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Modulation of striatum based non-declarative and medial temporal lobe based declarative memory predicts academic achievement at university level

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ABSTRACT

Background: There is a dearth of research on the roles of non-declarative (implicit) learning linked to the striatum and declarative (explicit) learning associated with the medial temporal lobes as predictors of academic attainment.

Methods: Participants were 120 undergraduate students, studying Psychology or Engineering, who completed several long-term memory tests.

Results: There was a significant interaction between the groups (Psychology or Engineering) and task type (declarative or non-declarative): Engineers performed better at declarative and psychologists at non-declarative learning. Furthermore, non-declarative but not declarative learning scores were significant correlates of academic achievement ($r = 0.326$, $p < .05$). Moreover, competitive modulation (activation of non-declarative learning in conjunction with deactivation of declarative learning) was a significant predictor of future academic achievement in both psychology ($r = 0.264$, $p < .05$) and Engineering ($r = 0.300$, $p < .05$) groups.

Conclusions: The results confirm that these declarative and non-declarative systems interact competitively and that the extent of this competition may have implications for understanding educational attainment.

1. Introduction

Intelligence testing is often used with varying success to predict academic achievement. Indeed, intelligence tests were originally developed for that very reason [1]. The predictive value, as measured by correlation, can be quite high for younger learners [2] but fairly meager at the level of higher education [3]. There is also some evidence that the relationship between achievement (as measured by grades) and intelligence is dependent on the field of study, as intelligence seems to be much better predictor of grades in technical subjects such as mathematics and science than it is in humanities subjects [4]. However, at face value at least, higher education is principally about learning information or skills, rather than the on-line novel problem solving that characterizes most intelligence tests. Therefore, the association of academic performance with learning ability may be a more productive line of enquiry, but one that has strangely been neglect in academic research.

On the one hand, pedagogical science has often drawn on the cognitive psychology of learning and memory to enhance teaching practices. A good example of this is the concept of deep and surface learning which has been very influential in educational circles. The principle is that the strategy applied by the learner greatly influences the quality of later demonstrated learning [5]. This approach stems directly from the Levels of Processing framework on memory structure proposed by Craik and Lockhart in 1972 [6]. Similarly, there is a large corpus of research on working memory and academic achievement, generally suggesting that at least in young people, working memory capacity (as measured by tests such as reading span and counting span) is a significant

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predictor of academic ability, particularly in language and mathematics learning [7–10]. In fact, it is perhaps a better predictor than intelligence testing [7]. This line of research has been successful because it took the concept of working memory developed in cognitive science and neuropsychology [11,12] and examined it as an individual difference metric, commonly referred to as working memory capacity [9] that could then be applied to education.

However, working memory is conceptually and functionally distinct from long-term memory [11–13]. Working memory is involved with storage of information over periods of seconds, with separate long-term storage systems responsible for longer-term storage [13,14]. This functional separation suggests that any contribution to academic attainment by variation in working memory capacity is likely to be independent of that which stems from variation in the capacity of long-term memory processes. Furthermore, although working memory capacity is a good predictor of performance in schools [7,8,10], it appears not be predictive of performance in higher education [15].

In contrast to the many studies of working memory capacity and academic achievement, there is very little research on the contribution of long-term memory capacity as a predictor of academic attainment. As students in higher education are required to learn facts and develop skills for use over the long term, this is quite a conspicuous absence from the pedagogical and cognitive sciences literature. There is evidence that acquired knowledge of word forms is a strong predictor of academic achievement, which may be a consequence of the strength of declarative learning ability [16]. Another study has reported that with deep, but not shallow, processing of verbal material, students who had achievement goals defined by self-improvement performed better on delayed recognition than students in whom the goal was to outperform other students (who conversely were better on immediate recall) [17]. However, this tells us little about individual differences in long-term memory capacity and achievement. Another study measured subjective memory functioning with a self-rated neuropsychological scale: the Everyday Memory Questionnaire (EMQ) [18]. Scores on the scale were found to be the best predictor of university students' grades among several other scales focusing on self-efficacy and locus of control [19]. In fact, there was a relatively strong correlation of $r = 0.47$ between EMQ scores and grades. The EMQ scale appears to measure subjective strength of factors identified as retrieval, task monitoring, conversational monitoring, spatial memory and memory for activities [20] and so includes a range factors from working memory and long-term memory processes. Therefore, the contribution of longer-term memory processing to academic achievement still remains unclear.

A fundamental distinction within long-term memory is between declarative and non-declarative processes [21–25]. This is suggested particularly by neuropsychological studies. It has frequently been observed that patients with dense anterograde amnesia for episodic information can nevertheless learn various skills. Such cases are generally associated with damage to medial temporal lobe (MTL) structures or midline diencephalic structures [23]. A classic example is the patient Henry Molaison (formerly known as HM) who in 1953 developed dense amnesia following bilateral surgical ablation of his hippocampi and other MTL tissue [26]. However, he was shown to be able to learn mirror drawing and maintain the learning despite having no conscious recall of the learning trials [27]. Since then various other forms of learning have been demonstrated in patients who show the classic amnesia syndrome due to MTL damage, these include eye-blink classical conditioning [28] and perceptual priming [29]. These studies have led to the distinction between declarative memories that can be reported verbally or represented in images [30], usually identified primarily as stemming from an MTL system [31], and non-declarative memory that is dependent on other brain systems including the cerebellum (skeletal responses such as eye-blink conditioning) and the neocortex (priming) [24].

In particular, there has been considerable interest in probabilistic category classification tasks as these seem to show a non-declarative learning system dependent on the striatum. The Weather Prediction Task is one such task. Performance involves prediction of either 'sun' or 'rain' based on abstract visual displays that only have a probabilistic contingency relationship with the outcome. Therefore single learning trials are less useful in developing accurate predictions than the sum of experiences [25]. It is this multi-trial aspect which seems to prevent declarative learning, but with participants nevertheless showing above guessing-rate improvement over time. This form of non-declarative learning appears to be analogous to habit learning in animal research which is also dependent on the striatum [25]. In a classic neuropsychological study, patients with impaired MTL function demonstrated significant learning on the Weather Prediction Task. In contrast, patients with impaired striatal function (Parkinson's disease) did not [32]. Taken together with episodic memory loss seen in classic amnesia, this double dissociation strongly suggests parallel memory systems subserving non-declarative learning in the striatum and declarative learning in the MTL. Additional evidence from single-cell recordings with rats [33] and functional magnetic resonance imaging (fMRI) have also implicated the striatum in non-declarative habit learning [21,22]. However, although the striatum and MTL are anatomically distinct it is likely that in many learning contexts they work together. There is evidence of simultaneous activation in both areas with early learning occurring in the MTL regions and at a later stage changes in the striatal system, as well as antagonistic modulation in which activity in one system down regulates activity in the other [21,22]. A recent example of this was a reward based (non-declarative) learning study conducted during fMRI with declarative memory testing of the task materials the following day. It was found that good declarative performance was related to poor non-declarative in-scanner learning, and this was also shown in the brain activations, good declarative performance was associated with decreased error-related signals in the striatum, and enhanced striatal-hippocampal connectivity [34].

