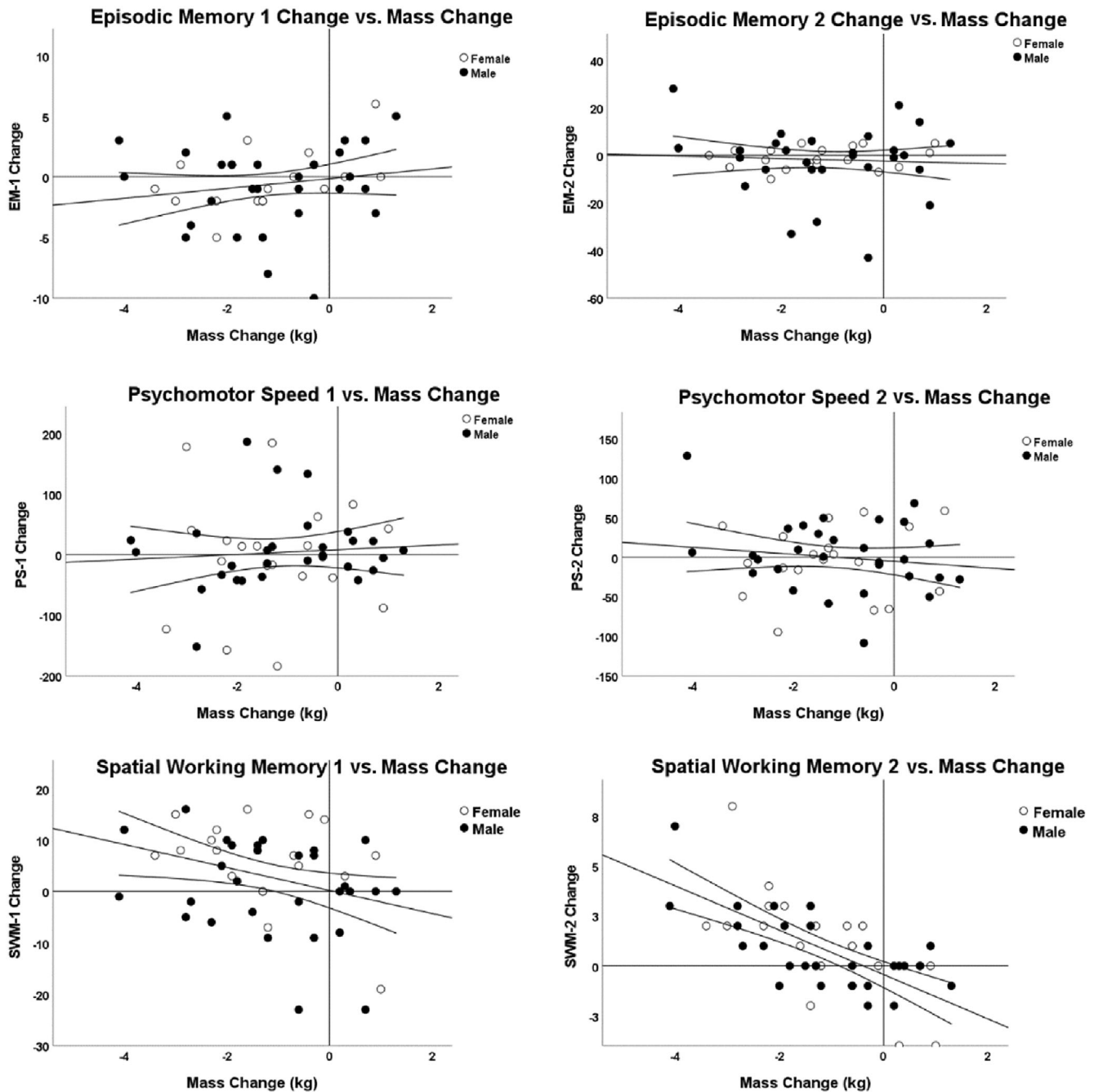


FIGURE 2 Scatter plots showing a significant relationship between mass change and measures of SWM (SWM-1 $r = -0.33$, $p = 0.023$; SWM-2 $r = -0.67$, $p < 0.001$). There was no significant correlation between mass change and EM (EM-1 $r = 0.19$, $p = 0.207$; EM-2 $r = 0.06$, $p = 0.673$) or PS (PS-1 $r = -0.07$, $p = 0.646$; PS-2 $r = 0.14$, $p = 0.359$). Error bars represent a 95% confidence interval. All $n = 48$.

