Running head: Everyday-life and experimental habits

An fMRI meta-analysis of the role of the striatum in everyday-life vs laboratory-developed habits

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Abstract

The dorsolateral striatum plays a critical role in the acquisition and expression of stimulus-response habits that are learned in experimental laboratories. Here, we use meta-analytic procedures to contrast the neural circuits activated by laboratory-acquired habits with those activated by stimulus-response behaviours acquired in everyday-life. We confirmed that newly learned habits rely more on the anterior putamen with activation extending into caudate and nucleus accumbens. Motor and associative components of everyday-life habits were identified. We found that motor-dominant stimulus-response associations developed outside the laboratory primarily engaged posterior dorsal putamen, supplementary motor area (SMA) and cerebellum. Importantly, associative components were also represented in the posterior putamen. Thus, common neural representations for both naturalistic and laboratory-based habits were found in the left posterior and right anterior putamen. These findings suggest a partial common striatal substrate for habitual actions that are performed predominantly by stimulus-response associations represented in the posterior striatum. The overlapping neural substrates for laboratory and everyday-life habits supports the use of both methods for the analysis of habitual behaviour.

Keywords: habits, everyday-life, probabilistic learning, cortex, striatum, meta-analysis, fMRI

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Introduction

Repetition gradually enables human behaviour to become automated to the point where it can be executed without conscious thought and attention. Thus, over a lifetime, a vast array of sometimes sophisticated movements, thoughts, and motivations are assumed under automatic stimulus-response control. Typically, we refer to such behaviour as *habits*. Repeated associations between representations of specific stimuli and particular responses enable stimulus-evoked reactions to be enacted without conscious intervention (Haith and Krakauer, 2018). This allows us to perform established stimulus-response associations automatically, thereby allowing conscious attention to be directed to less predictable aspects of the world. An obvious example would be not having to think *how* to walk when consciously thinking about *where* to walk. Hence, the development of habitual routines enable us to perform predictable and less predictable tasks simultaneously – walking and talking (Sun, 2004).

A defining feature of habitual behaviour is once a stimulus-response association has been established, it proceeds independently of any change in the outcome value of the response (Dickinson et al., 1985; Miller et al., 2019). An example would be pressing the lift/elevator button taking you to the floor of your old office, (the previous stimulus-response outcome), rather than the new office. Here the lift is the stimulus while the habitual response would be pressing the old floor button. The move to the new office has devalued the outcome value of this response yet, when conscious attention is directed elsewhere, it is still performed. This so-called action slip example satisfies the outcome-devaluation criteria and would confirm its status as a habit. Automatic habitual control is often contrasted with conscious goal-directed processing where the action selected is determined by the value/appropriateness of the predicted outcome (Daw et al., 2005; Dickinson et al., 1985; Gläscher et al., 2010). Typically, before statistical regularities of a task are determined, adaptive goal-directed control is used flexibly to achieve the desired outcome at the expense

of speed and efficiency. Consequently, early in instrumental learning, and in uncertain situations, flexible goal-directed control is specifically deployed for aspects of the task that cannot easily be predicted.

Human neuroimaging studies have revealed activation of the rostro-medial (associative) striatum during goal-directed instrumental learning, a pattern that gradually shifts to caudo-lateral (sensorimotor) regions when habitual control takes over (Brovelli et al., 2011a; de Wit et al., 2012a; Jankowski et al., 2009; Lehéricy et al., 2005a; Patterson and Knowlton, 2018; Tanaka et al., 2008; Tricomi et al., 2009). These findings concur with those described in non-human animals that demonstrate a similar involvement of the rostro-medial striatal territories early, and caudo-lateral regions later in the acquisition of instrumental tasks (Balleine and O'Doherty, 2010). Several neuropsychological studies including patients with striatal abnormalities provide converging evidence for a critical involvement of the caudal striatum in automatic habitual behaviour. The loss of dopaminergic input from the midbrain to the striatum in Parkinson's disease is initially concentrated in the posterior putamen (Pineda-Pardo et al., 2022; Redgrave et al., 2010a). This selective loss seems to alter automatic moves such as arm swinging during walking or facial expressions in social interactions. More recently habitual components of typing (Bannard et al., 2019) and associative learning (Mi et al., 2021) seem to be reduced in Parkinson's disease. In contrast, Huntington disease induces neural atrophy specifically in the head of the caudate (Vonsattel and DiFiglia, 1998) preventing the initial associations needed to integrate the repetition of stimulus-response associations into habits (Holl et al., 2012; Willingham and Koroshetz, 1993). Thus, evidence from experimental animal studies, functional imaging in healthy humans, and behavioural studies in human patients with selective dysfunction in different sub-regions of the basal ganglia, all point to the conclusion that conscious goal-directed and automatic habitual control are exercised by regionally segregated regions in the striatum.