A further example of the interactive nature of striatal and MTL-based memory systems comes from the effects of estrogen on learning. Both the dorsal striatum and the hippocampus contain estrogen receptors [35] and it has been shown that the natural estrous cycle in rats dynamically alters their preference for learning style. Specifically, when estrogen levels are high in the proestrous phase rats tend to spatial-based learning linked to hippocampal function, conversely when estrogen levels are low in the estrus phase they tend to use a habit-response strategy linked to striatal functioning [36]. Furthermore, experimental infusions of estrogen into the hippocampus of female rats enhances spatial learning while infusions into the striatum impair habit-response learning [37] suggesting that estrogen levels actively modulate the dual-learning systems biasing towards striatal learning in low estrogen states and to hippocampal learning during high estrogen states. This may be one reason why in mice at least, females show better striatal-based habit learning than males [38]. In women, the same form of modulation between memory systems seems to occur. When women are tested during different phases of the menstrual cycle, high estrogen levels are associated with enhanced MTL-based declarative verbal memory performance and low levels are associated with a preference for a striatal-based non-declarative learning strategy during spatial navigation [39]. Again, this suggests that declarative and non-declarative systems can be differentially active.

As an exploratory study into the role of long-term memory capacity and interaction in academic achievement at university level, we used this striatal non-declarative and MTL-based declarative dichotomy. This is a useful starting point because on the one hand students are required to learn facts when exposed to them and use them in alternative forms, a seemingly very declarative requirement [40]. On the other hand, non-declarative striatal learning appears to be necessary in learning from complex stimuli over time, in a sense developing intuitions about how to respond in adaptive ways, which also appears to reflect the types of learning seen in higher education. We examined the capacity of these two systems as individual difference measures, comparing them between two different groups of university students (Psychologists and Engineers). These were included so that memory capacity differences between technical and humanities students could be examined. However, we were particularly interested in examining how long-term memory capacity in these two groups could predict Grade Point Average (GPA) data. In addition, we examined the interaction of the two systems as a potential predictor. It was hoped that the findings would help us better understand why some students excel in higher education and others do not, and more generally, to understand the ways in which neurocognitive systems identified in laboratory work are related to adaptive (successful) behavior in the real world.

2. Method

2.1. Design and analysis

Participants were recruited from two different university faculties, Education and Engineering, and all were assessed with two different memory tests. In addition, the Grade Point Average (GPA) data of each participant was acquired from the university systems. In one strand of analysis the learning of the two groups was compared with standard between-groups analyses. In the other strand of analysis, the relationships between the memory test scores and GPA scores were examined. All analyses used a significance threshold set at 0.05 and were two-tailed unless stated otherwise (one-tailed analyses were used where one-directional hypotheses were being tested). For all analyses the data distributions were assessed by examination of the Q-Q plots. Where the distributions appeared to be normal, parametric tests were used, otherwise non-parametric alternatives were employed (e.g. Mann–Whitney U tests). To compare normally distributed continuous data (e.g., the participants test scores) with an expected value one-sample t-tests were employed. To make between group comparisons on normally distributed continuous data ANOVA tests were employed. To assess strength of relationship between pairs of uncontrolled variables (e.g., test scores, GPA) correlation tests were employed, or when predicting GPA with uncontrolled variables linear regression was employed. Standard effect sizes are given were appropriate (i.e., r values for correlations, Cohen's d for t-tests and partial eta^2 ($\eta_p{}^2$) for ANOVAs). Where descriptive statistics are given, for normally distributed data, numbers less than 10 are given to two decimal places, between 10 and 100 to one decimal place and above 100 to zero decimal places. When data distributions are not normal we have used the median plus the score range.

2.2. Participants

An overall sample of 120 undergraduate students at Universidad Nacional de Chimborazo, Ecuador, was recruited. All had already completed at least three semesters of university study at the point of participation. The median age in years of the full sample was 22.5 (range = 20.1–36.8) and 61/120 (50.8%) were female. All were Spanish speakers. The sample of 120 participants was comprised of two subsamples recruited from different faculties within the University. The first subsample (n = 60) were studying Educational Psychology as a major (median age = 22.1, range = 20.1–30.3; 47/60 female). The second subsample (n = 60) were all studying Industrial Engineering as a major (median age = 22.8, range = 20.4–36.8; 14/60 female). There were no significant differences between the groups for age (U = 1606.000, p = .309), ethnicity ($X^2_{(1)}$ = 0.00, p = 1.00) or family socioeconomic background (U = 1,863.5, p = .728). However, there were significantly more female students in the Psychology group (78.3%) than in the Engineering group (23.3%), $X^2{}_{(1)}$ = 36.310, p < .001. As described in the Introduction, memory system activation may be linked to the menstrual cycle in women, which could affect the results given the sex imbalance in the two groups. For this reason sex as a binary variable was entered as a covariate in all the parametric between group and correctional analyses. In addition, potential sex differences on performance are explored with additional male – female comparisons.

2.3. Memory assessment

To provide a relatively pure test of MTL related declarative memory we used an incidental learning paradigm with later recognition testing. Incidental learning (i.e., the participant is presented with stimuli material but not told that they will be memory tested later) is appropriate in this context as it minimizes variation introduced by deliberate encoding strategies, which tend to invoke prefrontal systems [41]. In addition, recognition rather than recall is appropriate, as it also tends to invoke less prefrontal processing [42], focusing processing on the MTL. We developed a novel procedure rather than use an existing clinical test of memory as clinical tests can have ceiling effects when used with healthy and high-functioning participants such as university students. We used memory for abstract designs as these minimize verbalization strategy use, and memory for abstract designs has previously been shown to be sensitive to MTL lesions [43]. This form of learning would usually be considered to involve episodic declarative memory.