$p = 0.583$). Comparing the two races, the mass change in the Jordan Ultra was significantly larger than in the Sri Lanka Ultra ($t = -5.498$, $p < 0.001$). This difference is visualized in Figure 1.

3.1 | Correlation analyses

Among the 48 participants, measures in each of the three domains of cognitive performance were significantly positively correlated

pre-race to mid-race ($p < 0.05$ in each measure). Similarly, performance in the two tests within each cognitive domain were highly correlated with each other both pre-race ($p < 0.001$ for each domain).

Considering the complete athlete sample (combining races as well as male and female athletes), mass loss was associated with improved SWM performance (SWM-1 $r = -0.33$, $p = 0.023$; SWM-2 $r = -0.67$, $p < 0.001$). In contrast, there were no statistically significant relationships between mass change and performance in tasks of

TABLE 2 Regression of change in cognitive performance on baseline cognitive performance, sex, race, and Δ weight.

	Unstandardized B	Coefficients SE	Standardized coefficients Beta	t	Sig	95% confidence interval for B	
						Lower bound	Upper bound
ΔEpisodic Memory 1							
(Constant)	-1.15	2.32		-0.49	0.627	-5.82	3.55
Baseline score	-0.33	0.12	-0.35	-2.64	0.011	-0.56	-0.08
Sex	-1.00	0.84	-0.16	-1.19	0.240	-2.68	0.69
Race	3.48	1.07	0.56	3.26	0.002	1.33	5.63
Δ Weight	-0.37	0.39	-0.16	-0.95	0.348	-1.15	0.42
ΔEpisodic Memory 2							
(Constant)	29.805	7.18		4.15	<0.001	15.32	44.29
Baseline score	-0.41	0.15	-0.34	-2.69	0.010	-0.71	-0.10
Sex	3.58	3.05	0.15	1.18	0.246	02.56	9.72
Race	-14.23	3.816	-0.61	-3.74	<0.001	-21.90	-6.55
Δ Weight	4.02	1.41	0.47	2.86	0.007	1.18	6.86
ΔSpatial Working Memory 1							
(Constant)	3.45	1.27		2.71	0.010	0.88	6.02
Baseline score	-0.13	0.10	-0.14	-1.35	0.184	-0.32	0.06
Sex	0.45	0.49	0.10	0.93	0.359	-0.53	1.43
Race	-1.41	0.61	-0.31	-2.30	0.026	-2.64	-0.17
Δ Weight	1.39	0.23	0.83	6.09	<0.001	0.93	1.85
ΔSpatial Working Memory 2							
(Constant)	6.54	6.07		1.08	0.287	-5.69	18.79
Baseline score	-0.32	0.14	-0.30	-2.31	0.026	-0.61	-0.04
Sex	4.36	2.49	0.23	1.75	0.087	-0.66	9.37
Race	-3.36	3.13	-0.18	-1.08	0.288	-9.66	2.94
Δ Weight	2.89	1.15	0.42	2.51	0.026	0.57	5.21

TABLE 3 Correlation analysis showing a significant relationship between mass change and measures of SWM in both male and female athletes.

	Episodic memory 1	Episodic memory 2	Psychomotor speed 1	Psychomotor speed 2	Spatial working memory 1	Spatial working memory 2
Δ Weight Female (n = 19)	$r = 0.45$ $p = 0.055$	$r = 0.21$ $p = 0.397$	$r = 0.02$ $p = 0.953$	$r = 0.11$ $p = 0.667$	$r = -0.40$ $p = 0.088$	$r = -0.69$ $p = 0.001$
Δ Weight Male (n = 29)	$r = 0.08$ $p = 0.678$	$r = -0.11$ $p = 0.566$	$r = 0.11$ $p = 0.562$	$r = -0.28$ $p = 0.141$	$r = -0.28$ $p = 0.144$	$r = -0.68$ $p < 0.001$

Note: Associations achieving (or near to) statistical significance are highlighted in bold.