A complication in the study of habits is the likely overlap with a wide range of other psychological concepts, including skills, automatic, routines, autonomous, inflexible, unconscious behaviour (West and Brown, 2013). We have already established that the formal definition of a habit is a stimulus-response association that proceeds automatically and is not modulated by outcome expectations (Dickinson et al., 1985). This perspective focuses on the stimulus evoked nature of habitual responses. Other definitions point more to the acquisition of habitual behaviours (Gardner, 2015), where the role of statistical regularities within tasks and the necessity of repetition are emphasised. Further, more recent analyses consider the way ultimate goals and motivation can influence habitual performance (Wood et al., 2021; Wood and Neal, 2007). However, due to the descriptive terminology used in different literatures, where the extent of conceptual overlap is unclear, inconsistencies and discrepancies between the previous studies of habitual behaviour should be expected (De Houwer, 2019). The purpose of the present meta-analysis was therefore, to determine the extent to which different forms of automatic stimulus-response behaviour engage the same or different neural substrates.

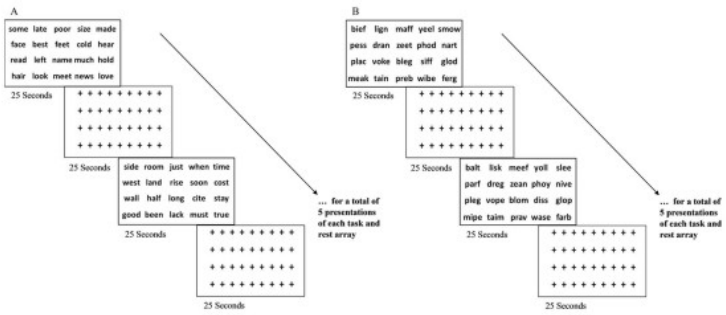
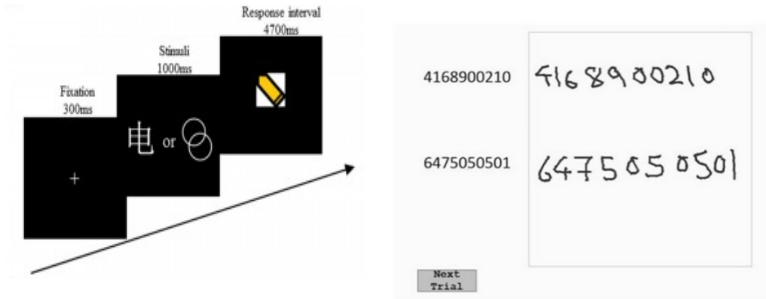
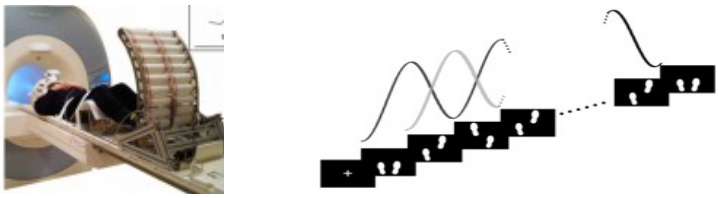
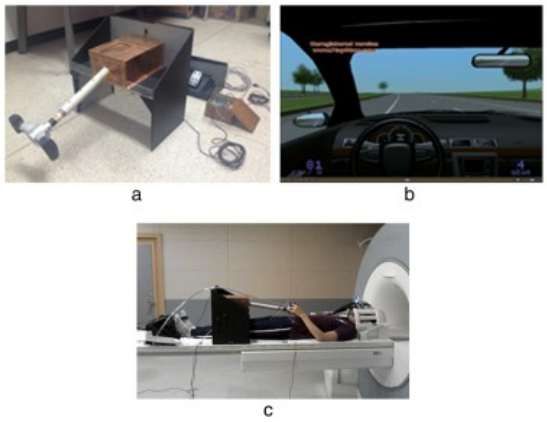
Until recently, most studies of habits have been in experimental settings where new stimulus-response relationships are learned in the laboratory. However, the relationship between these newly acquired stimulus-response associations and those acquired naturally over a lifetime when conducting everyday activities, is uncertain. It is equally important to understand how these important functional systems might malfunction, as reflected in brain disorders such as Parkinson’s disease (Bannard et al., 2019; Redgrave et al., 2010b), obsessive-compulsive disorder (Gillan, 2021), and drug addictions (Sjoerds et al., 2013), where dysfunctional patterns of habits are evident. Despite the obvious importance of habitual control, formal investigations of stimulus-response associations established in everyday-life are notably absent. An important step to remedy this would be to ask whether the neural circuits engaged by stimulus-response behaviour acquired in daily life are the same or different to those activated by newly learned habits in the laboratory. The specific

purpose of the present investigation was therefore to compare the patterns of neural activation evoked by long-acquired habits brought into the laboratory with those newly acquired under formal experimental conditions.