In the learning phase a task was used in which 27 different abstract designs were presented sequentially on a 10-in. Tablet computer. The learning phase was presented to the participants as being a Size Judgment Task in which each abstract design appears on the screen twice in a vertical alignment. The area of the two shapes (maximum height * maximum width) was always different, ranging from 11.7% difference in area to 15.5% difference in area. On average the square area of each shape on the screen was 1425 mm^2. In 14 trials the larger object was the one below and for the other 13 it was the one above. Each pair of designs was shown for 1500 ms with a 3000 ms interstimulus interval consisting of a blank screen followed by a fixation cross for 1000 ms. An example slide trial from the learning phase (the Size Judgment Task) is shown in Fig. 1 (panel A).

For the recognition phase, each of the designs from the learning

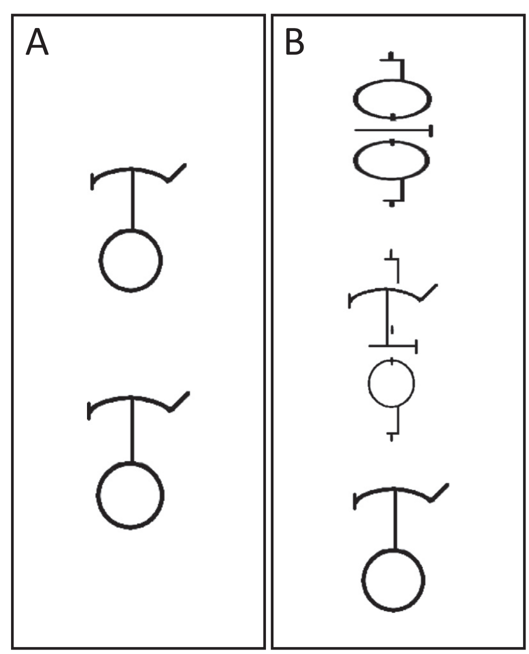

Fig. 1. Sample images used in the incidental learning paradigm: First participants were presented with stimuli such as in Panel A and were asked to judge which was the larger of the two. Approximately 100 min later they were presented with a surprise recognition test. For this, stimuli such as shown in Panel B were shown and the task was to identify the symbol that was included in the original size judgement task.

phase was presented with two similar designs that had not been shown previously. The actual 'old' design appeared in the top, middle and bottom positions 9 times in a pre-set random pattern. Progression through the recognition trials was participant paced. An example of a trial from the Abstract Design Recognition Task is shown in Fig. 1 (panel B).

As a measure of striatal-based non-declarative learning we used a probabilistic category classification task. The Weather Prediction Task involves participants being shown a configuration of shapes and their task is to decide whether it will be followed by 'sun' or 'rain'. This is repeated multiple times and the participant learns from the feedback from repeated associations. Importantly, the contingency between the different shape configurations and the outcome (sun or rain) is not fixed but varies probabilistically, such that a particular configuration may for example have a 75% probability of predicting rain and 25% probability of predicting sun. This probabilistic feedback aspect appears to be unconducive to MTL declarative learning systems, but can be learnt in a non-declarative manner. Learning in this paradigm is demonstrated by a gradual increase in performance above the chance guessing rate of 50%. The role of the striatum in performance of this task has been shown in human neuropsychological [32] and brain imaging studies [21,22], and similar learning has been linked to the striatum in animal lesion research [44]. Also, it can be performed without contingency awareness indicating that it can measure non-declarative learning [45].

We used 50 learning trials as this has been found sufficient to reveal significant improvements in performance above chance levels [32]. The visual stimuli and contingencies with prediction of rain or sun were the same as those described in a previous study with the Weather Prediction Task [46]. In brief, the stimuli were configurations of 1–3 different shapes comprised of squares, triangles, circles or diamonds. Each configuration was shown several times and had a set probability of predicting rain or sun. All trials were presented with black text and images against a white background. The individual shapes had a square on-screen area of approximately 1130 mm^2. Text was slightly smaller, in Calibri font, size 138. In each individual trial the configuration was shown for 1000 ms, this was followed by a screen showing only the word 'Responda' (respond) for 2500 ms, and then original configuration was shown above the outcome in words and pictorially "sol" (sun) or "lluvia" (rain) for 1000 ms. There was then a blank screen for 1000 ms before the start of the next trial. A schematic representation of this can be seen in Fig. 2. There were two blocks of 25 trials separated by a 10 s rest period. The 50 trials (in two blocks) where prepared in Microsoft PowerPoint but presented continuously as a movie file. The tasks described above were all administered on a 10-in. tablet computer.

Finally, we used a drawing task to assess declarative awareness of the stimulus-outcome contingencies in the Weather Prediction Task. This was included so that we can examine the interaction between the non-declarative prediction performance and declarative recall of the same stimuli. After the Weather Prediction Task was completed and the stimuli were out of sight, we asked each participant to draw the configuration that best predicated 'sun'. They were then asked to draw the configuration that best predicated 'rain'. As the different configurations had different probabilities of association with 'sun' and 'rain' these probabilities were awarded as points. For example, a square and a circle together were associated with 'sun' on 75% of trials and with rain on 25% of trials, therefore a participant who draw a square and a circle for the best predictor of 'sun' received 0.75 points. However, if they had drawn that for the best predictor of rain they would receive only 0.25 points. Therefore, a pure guessing rate would produce at best a score of 0.5 on average for each drawing. We took the sum of the two scores (guessing rate = 1.0) with scores greater than 1.0 indicating declarative knowledge of stimuli-outcome contingencies. Such knowledge would conform to definitions of declarative memory which refers to information that can be consciously recalled and represented in image form, whereas non-declarative memory is not amenable to imagetic representation [30]. This task is therefore referred to as the Declarative Drawing Task.