EM or PS. See Figure 2 for scatter plots of the associations of mass loss with cognitive outcomes.

3.2 | Regression analyses

Regression analyses were performed to investigate the effects of mass change on cognitive variability. After controlling for baseline test

score, sex, and competition, it was revealed that for every standard deviation reduction in mass, performance in EM-2 decreased by 4.02 units (95% CI -1.18, -6.86), performance in SWM-1 improved by 1.39 units (95% CI 0.93, 1.85) and that performance in SWM-2 improved by 2.89 units (95% CI 0.57, 5.22). Mass change did not significantly explain performance in EM-1, nor for either measure of psychomotor speed after controlling for baseline test score, sex, and race. See Table 2.

3.3 | Sex differences

The association between mass loss and improved performance in tests of SWM was evident in both the male and female athletes. However, a near-significant trend for an association between mass loss and decreased performance in EM was evident in female, but not male, athletes. See Table 3.

3.4 | Comparison of the Jordan Ultra and the Sri Lanka Ultra

The observed mass loss of the Jordan Ultra cohort was accompanied by significant changes in whole-cohort cognitive function. Not only did performance in SWM increase (SWM-1 $t(25) = 2.635, p = 0.014$; SWM-2 $t(25) = -2.674, p = 0.007$), but the athletes also exhibited a