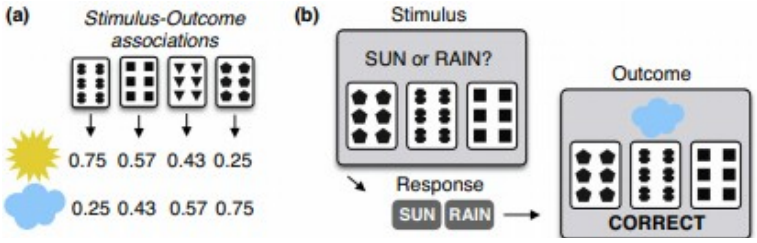
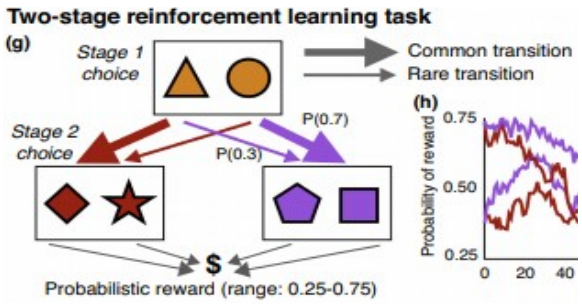
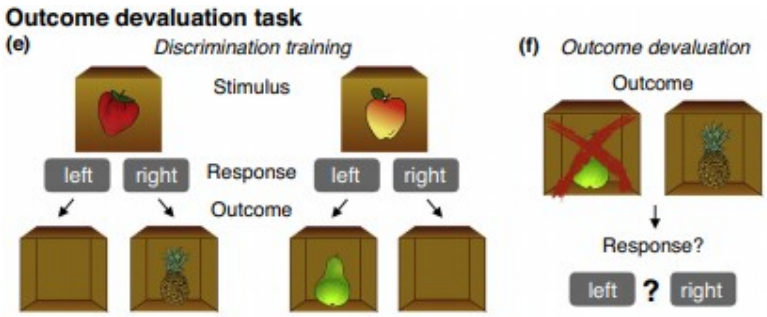
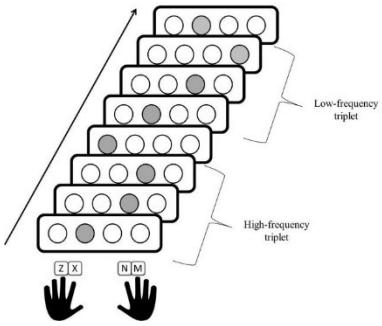
Experimental research with animals has shown how instrumental learning occurs initially through goal-directed computations where behaviour is influenced by predicted outcome values and then later transitions into outcome-independent stimulus-response mappings (Balleine and O'Doherty, 2010). Specific tests have been devised to demonstrate the insensitivity of habitual responding to changes in outcome value or the stimulus-response relationship. For example, when instrumental performance is seen to persist after the outcome has been devalued, or the association between stimulus and response outcome degraded (see Box 1 for a summary), then the observed behaviour is considered under habitual rather than goal-directed control (Adams, 1982; Balleine and O'Doherty, 2010; Dickinson et al., 1985; Perez and Dickinson, 2020; for a review see Foerde, 2018). The formal procedures developed in animal studies have been imported into experiments investigating habits in humans (Luque et al., 2020; Tricomi et al., 2009; Valentin et al., 2007; Watson et al., 2014; Watson and de Wit, 2018).

To date, most of the literature investigating the neural basis of human habits has relied on subjects developing new stimulus-response associations under formal laboratory conditions (Box 1B). This approach has provided important information about the transitions between goal-directed and habitual neural systems (Balleine and O'Doherty, 2010), and the factors (repetition, rewards or schedules of reinforcement) that promote the formation of habitual control (Dickinson et al., 1985; Omar D. Perez and Dickinson, 2020; Smith and Graybiel, 2016). However, this approach faces several challenges. Most pressing is the assumed equivalence of stimulus-response habits learned in the laboratory with those developed naturally in everyday-life. For example, one of the basic tenets of habitual behaviour is that the potency of stimulus-response associations should become stronger

with repetition. It is therefore, not inspiring that several studies have failed to report a positive relationship between the amount of training and the strength of habitual responses measured in their experimental settings (de Wit et al., 2018; Pool et al., 2022.).

Everyday-life	Main habitual outcomes	Task example
READING Real words are read aloud and compared to pseudo-words reading. Depending of the nature of the study, content of words may vary (neutral, emotional, language, non-words, etc) as well as naturality (own language vs new unknown words).	Reading own language with highly familiar/frequent words	 (1)
WRITING Participants are asked to handwrite by free natural writing, copying sentences/words, air-writing (sensorimotor control), creative writing, naming or drawing different figures.	Writing own language, familiar words (compared to baseline or control conditions)	 (2) (3)
WALKING While lying down inside the scanner, participants generate walking programmes on different block conditions, including voluntary alternating strides of the lower limbs, ankle moves, stepping, rapid walking or self-paced vs externally-paced.	Walking naturally at self-paced conditions	 (4)
DRIVING MR-compatible driving simulator is often used where participants are asked to naturally drive with different environmental conditions (driving only, stopping at traffic lights, turning curves, avoidance of particular stimuli) and control conditions (driving with sub-task, sub-task only, passive viewing, resting).	Driving in a natural environment (without distractors or dual tasks)	 (5)

- Cummine et al., 2016; (2) Yang et al., 2018; (3) Karimpoor et al., 2015; (4) Martínez et al., 2016; (5) Choi et al., 2017.