2.4. Procedure

The protocol was approved by the local research ethics committee and all participants provided written informed consent prior to data collection. All were assessed in a quiet private room at the university and received course credits for their participation. Assessments were performed individually for each participant with two experimenters (one assisting the other). Three pairs of experimenters worked in this way. The tasks described here were part of a larger neurocognitive and neurobehavioral test battery to be reported later. The first task in this battery was the Size Judgment Task. This was presented to the participants as being a perceptual task, but this was to mask its true

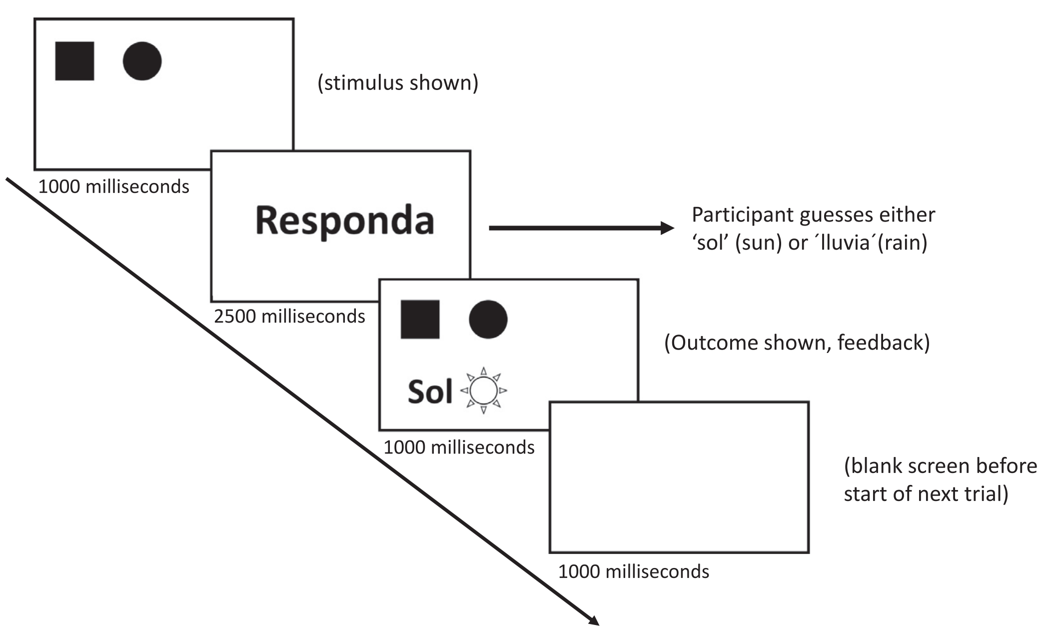

Fig. 2. Schematic representation of a single trial from the Weather Prediction Task. A configuration is shown and the participant is asked to guess whether this will be followed by sun or rain. Then they receive feedback showing whether it was in fact sun or rain.

objective as being the learning phase in an incidental learning paradigm. In each of the 27 trials the participant was asked to simply say which of the two shapes (identical in all aspects except size) was the larger. One of the researchers recorded responses by hand. Approximately 45 min further into the assessment the Weather Prediction Task was administered, again the responses were recorded by hand. Following that task, the Declarative Drawing Task was administered in which the participants were asked to draw from memory the configurations from the Weather Prediction Task that best predicted 'sun' or 'rain'. There were then about 30 min of further (non-memory) cognitive tests before the final assessment, this was the Symbol Recognition Task. Again, responses were recorded by hand. The entire assessment took around 100 min. All 120 participants were assessed within a single university semester. GPA scores were later obtained from the University databases. These were for the semester of research participation and the three preceding semesters. This was to be used for studying associations between cognitive test performance and concurrent academic attainment. We also waited for one additional semester after cognitive data collection had completed and recorded that GPA too. This was to be used for prediction of future academic performance.

3. Results

For the declarative memory task, the first stage, the learning phase, was administered to the participants as the Size Judgment Task. Although this task was used merely to present the stimuli for the later recognition test, we did record performance as this gives a measure of the initial processing of the stimuli items. The Psychology group scored a median of 25/27 correct (range = 15–26) which is slightly higher than the Engineering group median of 24/27 (range = 10–26), but not significantly ($U = 1949.5$, $p = .423$). Sex was not covaried in that non-parametric test, but we confirmed that there was no significant sex difference for performance on the task ($U = 1{,}720.5$, $p = .672$)

Next, we examined the recognition of the symbols that were used in the Size Judgment Task. To confirm that the Symbol Recognition Task did indeed measure memory performance we compared the scores of the whole sample to the guessing rate mean score of 9 (27 test recognition trials of one target with two distractors). This was achieved with a one-sample *t*-test (one-tailed). The whole sample's mean score of 13.5 (SD = 2.81) was significantly above chance ($t(119) = 17.360$, $p < .001$, $d = 1.59$). Despite the similar initial processing of the items (Size Judgment Task), in the later surprise recognition test the Engineer group achieved higher recognition scores (mean = 14.0, SD = 2.72) than the Psychology group (mean = 13.0, SD = 2.83), however, this difference did not reach statistical significance ($F(1,117) = 2.211$, $p = .140$, $\eta_p{}^2 = 0.019$).

For the supposed non-declarative test, the Weather Prediction Task, we also first ascertained that improvement was taking place and therefore that the task is indeed sensitive to learning. There were 50 trials and the average score in each block of ten trials was calculated and compared to the expected chance guessing rate of 5/10 (50%). Overall, the mean in each of the first three blocks of ten trials was close to and in fact slightly below the guessing rate (4.92, 4.93, and 4.43). However, in each of the penultimate and ultimate blocks of ten trials, the mean scores were 5.32 (SD = 1.61) and 5.74 (SD = 1.60) and both sets were significantly above chance ($t(119) = 2.156$, $p = .016$, $d = 0.197$ and $t(119) = 5.742$, $p < .001$, $d = 0.463$, one-tailed tests). This confirms that learning was occurring in the Weather Prediction Task, being most evident in the final 20 trails.

The Psychology group scored a mean of 11.6 (SD = 2.43) correct in the final 20 trials which was significantly higher than the mean of the Engineering group mean of 10.5 (2.72) and this difference was significant, $F(1,116) = 5.757$, $p = .018$, $\eta_p{}^2 = 0.047$). As the Engineering students scored significantly worse than the Psychology students on the overall measure of the non-declarative task (Weather Prediction) but better than the Psychology students on the declarative task (Symbol Recognition) these scores were compared directly with a mixed-model ANOVA. To allow comparison within the same model, z scores were used for each measure. Task type (Weather Prediction or Symbol Recognition) was used as a within-subjects factor and Group (Psychology or Engineering) as a between-subjects factor. This confirmed that there was a significant interaction between Task type and Group ($F(1,116) = 7.532$, $p = .007$, $\eta_p{}^2 = 0.061$), with Engineering students performing better on the declarative Symbol Recognition Task, in contrast to the Psychology students performing better on the non-declarative Weather Prediction Task (trials 31–50).