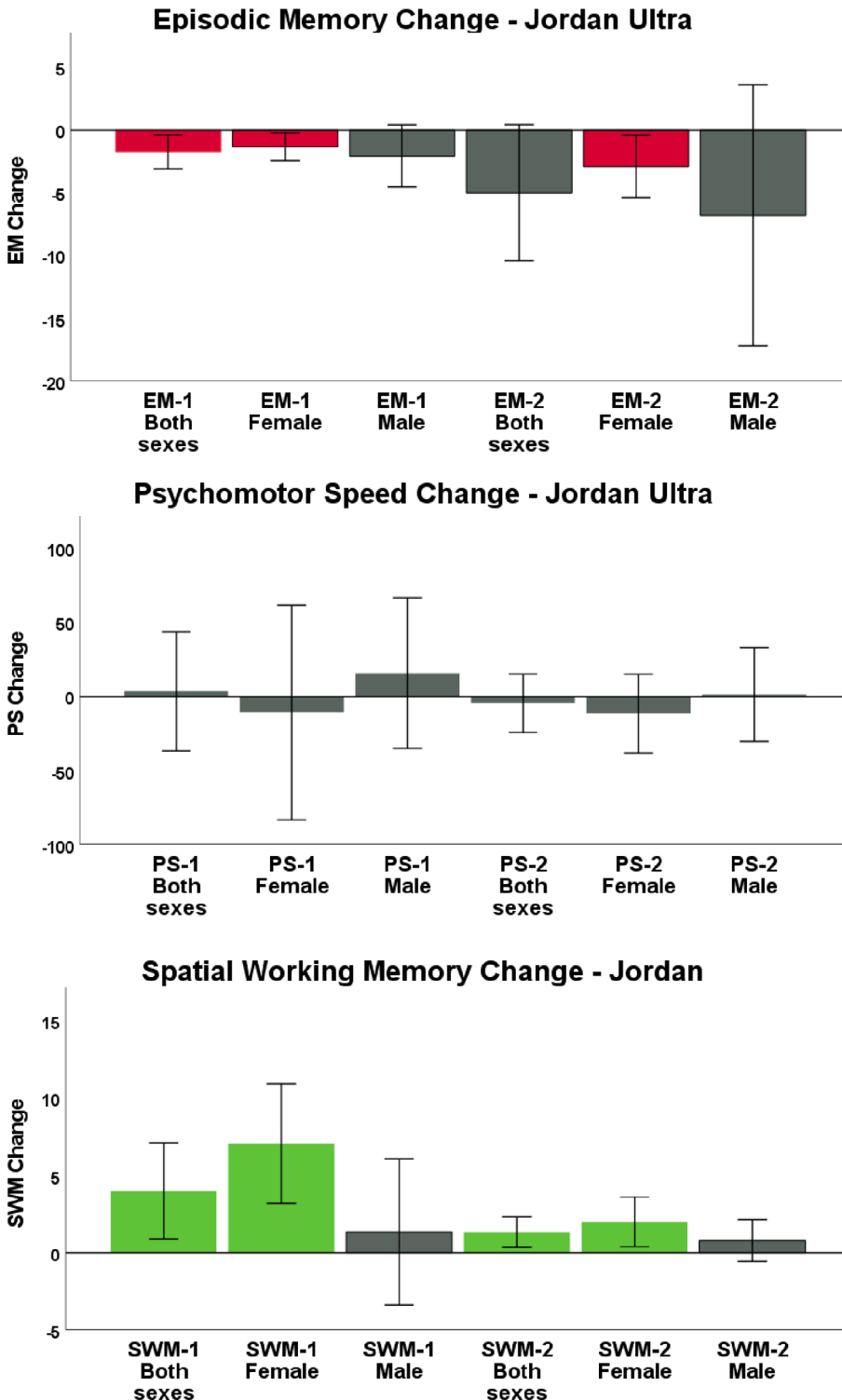


FIGURE 3 Bar charts showing sex differences in the change in each cognitive domain variable pre- to post-Jordan Ultra. A green bar represents a statistically significant improvement in performance, a gray bar no change, and a red bar a statistically significant decrease in performance. Error bars represent a 95% Confidence Interval.

decrease in performance in EM (EM-1 $t(25) = 2.651, p = 0.014$; EM-2 $z(25) = -2.373, p = 0.018$). There was no change in PS.

In contrast, athletes competing in the Sri Lanka Ultra, where the athlete cohort did not experience a change in body mass, there was no change in any of the three cognitive functions. See Tables S1 and S2 for further detail.

Figure 3 shows the changes in each cognitive domain for athletes participating in the Jordan Ultra, split by sex. A possible sex difference is apparent, whereby the female subsample drove the observed changes in cognitive performance. While there were no changes for either sex in PS, female performance in both tests of SWM improved (SWM-1 $t(11) = 4.015, p = 0.002$; SWM-2 $t(11) = 2.746, p = 0.019$),