B. Experimental learning	Main habitual outcomes	Task example
PROBABILISTIC CLASSIFICATION TASK (PCT) Participants are shown visual cues that are probabilistically related to outcomes. Participants gradually learn the cue–outcome relationships through trial-by-trial feedback	Optimal responses to stimuli	 (1)
TWO-STAGE REINFORCEMENT LEARNING TASK Choices at stage 1 determine which state is more probable to occur in Stage 2 that leads to reward. At each Stage 2, participants choose between two stimuli and discover whether they receive a reward or not.	Reward sensitivity without sensitivity to transition probabilities	 (1)
OUTCOME DEVALUATION TASK During the discrimination training, participants learn to discriminate cues related to right-left key presses with rewarded outcomes. During the test phase, some of these outcomes are devalued and no longer worth any points. Participants are asked to press the correct key when a stimulus signals the still-valuable outcome or withhold responding if outcome is no longer valuable	Continued responding for devalued outcomes	 (1)
MOTOR SEQUENCE LEARNING Motor finger movements are repeated or alternated in high-frequent vs low-frequent sequences. Through repeated practice, participants learn the repeating sequences, as demonstrated by improvements in performance (speed and accuracy).	Accuracy differences between high-frequency and low frequency sequences	 (2)

- *Images obtained from Foerde et al., 2018; (2) Cellini, 2017*

Box 1. *Description of most used paradigms to assess everyday-life* ***(A)*** *behaviours and experimental learning* ***(B)*** *in fMRI contexts.*

An alternative and increasingly important way forward to study habits in humans would be to have everyday habitual behaviour learned over a subject's lifetime brought into the laboratory for investigation. Many behaviours in normal life including aspects of driving, eating, dancing, reading, talking or walking have significant stimulus-response components that can be performed automatically without thought while the person's conscious attention is directed elsewhere (Wechsler et al., 2018; Worringer et al., 2019). Such components have been acquired through frequent repetition throughout a life-time of everyday trials. Such associations come to the laboratory fully formed and are independent of any new learning.

The principal challenge in studying everyday-life habits is getting subjects to express their long-established stimulus-response associations in laboratory settings. This is necessary so both the automatic behaviour and associated neural activity can be measured quantitatively. Consequently, investigators have chosen behaviours that have significant automatic stimulus-response components (Ceceli et al., 2020) and can be performed in the laboratory while both behaviour and fMRI BOLD signals are measured simultaneously. Examples of such tasks include reading, where comparisons are made between real words of different familiarity and emotional content, foreign words and pseudo-words (Cummine et al., 2016); writing and drawing (Lin et al., 2021; Yang et al., 2018) walking on a special apparatus (Martínez et al., 2018); and driving an MR-compatible driving simulator (Box 1A; Choi et al., 2017; Cummine et al., 2016; Huth et al., 2016; Karimpoor et al., 2015; Martínez et al., 2016, 2018; Oberhuber et al., 2013; Varotto et al., 2020; Yang et al., 2018). The specific question we addressed in the current study is whether the BOLD activity patterns reported for stimulus-response associations acquired in everyday life are the same, partially overlapping or separate from those described for recently established laboratory habits (Figure 1).

To answer this question, we conducted a quantitative meta-analysis to investigate the neural substrates of everyday-life and experimental habits. This novel approach allowed a

direct comparison of the respective neural signatures. Special interest was focused on the system-level circuits involving the basal ganglia (Figure 1). The resulting information provides important clues into the organisation of life-time habits against which pathologies of habit and the results of therapeutic interventions can be referenced.