The Weather Prediction Task is designed to be difficult to perform in a declarative manner and so performance improvements are assumed to be indicative of non-declarative learning. However, since its inception as a non-declarative memory test, it has become clear that the associations between stimuli and outcome can be learnt in a declarative way [45,47]. To assess the extent that this was happening we included a task in which participants were asked to draw from memory the patterns that they thought were the best predictors of the two different outcomes- rain or sun (the Declarative Drawing Task). Scores were awarded proportional to the actual probabilistic prediction value; therefore, the guessing score would be 0.5 for each of the two drawings, the sum guessing rate would be 1.0. The actual observed mean score for the whole sample was 1.21 (SD = 0.444) and this was found to be significantly above the expected chance guessing rate with a one-sample *t*-test ($t(119) = 5.145$, $p < .001$, $d = 0.470$). This was true for both the Psychology ($t(59) = 4.689$, $p < .001$, $d = 0.605$) and Engineering ($t(59) = 2.746$, $p = .008$, $d = 0.355$) groups. Therefore, it appears that some declarative learning of the task had been occurring.

To further examine the main performance measure on the Weather Prediction Task, we divided the whole sample into two groups based on a median-split of the drawing test scores. The low declarative knowledge group ($n = 59$) had a mean knowledge score of 0.857 (SD = 0.330) and the high declarative knowledge subgroup ($n = 61$) had a mean of 1.55 (SD = 0.217). Note that scores above 1.0 imply declarative knowledge of the contingencies. Not surprisingly, one-sample *t*-tests confirmed that the low-declarative knowledge sub-group scored significantly below chance on the drawing task ($t(58) = -3.348$ $p = .001$, $d = 0.436$) while in contrast the high-declarative knowledge group scored significantly above chance ($t(60) = 19.778$, $p < .001$, $d = 2.53$).

We then examined performance of these two subgroups on each block of ten trials in the Weather Prediction Task, testing whether they scored above the expected guessing rate (one-tailed). The group with low declarative knowledge performed significantly above chance on the last block of trials ($t(58) = 1.969$, $p = .027$, $d = 0.256$), but at chance on the earlier blocks, while the subgroup with high declarative knowledge scored significantly above chance on the final two blocks ($t(60) = 2.650$, $p = .005$, $d = 0.339$ and $t(60) = 5.466$, $p < .001$, $d = 0.700$). This confirms that declarative knowledge was associated with better performance, but also that this was not essential as the participants in the subgroup lacking declarative knowledge of the contingencies were still able to improve performance through learning and perform significantly above chance.

In the analyses above we reported with a mixed-ANOVA that the Engineering students were better at declarative Symbol Recognition Task, compared to the Psychology students, but the reverse pattern was true with the ostensibly non-declarative Weather Prediction Task. To assess this interaction with the more stringent criteria for non-declarative memory, we repeated the mixed-ANOVA limiting the cases to those with low declarative knowledge according to the Declarative Drawing Task ($n = 59$). The interaction between Task type and Group remained significant ($F(1,55) = 4.293$, $p = .043$, $\eta_p{}^2 = 0.072$).

Next, we examined the relationship between academic achievement and cognitive task performance. The total scores for concurrent GPA over the 4 most recent semesters had a potential range from 0 to 40.

The mean GPA of the Psychology student group was 34.2 (SD = 1.92) which was significantly higher than the Engineering student group mean of 29.9 (SD = 2.99), $F(1,117) = 78.872$, $p < .001$, $\eta_p^2 = 0.403$. This difference likely indicates differences in grading standards between university faculties. To control for that difference z scores were calculated separately for the two groups (i.e., the mean GPA in each group was transformed to 0 with an SD of 1).

We then used GPA z scores to identify groups of high-GPA and low-GPA students. This was achieved with a median-split based on GPA scores in each of the Psychology and Engineering groups. Then we compared the 61 high-GPA students (Psychology $n = 31$, Engineering $n = 30$) with the 59 low-GPA students on the different memory test measures. On the declarative Symbol Recognition Task the high-GPA students scored similar scores to the low-GPA students (mean = 13.5, SD = 2.82 and mean = 13.4, SD = 2.83, respectively) and the small difference was not significant ($F(1,117) = 0.073$, $p = .788$, $\eta_p^2 = 0.001$. In contrast, for the Weather Prediction Task probabilistic classification performance (trials 31–50) there appeared to be a performance difference, the high-GPA group scored 11.5 correct (SD = 2.20) compared to 10.6 (SD = 2.96) for the low-GPA group. The difference was approaching but did not reach statistical significance, $F(1,117) = 3.212$, $p = .075$, $\eta_p^2 = 0.027$. However, one-sample tests revealed that while the high-GPA group scored significantly above chance ($t(60) = 5.288$, $p < .001$, $d = 0.677$) on the task, the low-GPA group did not ($t(58) = 1.584$, $p = .119$, $d = 0.206$).

For the measure of declarative task knowledge on the Weather Prediction Task we observed the opposite between-group difference, the high-GPA group scored significantly lower than the low-GPA group ($F(1,116) = 8.233$, $p = .005$, $\eta_p^2 = 0.066$) with means of 1.09 (SD = 4.28) and 1.33 (SD = 0.433) respectively. In fact, the high-GPA group did not appear to have developed declarative knowledge of the task contingencies in the Weather Predication Task, as their scores were not significantly higher than the chance guessing rate of 1.0 ($t(60) = 1.712$, $p = .092$, $d = 0.219$). However, the group with relatively lower GPAs did score significantly above chance ($t(58) = 5.814$, $p < .001$, $d = 0.757$).

Thus, during processing of the same task, the high-GPA group demonstrated significant levels of non-declarative learning but no significant declarative learning. We can assume the probabilistic classification task was performed non-declaratively due to the absence of declarative recall. In contrast the low-GPA group demonstrated no significant non-declarative learning, but significantly above chance declarative learning. To explore this further we performed a mixed-model ANOVA with one within-subjects factor (Measure type, non-declarative or declarative) and two between-subjects factors (GPA: high or low and Major: Psychology or Engineering). This revealed a significant Measure x GPA group interaction, $F(1,117) = 16.958$, $p < .001$, $\eta_p^2 = 0.129$. There was no 3-way interaction with study major indicating that both subject groups showed the GPA*Task interaction equally. In fact, when analyzed separately, this interaction of GPA group and memory measure remained significant in both the Psychology ($F(1,57) = 10.639$, $p = .002$, $\eta_p^2 = 0.157$) and Engineering ($F(1,57) = 8.308$, $p = .006$, $\eta_p^2 = 0.127$) groups. These interactions are shown in Fig. 3. Thus, it appears that regardless of student group, Engineering or Psychology, there was a tendency for antagonistic competition between declarative and non-declarative learning strategies on the Weather Prediction Task. This was manifest with high-GPA students tending to favor non-declarative learning at the expense of declarative learning and low GPA students tending to show the opposite pattern.