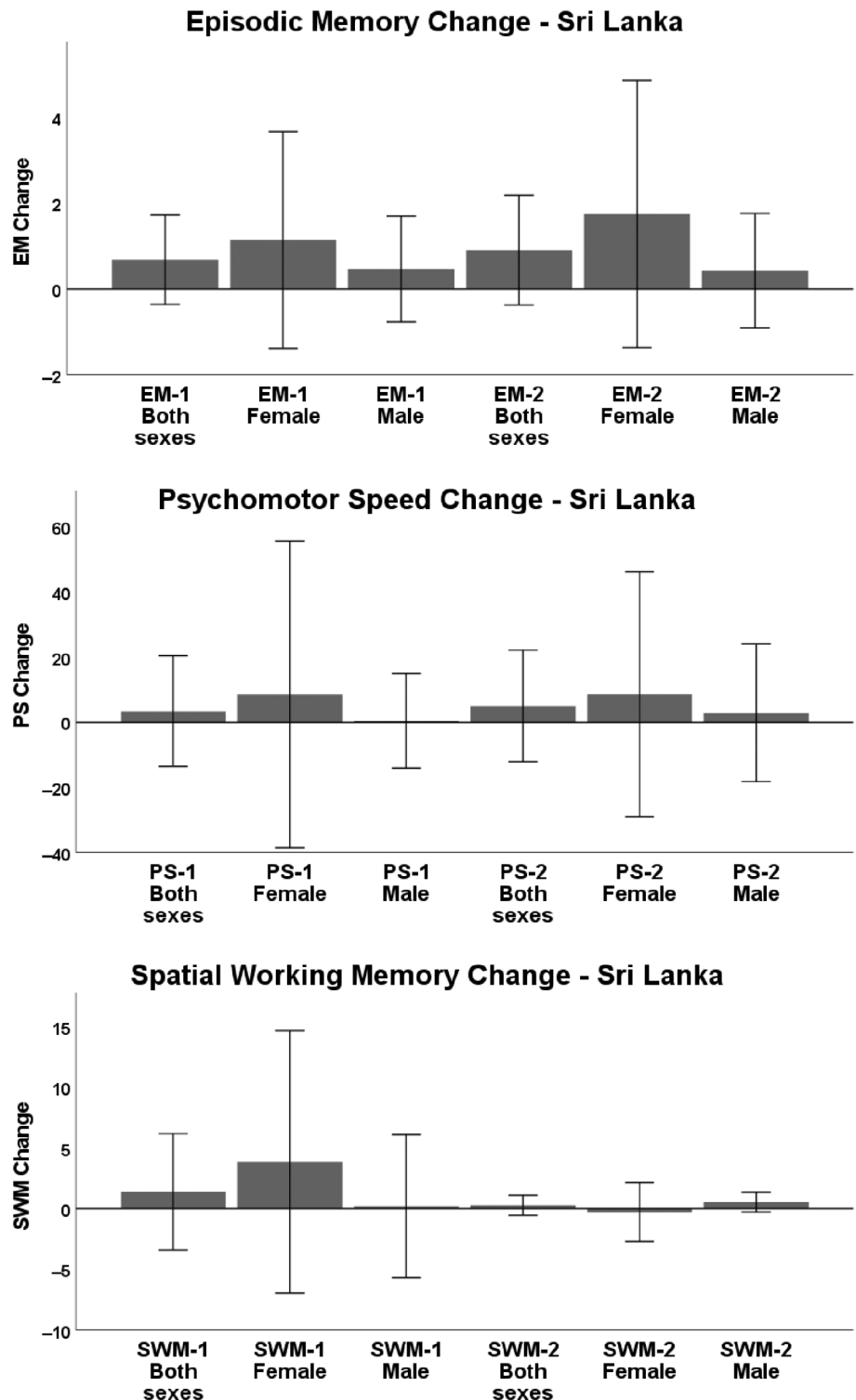


FIGURE 4 Bar charts showing sex differences in the change in each cognitive domain variable pre- to post-Sri Lankan Ultra. There were no statistically significant changes in cognition. Error bars represent a 95% Confidence Interval.

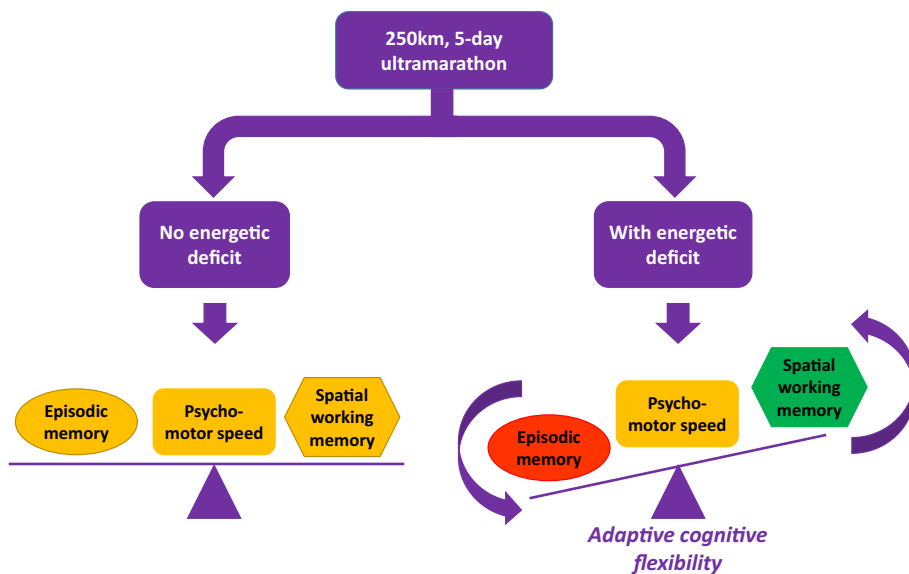


FIGURE 5 Schematic diagram illustrating adaptive cognitive flexibility prioritizing SWM at the expense of EM under conditions of energetic deficit. Red colouration indicates a decrease in performance, yellow colouration no change, and green colouration an increase in performance.