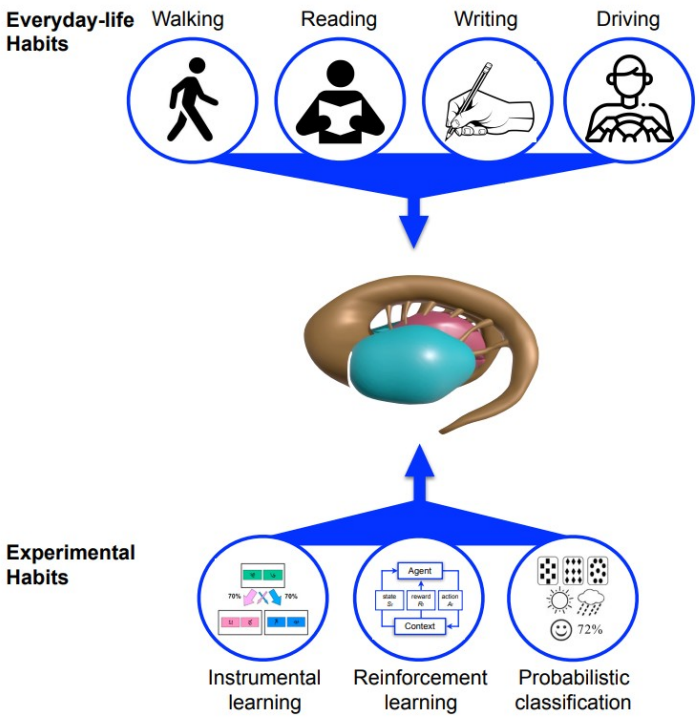


Figure 1. *Hypothesis diagram on striatal role in both everyday-life and experimental habits. Activities part of daily life such as writing, reading, walking or driving were selected as everyday-life habits (see Box 1 for task measurements and details) to expect a critical striatal role in executing these habits forms. Similar striatal activities can be expected compared to experimental paradigms commonly used in the cognitive science literature.*

Methods

Selection of studies. We conducted 2 independent searches in PubMed and Web of Science databases to identify fMRI studies investigating stimulus-response habits acquired: (1) in everyday-life; and (2) in experimental laboratories. The search of articles related to everyday-life habits was focused on natural behaviours expected to have significant automatic stimulus-response components: walking, driving, reading and writing.

The selection of these activities was in part based on their potential link to fundamental basal ganglia functions (Figure 1) and were based on 3 additional criteria: (i) behaviours that are testable within an MR scanner; (ii) entail a strong component of stimulus-response learning; and (iii) acquired through lifetime repetition. A summary of typical measures used in these studies is presented in Box 1. In the search for laboratory based habits we included articles referenced by Patterson & Knowlton (2018) plus all new relevant articles published since their last search (June 22, 2017) and June 1, 2022. To enable direct comparison with, and the extension of the Patterson and Knowlton review (2018), we conducted literature searchs using the same key search terms and included the task categories – probabilistic learning, discriminative learning and sequence learning (see Box 1). We also included relevant MeSH terms available in Pubmed. This allowed us to find articles that do not include targeted keywords in the title or abstract but have proper MeSH terms linked to their metadata. The complete list of our search terms can be found in Supplementary Material. To set limits on inclusion, the articles were filtered further according to the following criteria:

(1) Neuroimaging modality and analyses: spatial coordinates from human brain fMRI reported in standardized stereotaxic space (MNI or Talairach space). Thus, other functional imaging methods (e.g., PET, EEG source imaging, etc) were excluded;

(2) Sample selection and signal sensitivity: healthy subjects over 18 years old were included, as were the healthy control participants within clinical studies with independent analyses. Since brain activity in sensorimotor-related regions of the basal ganglia can deteriorate with neurological conditions (Redgrave et al., 2010), we included studies only with healthy adult controls. Moreover, following other fMRI meta-analysis (Murphy and Garavan, 2004; Sescousse et al., 2013), we did not include studies with potential low sensitivity (less than 6 subjects);

(3) Whole-brain analysis: ROI analyses were excluded as they can be biased by the study hypothesis and may not report all significant regions;

(4) Computational models: for studies using computational model parameters (i.e., model-free and/or model-based parameters), we only selected those corresponding to the reward prediction error (RPE) and the 2-step probabilistic task (a task validated to assess the duality between habitual/goal-directed modelling (Daw et al., 2011). Model-based related parameters of any kind (e.g., state prediction error, SPE) were not considered in the analysis, as they are characteristics of goal-directed behavior;

(5) Type of studies and language: studies reporting original data and published in English peer-reviewed journals (other reviews and meta-analysis were excluded).

We then performed a second-step control using reference lists from already included articles. From the list of references, we first excluded articles whose title had no direct link to any of our inclusion criteria. From the remaining articles that met our inclusion criteria we found 17 that had investigated everyday-life habits and 14 articles that had investigated laboratory-developed habits. Since our second exclusion step involved manual, rather than online searching, we were able to include articles published before 2017 not included in Patterson and Knowlton (2018). These additional references were selected because: (1) we checked all references from the list of accepted papers, not only those in major review articles; and (2) our criteria allowed us to include studies that did not report putative habit-related activation of the dorsal striatum (caudate, putamen, or both). Figure S1 depicts the identification, screening, eligibility and selection stages we used to select studies for inclusion. Foci, scripts and statistical maps can be accessed in the Open Science Framework (https://osf.io/w5ftm).