We also examined how the different cognitive measures correlate with concurrent GPA as a continuous variable. For the modulation of declarative and non-declarative memory we created a metric based on the sum of z scores for Weather Prediction Task probabilistic classification (trials 31–50) and the additive inverse of the z score for declarative drawing scores. Such scores would sum to zero if performance on the two measures were measuring the essentially same phenomenon

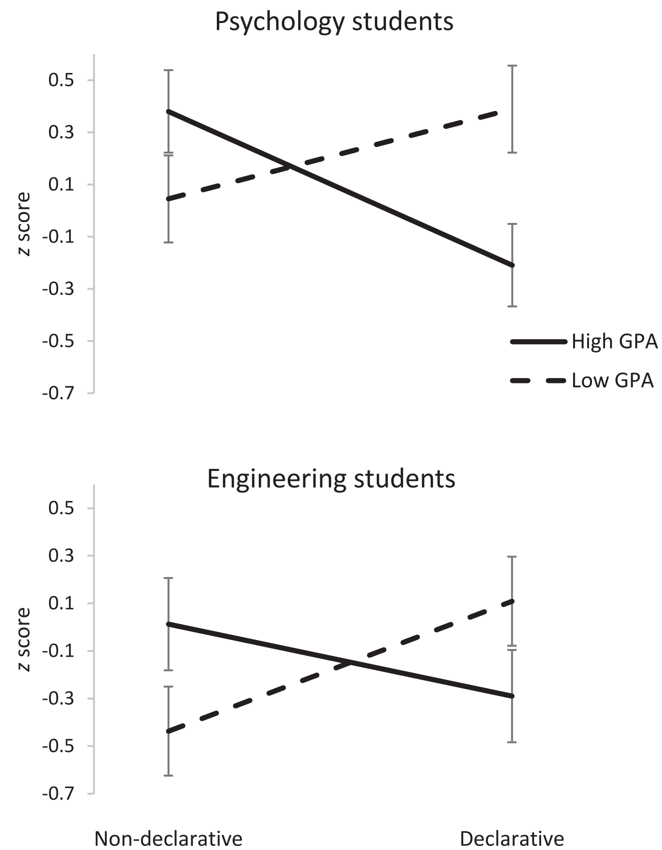

Fig. 3. Adjusted mean z scores (with standard error bars) for the Psychology and Engineering groups in the Weather Prediction Task. Non-declarative refers to their weather prediction guessing scores, Declarative refers to their ability to draw from memory the best predictors of 'sun' and 'rain'.

(e.g., task difficulty), on the other hand, the strength of tendency for better non-declarative learning to be linked to worse declarative learning would produce higher values. These correlations are shown in Table 1. As can be seen rather than cancelling each other out, the modulation metric was a consistent correlate of concurrent GPA, showing significant positive associations in both student groups. It is worth noting that the modulation metric is positive when calculated as we have described above. However, if it were calculated the other way around, as the sum of the additive inverse of probabilistic classification z scores and the z of the declarative knowledge scores, then the correlation r values would be exactly the same value but would become negative. Therefore, the modulation metric and GPA correlations can be seen as indicating either that good non-declarative paired with poor declarative performance is associated with good GPA, or poor non-declarative paired with good declarative is associated with poor GPA.

As an alternative to the modulation metric, we also examined the correlations of GPA with performance on the Weather Prediction Task when performance was limited to the participants identified as not having developed declarative knowledge of the task. These values are also shown in Table 1 as 'Weather Prediction Task (sub-group)'. The performance of these participants on the Weather Prediction Task represents the purer measure of non-declarative learning and these in fact showed the strongest correlations with concurrent GPA. Indeed, there was a very large positive correlation in the Engineering group ($r = 0.726$). It should be noted that these correlations should be interpreted with some caution, as the subsample sizes were small (Psychology $n = 28$, Engineering $n = 31$). This is also why the correlation within the Psychology group did not reach significance. Nevertheless, in the larger combined sample ($n = 59$) there was still a significant medium sized correlation of $r = 0.326$.

Table 1
Correlations between the various measures of long-term memory performance and concurrent GPA. For Weather Prediction Task we have included analysis of the median-split derived sub-group of participants who showed the least declarative knowledge (based on the Declarative Drawing Task).

Measure	Psychology	Engineering	Combined sample
Symbol Recognition Task	−0.044	0.195	0.061
Weather Prediction Task (all participants)	0.135	0.213	0.145
Weather Prediction Task (sub-group)	0.231	0.726***	0.326*
Declarative Drawing Task	−0.321*	−0.102	−0.211*
Declarative/Non-declarative Modulation	0.352**	0.274*	0.301**

* $p < .05$.
** $p < .01$.
*** $p < .001$.

We also collected data on prospective academic achievement (GPA accrued in the semester subsequent to cognitive data collection). This was to test how neurocognitive performance could predict later academic performance. We used linear regression with prospectively collected GPA scores as the dependent variable and cognitive scores as the independent variables, sex was also included as an independent variable. First, we analyzed the whole sample, and only where significant models were found did we perform further analysis on the Psychology and Engineering groups independently. Performance on the Symbol Recognition Task (a measure of declarative learning) did not produce a significant equation predicting GPA ($F(2,117) = 1.626$, $p = .201$, adjusted $R^2 = 0.010$. To examine performance on the Weather Prediction Task we entered both the probabilistic classification scores and the declarative drawing scores. This produced a significant model predicting GPA ($F(3,116) = 4.950$, $p = .003$, adjusted $R^2 = 0.091$). Interestingly, this time probabilistic classification performance was not a significant predictor with the other variables held constant ($t = 1.542$, $p = .126$, partial correlation $r = 0.142$); however, declarative drawing performance was ($t = -3.494$, $p = .001$, partial correlation $r = -0.309$). Therefore, although non-declarative performance could not predict GPA, declarative task knowledge could, but good task performance predicts *lower* GPA. When we repeated this linear regression with only the Psychology group or only or the Engineering group, more or less the same results were found. Neither analysis produced significant models (Psychology: $F(3,56) = 2.750$, $p = .051$, adjusted $R^2 = 0.082$; Engineering: ($F(3,56) = 2.398$, $p = .078$, adjusted $R^2 = 0.066$). However, within both models declarative task knowledge significantly predicted GPA (Psychology: $t = -2.351$, $p = .022$, partial correlation $r = -0.300$; Engineering: $t = -2.394$, $p = .020$, partial correlation $r = -0.305$). In both groups therefore, poor declarative task knowledge predicted higher GPA.