while male performance did not change. Similarly, performance in EM significantly decreased for female athletes (EM-1 $t(11) = 2.602$, $p = 0.025$; SWM-2 $t(11) = -2.578$, $p = 0.026$), while male performance remained unchanged. See Supplementary Information 3 for further detail.

Figure 4 shows the same data for the athletes participating in the Sri Lanka Ultra, where athletes did not lose mass, split by sex. No significant changes in cognitive function were observed.

4 | DISCUSSION

This study aimed to assess human cognitive plasticity under conditions of energetic deficit by evaluating variability in performance in three key cognitive domains under conditions of energetic deficit. We hypothesized that, due to its role in facilitating calorie-acquisition, conditions of energetic deficit would lead to upregulation of SWM relative to the other cognitive domains measured. The data, both as a whole and split by race, was consistent with this prediction.

Correlation analysis combining the Jordan Ultra and Sri Lanka Ultra athlete cohorts revealed that loss of body mass was associated with improved performance in both measures of SWM (in male and female athletes) and decreased performance in a measure of EM (in female athletes only). Regression analysis, controlling for baseline test score, sex, and race, also revealed that loss of body mass led to decreased EM and increased SWM performance. The results of this regression should, however, be considered in the context of the limitation of a relatively small sample size.

These results were supported by analyses considering each race separately. The body mass loss experienced by athletes competing in the Jordan Ultra was accompanied by a statistically significant decrease in performance in EM, no change in PS, and a statistically significant increase in performance in SWM. These changes were

largely due to changes in the female, rather than the male, subsample (this is discussed in more detail below). In contrast, athletes participating in the Sri Lanka Ultra did not lose body mass and exhibited no change in cognitive performance. Taken together, the combination of results reported here suggest that adaptive cognitive flexibility is driven by negative energy balance, rather than simply a high energy turnover. See Figure 5 for a schematic diagram illustrating this.

We suggest that prioritization of SWM function during conditions of negative energy balance represents an adaptive response. SWM temporarily stores location information, enhancing an individual's ability to navigate a landscape. This could be beneficial during energetic deficit because it may improve (a) ability to find the way home following a foraging or long-distance hunting trip, and (b) ability to acquire food by facilitating recollection of the location and quality of previously visited feeding sites. Preservation (or enhancement) of functions providing the greatest immediate survival advantage during negative energy balance is consistent with our previous observations with physiological functions (Longman, Prall, et al., 2017; Longman, Stock, & Wells, 2017). The resiliency of PS to energetic deficit may reflect the unchanging importance of a quick reaction to danger, regardless of energetic state.

Hot-dry conditions, such as those experienced by athletes competing in the Jordan Ultra, are known to cause a greater rate of sweating than hot-humid conditions, such as those found in Sri Lanka (Frye & Kamon, 1983; Morimoto et al., 1967; Shapiro et al., 1980). Despite the detrimental effects of dehydration on both general cognitive function (Adan, 2012; Cian et al., 2001; Sharma et al., 1986) and spatial cognition itself (Benefer et al., 2013; Cian et al., 2000; Lindseth et al., 2013), SWM performance improved in the Jordan Ultra. This context emphasizes the significance of the observed improvements.