Contrasts of interest. The selected contrasts were based on the task condition reflecting the least difficulty level and less goal-directed task demands as well as comparisons linked to stimulus-response behaviours (see Table S1 and S2). Of interest, and most relevant to the present work, was the use of activity maps that were not initially designed to measure motor or cognitive habits, but rather, general human behaviour. Hence, one strength of the current work is the study of common hubs for different measures not

initially intended to be directly compared. Ultimately, some contrasts are based upon validated mechanisms part of habitual behaviour, such as experimental situations (stress or time pressure) known to largely engage habits and were therefore selected from certain studies;

Data analysis. The latest version of the GingerALE software v3.0.2 (Eickhoff et al., 2009) was used to compute activation likelihood estimations (ALE) (Turkeltaub et al., 2002). From each of the accepted articles, the coordinates of peak activations were manually extracted and those in Talairach space were transformed to Montreal Neurological Institute (MNI) space using the inverse transform of icbm2tal from GingerALE (Lancaster et al., 2007). The ALE method was implemented as follows: (1) for each study a 3D Gaussian distribution was created around every peak activation (variance proportional to the sample size of the study). This allowed us to use the higher statistical power to reduce peak uncertainty in studies with larger sample sizes. This step was done for every peak to produce one modelled activation (MA) map per study. The value for each voxel in a MA-map represented the probability of that voxel containing an activation foci. (2) Voxel probabilities in all MA-maps were merged to produce an ALE map. Following recommendations of Eickhoff et al., (2016), the ALE map was thresholded using a cluster-level Family-Wise Error (FWE), with a cluster-forming threshold of .001 and a cluster-level FWE of .05 (as stated in the GingerALE manual; Fox et al., 2013).

The first step in applying a cluster-level FWE was to threshold the ALE map at the voxel-level (cluster-forming threshold). To do this, all possible combinations between all peaks from each MA-map were tested. The ALE values provided a null distribution which assumed the peaks would be randomly distributed following all potential combinations amongst them. Here, an uncorrected *p*-value was used since in the next step, a FWE correction was applied to correct for the possibility of multiple comparison errors.

Then, an additional threshold (cluster-level FWE) was applied to select only the largest clusters. Peaks in every MA-map were distributed randomly and then combined into a single ALE map, following the same union method described above for the voxel-level threshold. The ALE maps were also thresholded with the same method used at the voxel-level threshold. This procedure was repeated (1000 times for this meta-analysis) using Monte Carlo permutations method, selecting on every run the largest cluster in the thresholded ALE map (null distribution). Finally, we applied the selected threshold (0.05) to obtain the FWE-corrected results. Using a 0.05 cluster-level threshold resulted in a thresholded map where only 5% of the surviving clusters could have been introduced by chance (false positives), following guidelines to discard non-significant clusters (Eickhoff et al., 2009).

Contrasts between thresholded ALE maps were computed to compare between our conditions of interest (e.g. Everyday-life > Experimental maps). All foci in the selected studies were pooled into a single dataset, which we then split in two datasets by randomly assigning to each one the same number of foci in their original file. The ALE-scores of these two random maps were then subtracted in a voxel-wise manner generating the map of their ALE-scores differences (repeated 10000 times to record ALE-scores and generate a null distribution of randomly spatially distributed foci). Finally, the actual two ALE maps corresponding to the contrast were combined voxel-wise by subtracting the ALE-score of one map from the other. The resulting map of ALE-scores were then thresholded voxel-by-voxel by comparing them with the null distribution previously obtained. We used the default *p*-value suggested in GingerALE (0.01 uncorrected). All computations were run via in-house python scripts to automate analyses in the GingerALE's interface. Thresholded maps are reported in MNI152 space (Mazziotta et al., 2001).

Complementary analysis. To ensure the results were not driven by a small number of studies from specific categories (i.e. heterogeneity), several additional tests were conducted (as indicated by Müller et al., 2018). We categorized possible differences by

dividing each category (experimental, everyday-life) into subgroups and analysed independently. Studies of experimental habits were separated into two subcategories: probabilistic learning vs other experimental tasks (Table S2), on the ground that probabilistic classification typically activates more anterior portions of the caudate and the putamen, compared with other tasks (Patterson and Knowlton, 2018). Meanwhile, we included categorical variables that separated motor (walking, driving) and cognitive (reading, writing) habits acquired in everyday-life, a further sub-division motivated by the anatomo-functional gradient along fronto-striatal circuits (Haynes and Haber, 2013). To best isolate the sensorimotor properties of habitual driving as part of the motor category, we selected contrasts including less cognitive demands. We also ensured to include > 20 studies in the experimental and everyday-life categories in order to fulfil the expected effect (Eickhoff et al., 2016). Finally, we also performed an additional check for heterogeneity and individual study bias which consists in counting the number of studies that contribute to a specific ROI which was significant in the ALE analysis (Müller et al., 2018). To do so, we applied an FWHM smoothing, whose value depended on the number of subjects per study which was configured according to recommendations in the GingerALE manual. Then, we reviewed the clusters to check if the foci of each study had any influence for each ROI that resulted significant in the group analysis.

Results

Study selection

First, to select a cohort of studies investigating everyday-life habits, we analysed data from 57 studies (a total of 1536 subjects) that used diverse stimulus-response paradigms (walking, reading, writing and driving). Imaging models that included automatic parameters on each task were chosen (Tables S1-S2). Second, we sought to confirm the neural basis of

newly learned experimental habits in the 38 studies (a total of 938 subjects) that had used probabilistic or discriminative learning, 2-step learning or sequential tasks (Box 1B).