Similarly, significant models predicting future GPA were found when we considered the modulation metric. Within the combined student sample a significant regression equation was found ($F(2,117) = 5.960$, $p = .003$) with an adjusted R^2 of 0.077. Within the model only the modulation metric score was a significant predictor with sex held constant ($t = 3.093$, $p = .002$) and the partial correlation with GPA was $r = 0.275$. Based on the standardized coefficients, a one standard deviation increase in scores on the modulation score was associated with 0.275 standard deviations increase in GPA in the combined student sample. Similar results were found in the Psychology students only where there was a significant equation, $F(2,57) = 3.384$, $p = .041$, adjusted $R^2 = 0.075$. Within this model only modulation was significant ($t = 2.064$, $p = .044$) and the partial correlation was $r = 0.264$. A slightly stronger predictive relationship was found in the Engineering students sample, again the model was significant ($F(2,57) = 3.333$, $p = .043$, adjusted $R^2 = 0.073$). And again, only modulation was significant within the model, $t = 2.378$, $p = .021$, with a partial correlation of $r = 0.300$ with GPA scores. The partial correlations indicate that with sex held constant, modulation of memory systems in the Weather Predication Task towards non-declarative learning and away from declarative learning was predictive of future GPA in both the Engineering and Psychology student samples.

Finally, as described in the introduction, biological sex differences in ability related to declarative and non-declarative memory have been previously reported [38,48]. This is important to consider here because of the high male:female ratio in the Engineering group and the opposite ratio in the Psychology group. To examine this, we first compared all the male with all the female participants on the various measures of memory described above using between-subjects ANOVA. We also performed the same analyses adding group (Psychology or Engineering) as a covariate. For the Symbol Recognition task there was no significant effect of biological sex on performance ($F(1,118) = 1.864$, $p = .175$, ${\eta_p}^2 = 0.016$), even with Group covaried ($F(1,117) = 0.108$, $p = .744$, ${\eta_p}^2 = 0.001$). Similarly, there was no biological sex difference on the scores for the Weather Prediction Task ($F(1,118) = 0.428$, $p = .514$, ${\eta_p}^2 = 0.004$) even with Group covaried ($F(1,117) = 0.578$, $p = .449$, ${\eta_p}^2 = 0.005$). In contrast, although in the ANOVA calculation there was no effect of biological sex on the Declarative Drawing Task ($F(1,118) = 1.189$, $p = .278$, ${\eta_p}^2 = 0.010$) when Group was covaried there was a significant difference ($F(1,117) = 3.923$, $p = .050$, ${\eta_p}^2 = 0.032$). Analysis of the adjusted group means suggested that male participants tended to score higher than female participants (male mean = 1.25, SD = 0.475, female mean = 1.17, SD = 0.412). However, this effect seemed to be confined to the level of declarative learning in the Weather Prediction Task- there were no significant differences based on biological sex in for the modulation metric that we previously found to be statistically associated with GPA. Either in the ANOVA ($F(1,118) = 2.180$, $p = .142$, ${\eta_p}^2 = 0.018$) or the ANCOVA with Group covaried ($F(1,117) = 1.039$, $p = .310$, ${\eta_p}^2 = 0.009$) there were no significant differences.

4. Discussion

The aim of the current research was to investigate how capacity and interactions of non-declarative and declarative long-term memory systems may be contributing to academic achievement. We found absolutely no relationship between a pure measure of declarative long-term memory capacity and GPA. This was with an incidental learning paradigm with recognition testing. The procedure was designed to focus most strongly on MTL mediated declarative memory functioning, specifically visual episodic processes. In contrast, the current results suggest that the capacity of a striatal-based non-declarative system may be linked to academic achievement at university level. Furthermore, the results revealed a further theoretically interesting interaction that was able to predict academic achievement. Although, the MTL linked declarative memory performance *per se* had no association with academic achievement when measured in the Symbol Recognition Task, its level of activation during non-declarative probabilistic learning may be important. This was revealed on a task of non-declarative learning (the Weather Prediction Task) in which a measure of concurrent declarative learning was taken.

Our results revealed that participants were developing declarative knowledge of the Weather Prediction Task during performance. This was shown by their ability to perform at above chance levels when drawing the configurations that best predicted 'sun' or 'rain'. Such declarative knowledge of supposedly non-declarative learning on this task has been reported previously [45,47]. Nevertheless, this was not a general phenomenon, some participants performed above chance on the Weather Prediction Task and some did not. In fact, with a median-split of their declarative drawing performance, on average the lowest performing group was performing below chance on the task but in contrast they still predicted the weather at significantly above chance levels. This confirms that Weather Prediction Task can indeed reveal non-declarative learning, and is consistent with recent evidence that performance of the Weather Prediction Task can be performed by either non-declarative or declarative means [45]. In fact, the individual differences in whether declarative or non-declarative processes are employed seem to be important when considering real-life learning in education contexts. We found a significant interaction between memory performance of Engineering and Psychology students: Engineers were better at declarative learning (in our incidental Symbol Recognition Task) and Psychologists better at non-declarative learning (in the Weather Prediction Task), even when we limited the analysis to those who had not developed declarative knowledge of the task contingencies.

We also found that biological sex may be an important factor, in that male participants seemed to perform better than female participants on the Declarative Drawing Task, a difference that cannot be attributed to the different study groups (Psychology or Engineering) as that was covaried. This result contrasts with evidence that, if anything, women tend to have better declarative memory than men [48]. However, the task in which the male participants exceled was not a straightforward declarative memory assessment, it was for declarative learning during a supposedly non-declarative response learning task (Weather Prediction). And there is some evidence that in mouse models non-declarative learning is better in females than males [38], although the evidence for such an advantage in women is limited to the observation that women seem more sensitive to development of substance dependence than men [49]. In the current research we observed no difference between male and female participants on non-declarative learning.

What is clear from the current research is that individual differences in learning styles in terms of non-declarative probabilistic learning is a significant predictor of academic achievement. And this effect cannot be caused by biological sex of the participants as that was statistically covaried. When we examined concurrent academic performance, there were significant positive correlations with non-declarative probabilistic category learning, particularly in the Engineering students. In contrast, within the Psychology student group there was no significant correlation of GPA with probabilistic category learning, however, GPA was negatively correlated with declarative knowledge of the same task. This suggests dual processing consequences of performance of the Weather Prediction Task that are linked to academic achievement: on the one hand there is non-declarative learning revealed by improving predication accuracy, on the other inhibition of declarative memory revealed by poor declarative recall of the material. Indeed, when we analyzed the Weather Prediction Task as a factorial study, this clearly revealed that high-GPA students, compared to low-GPA students, were characterized by relatively strong non-declarative learning coupled with relatively poor declarative learning on the same task. The low-GPA students showed the opposite pattern (Fig. 3). This suggests that in each group there was competition between activation of the two different memory systems. When the striatum-based non-declarative system was effective, the MTL-based declarative system was not and vice versa depending on the group of students (high- or low-GPA).