The results of this study suggest a potential trade-off between spatial working memory and episodic memory under conditions of

negative energy balance. Higher-order cognitive processes, including logical reasoning and decision-making, are very metabolically demanding. Such processes rely on a shared limited glucose and glycogen supply for fuel, deplete fuel reserves when active, and become impaired when fuel is in short supply (Gailliot, 2008; Gailliot & Baumeister, 2007). Competition between cognitive domains for fuel during the present study was likely intensified by the similar substrate demands of active skeletal muscle and the brain during the ultramarathon competitions (Brooks & Mercier, 1994; McArdle et al., 2001; Romijn et al., 1993; Wahren et al., 1971). The high glucose/glycogen demands of running, SWM, PS and EM function may therefore have combined to create competition for glucose and oxygen (Fehm et al., 2006), resulting in the observed negative covariation between cognitive domains.

It is likely that loss of body mass, representative of a breakdown of adipose/muscle tissue (as opposed to dehydration—the athletes had the opportunity to rehydrate prior to mid-race weighing and cognitive testing), was responsible for the observed cognitive plasticity. Consequently, limitations in circulating substrate, and subsequent reduced availability of metabolic resources, are expected to have played a central role in the observed trade-off. It is acknowledged, however, that dehydration could limit the body's ability to deliver substrate to metabolically active tissues.

The ability to respond to changing environmental pressures through cognitive flexibility may be a consequence of our evolutionary history. Environmental stimuli constantly mold our elaborate brains, underpinning learning and facilitating rapid responses tailored specifically to current environmental conditions (Pascual-Leone et al., 2005). We propose that by following an evolutionary trajectory focussed on encephalization, our species have increased our capacity to respond flexibly to changing environmental pressures via “adaptive cognitive flexibility.”

Within the Jordan Ultra cohort, under conditions of negative energy balance, the female athletes appeared to drive the group increase in SWM performance. We suggest that the heightened response in the female athlete subsample may reflect the unique energetic context of human female reproduction. Both pregnancy and lactation require the mother to provide a steady source of nutrition for her offspring to meet a metabolic demand intensified by the evolution of an enlarged brain (Butte & King, 2005; Ecuyer-Dab & Robert, 2007; Holliday, 1971). As males lack these direct metabolic reproductive demands, females potentially face a larger penalty than males if they are unable to successfully navigate when experiencing an energy deficit. While a continuum of responses exists between the sexes, the adaptive response to enhance SWM during conditions of energetic deficit appears to be stronger in females. Further investigation is required in this area. Similar sex differences in SWM have previously been reported by a number of investigators. While a 2017 meta-analysis found a small but significant male advantage in a variety of tasks of spatial working memory, a female advantage in a subdivision of tasks relating to location memory has been consistently reported (Voyer et al., 2017). In light of the relatively

small sample size of the current study, we suggest that future research with larger sample sizes should investigate potential sex differences in greater detail.

5 | CONCLUSION

To conclude, research seeking to understand the competitive allocation of resources between key biological processes is central to life history theory. Such work cuts to the heart of our nature as a phenotypically plastic, colonizing species (Wells & Stock, 2007). Here, we employed principles described by the recently defined field of human athletic palaeobiology (Longman et al., 2020) to investigate adaptive cognitive plasticity in humans. We demonstrated, for the first time, trade-offs between cognitive functions at the intra-individual level in human participants. Specifically, performance in SWM was prioritized at the expense of EM. We propose that, by following an evolutionary trajectory focussed on encephalization, we have increased the “adaptive cognitive flexibility” of our species.

AUTHOR CONTRIBUTIONS

Daniel P. Longman: Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (lead); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Jonathan C. K. Wells:** Conceptualization (equal); methodology (equal); writing – review and editing (equal). **Jay T. Stock:** Conceptualization (equal); funding acquisition (lead); project administration (lead); supervision (lead); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors report no competing interests.

DATA AVAILABILITY STATEMENT

The data has been uploaded to Loughborough University's online Research Repository and can be accessed via the link <https://figshare.com/s/e693eddc61cfd1d97dc4>.

ORCID

Daniel P. Longman  <https://orcid.org/0000-0003-3025-7053>

Jonathan C. K. Wells  <https://orcid.org/0000-0003-0411-8025>

Jay T. Stock  <https://orcid.org/0000-0003-0147-8631>

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