Striatal role in everyday-life and experimental habits

To find the neural signatures of everyday-life habits, we obtained cluster activity associated with stimulus-response behaviours learned throughout life, and compared these with the signatures of habits newly learnt in laboratory settings. The main effects of naturalistic habits revealed significant bilateral activity in the posterior putamen (Table 1; Figure 2A). Specifically, this was sustained by activity in dorsal sections and left putamen activation that expanded to its posterior boundary (Table 1; Figure 2A-B). For these tasks, other active regions were seen in the cerebellum and cortical areas including the premotor, SMA and inferior frontal gyrus pars opercularis (Table 1; Figure 2A-B).

Newly learned habits from laboratory settings were also associated with increased levels of activation in putaminal sections, but with larger representations in anterior striatum (Figure 2C). A gradient was seen along the rostro-ventral section of the putamen, right caudate and the nucleus accumbens bilaterally (Table 2; Figure 2C). The right insula was one of the extrastriatal hubs of activity associated with habits acquired in the laboratory (Table 2; Figure 2A).

Of particular interest was the possibility that despite the differences between neural activation patterns associated with everyday and experimental habits, there may be a common neural substrate accessed by both categories of stimulus-response behaviour. Specifically, we found common activations in anterior right putamen and posterior left putamen (Figure 2A). Although both categories of habits recruited dorsal sub-regions of the putamen bilaterally, the activation by everyday-life habits was stronger (Figure 2C). As expected, no activation in the caudate nucleus survived FWE-corrected thresholds with everyday-life habits. In contrast, habits acquired in the laboratory showed a differential

recruitment of the nucleus accumbens, and to a lesser extent, the most antero-ventral section of the right caudate nucleus and putamen (Figure 2C). Hence, while the striatum is a common hub for both categories of habitual behaviour, antero-posterior differences were reflected in the activation patterns of habits acquired in everyday-life and the experimental laboratory.