An educational implication of these findings is that the way that learning is approached will affect the outcome depending on the type of learning required. The concept of 'deep learning' is often invoked in pedagogy as it is thought to produce better or more durable learning [5,6]. However, if the required learning is more procedural or habit based, the form of learning associated with the striatal system [33], deep processing which invokes hippocampal meditated declarative networks [50] may have the opposite effect, as this hippocampal activity seems to down-modulate striatal based learning. This could be important for example in language learning, in which the evidence suggests vocabulary is learnt by the MTL-mediated declarative system but grammar by the striatal-based non-declarative system [51].

A further implication is that impaired non-declarative learning has been implicated in several developmental disorders that directly impact on educational attainment, including specific language impairment [52], dyslexia [53] and mathematical disability [54]. In contrast, declarative learning appears to unaffected in many neurodevelopmental disorders (including specific language impairment and dyslexia) and in fact, may play a role in learning where it compensates for deficits in non-declarative learning [55]. If, as we suggest, non-declarative learning is particularly important for achievement in higher education, the compensatory strategy of emphasizing declarative memory may be insufficient to fully compensate for difficulties in non-declarative learning at university level. Indeed, it is even possible that the low-GPA group in our research, who favored declarative over non-declarative learning, may contain an overrepresentation of learning difficulties such as dyslexia, as compared to the high-GPA group.

The concept of competition between MTL-based and striatal learning systems invoked here is supported by neuroscientific evidence. In animals such as rodents, hippocampal based declarative memory is closely linked to spatial learning, while the striatal processes are involved with stimulus-response habit learning. Experiments with mice have shown that lesions of the striatum impair stimulus-response learning but enhance spatial learning while lesions of the hippocampus impair spatial learning and enhance stimulus response learning [44]. Similar antagonistic affects have been observed in the human brain imaging literature. With fMRI of healthy participants performing the Weather Prediction Task, activations in the MTL and basal ganglia depend on whether declarative or non-declarative strategies are emphasized by the experimenters, and importantly the magnitude of these activations are negatively correlated [21]. And recently another fMRI study used a paradigm with parallels to ours. They found that in a reward-based decision learning task which included images to remember, good incidental learning of the images was linked to poor reward-based learning, suggesting functional inhibition. Furthermore, it was shown that the error reward signal in the striatum was significantly weaker in those participants with good episodic learning (revealed by a memory test the following day) [34]. This again suggests that activation of one system leads to deactivation of the other.

The interaction between academic performance and cognitive test performance in the current research supports the competition interpretation of the interaction between MTL based declarative learning and striatum based non-declarative learning. We have demonstrated that two different groups of participants seem to differ in their competitive activation of the supposed striatal based and MTL systems. One group tended to favor striatal processing at the cost of MTL processing, and the other group showed the reverse pattern. If there were no competition between the systems, then this interaction should not occur. The current results therefore contribute to our understanding of the antagonistic modulation of different brain systems during learning.

Furthermore, the modulation metric that we used to summarize that antagonistic modulation was correlated with concurrent GPA scores and also able to predict future GPA in two different samples of students. The correlations would be considered as medium sized (= > 0.3) by standard interpretations [56]. Although, these may seem relatively low (a correlation of $r = 0.3$ is equivalent to only 9% of shared variance between the two variables), this is in fact somewhat higher than the correlation of GPA with standard intelligence tests. Several studies have failed to detect any significant correlations between IQ scores and GPA at university level [57,58]. Although others have reported medium-sized positive correlations [15,59], a systematic review and meta-analysis revealed that the mean correlation between IQ and GPA at undergraduate level is only about $r = 0.2$, (or 4% of shared variance) [3]. Our correlations were generally larger than that and also, it is notable that while IQ score correlations with GPA tend to be strongest in technical subjects and weak or non-existent in humanities subjects [4], our significant predictions of GPA were independent of the subject matter, being similar with groups of Engineering and Psychology students.

The reason that non-declarative learning and antagonistic modulation of the declarative system is linked to GPA is less clear. One explanation may be that the ability to focus processes on non-declarative probabilistic learning may index the level of neurodevelopment. The striatum is richly involved with several circuits connecting it with the prefrontal cortex [60–62], and these circuits show much slower development than other brain regions, not maturing until early adulthood [63]. Furthermore, there is evidence from a similar category learning paradigm that children, compared to college age adults, have difficulty inhibiting declarative learning processes when non-declarative mechanisms are more appropriate, also suggesting development is an important factor [64]. An alternative, but related explanation may be that the ability to modulate between different memory systems requires top-down executive control from the prefrontal cortex. Evidence for this comes from a neuropsychological study in which patients with ventral prefrontal cortical lesions were impaired on a different non-declarative classification task. The impairment was driven by the use of sub-optimal learning strategies and was correlated with performance on the Wisconsin Card Sorting test, a neuropsychological test of cognitive control and attentional shifting [65].

These two possible explanations are not mutually exclusive, as development of the prefrontal-striatal circuits will impact on executive function development. There may be other explanations for the data, however efficiency of strategic antagonistic modulation has the benefit that it can explain the seemingly counterintuitive finding that high GPA is correlated with low cognitive performance (declarative knowledge developed during the Weather Prediction Task). In our modulation interpretation this would be due to poorer executive control (perhaps due to lagging prefrontal-striatal development) preventing the application of appropriate non-declarative processing.

Whether this or other interpretations are correct, we have nevertheless demonstrated that efficient striatal-based non-declarative learning, and down modulation of MTL based declarative processing appears to be a better predictor of academic achievement at university level than a relatively pure measure of MTL based declarative learning. And this seems to occur irrespective of the subject matter as we found equivalent associations in Engineering and Psychology students. This has implications for how we think about the neurocognitive basis of learning, and its role in real-life educational contexts. This topic deserves further investigation; to explore whether this modulation effect is common to achievement in other learning contexts, and indeed whether it represents a mechanism of adaptive behavior that lead to success in other, perhaps non-educational, real-life contexts.

Conflicts of interest

None.

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