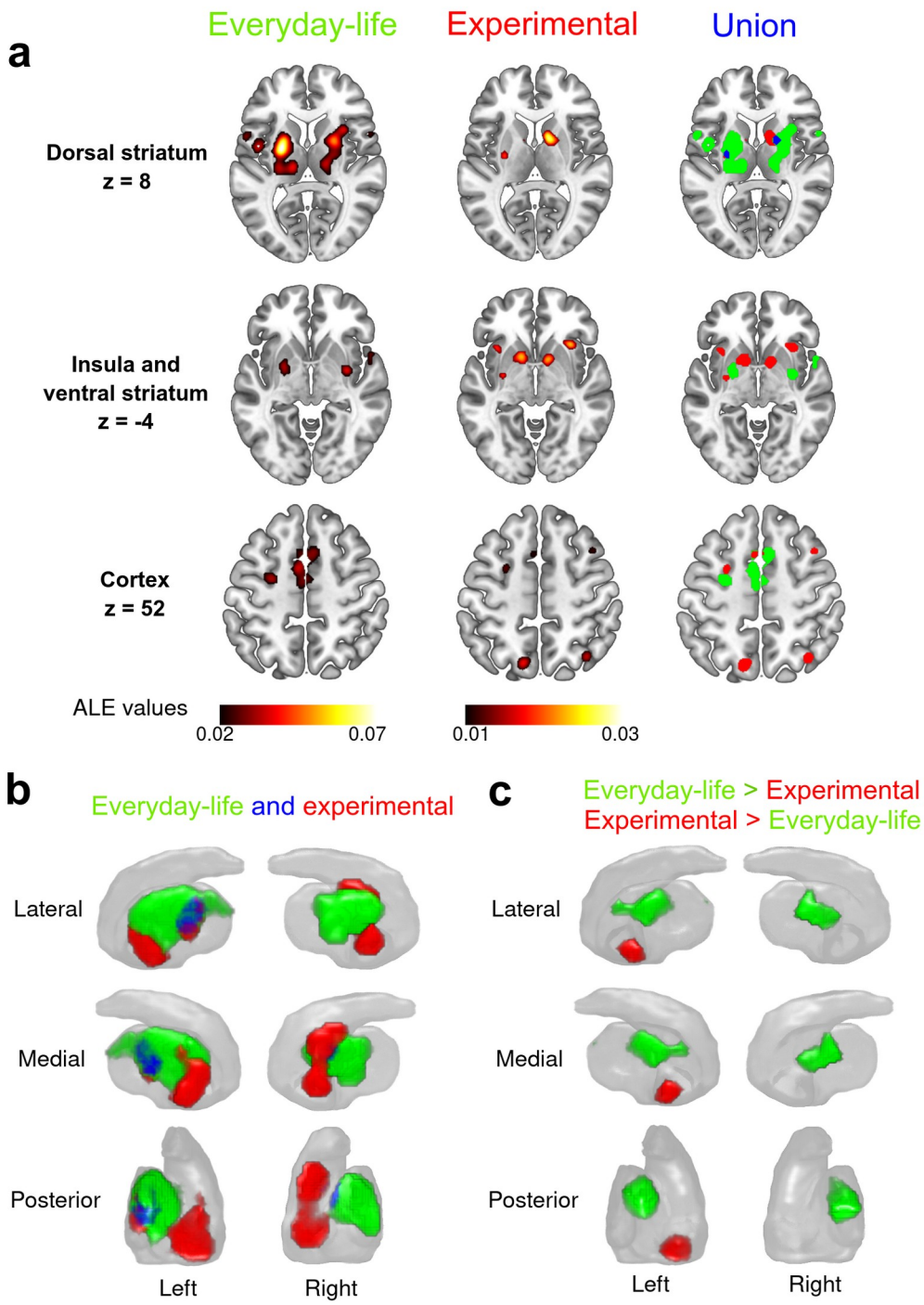


Figure 2. *Everyday-life and experimental thresholded activation maps.* ***a)*** *Axial views for the main regions. Overlap regions at the right column are shown in blue. Note that there exists activation in the cerebellar cortex for the case of everyday-life studies but it is omitted here for brevity. Z=52 view for the experimental studies is shown as an unthresholded map for visualization purposes (ALE value ≈ 0.01).* ***b)*** *3D striatum reconstruction showing all the activation that fall inside it. Overlap regions at the right column are shown in blue.* ***c)*** *3D striatum reconstruction showing the differential activation of the Everyday -life > Experimental contrast (in green) and the Experimental > Everyday-life contrast (in red).*

Cluster ID	Volume (mm^3)	Brain regions (%)	MNI peak coordinates			ALE value
			x	y	z	
1	9232	Left Putamen (54 %)	-24	-4	6	0.078
		Left Thalamus (28 %)	-14	-22	10	0.04
		Left Pallidum (16 %)	-23	-4	2	0.058
2	6616	Right Putamen (57 %)	24	4	6	0.056
		Right Thalamus (18 %)	16	-16	8	0.035
		Right Insula (12 %)	32	14	8	0.037
		Right Pallidum (11 %)	22	-8	8	0.04
3	4840	Left Supplementary Motor Area (40 %)	-6	0	52	0.035
		Right Paracingulate Gyrus (16 %)	6	14	50	0.031
		Left Paracingulate Gyrus (16 %)	0	8	53	0.031
		Right Supplementary Motor Area (14 %)	4	8	56	0.03
4	3088	Left Precentral Gyrus (97 %)	-54	-2	40	0.038
5	2288	Right-Cerebellum-Cortex (100 %)	8	-64	-20	0.037
6	2288	Left Central Opercular Cortex (54 %)	-46	-2	6	0.037
		Left Inferior Frontal Gyrus pars opercularis (19 %)	-54	8	24	0.027
		Left Precentral Gyrus (17 %)	-56	8	4	0.033
		Left Insula (7 %)	-44	-1	4	0.03
7	2152	Right Precentral Gyrus (76 %)	56	12	32	0.041
		Right Inferior Frontal Gyrus pars opercularis (19 %)	54	13	31	0.038
8	1072	Right Inferior Frontal Gyrus pars opercularis (34 %)	58	12	10	0.027
		Right Central Opercular Cortex (27%)	52	6	2	0.029
		Right Temporal Pole (13 %)	54	10	-2	0.034
		Right Precentral Gyrus (12 %)	3	-10	53	0.022
		Right Planum Polare (9 %)	53	5	-3	0.027
9	1016	Left Precentral Gyrus (43 %)	-26	-8	56	0.04
		Left Superior Frontal Gyrus (35 %)	-4	14	53	0.029
		Left Middle Frontal Gyrus (21 %)	-51	4	38	0.027

Table 1. *Everyday-life habits peaks coordinates in MNI152 space with region names from Harvard-Oxford atlas. Percentages of each brain region indicate how much activation from a cluster fall into such region. Coordinates of any activation comprising < 5% of its volume in a region are not shown for conciseness.*

Cluster ID	Volume (mm^3)	Brain regions (%)	MNI peak coordinates			ALE value
			x	y	z	
1	3000	Right Caudate (48 %)	12	6	10	0.028
		Right Pallidum (23 %)	14	4	0	0.023
		Right Accumbens (12 %)	10	8	-6	0.03
		Right Putamen (8 %)	14	9	-6	0.02
		Right Thalamus (7 %)	12	-1	10	0.018
2	2136	Left Putamen (30 %)	-14	5	-9	0.027
		Left Accumbens (28 %)	-12	6	-10	0.033
		Left Caudate (21 %)	-10	4	4	0.017
3	784	Left Putamen (99 %)	-28	-10	6	0.02
4	752	Right Insula (90 %)	32	22	-4	0.023
		Right Orbito-Frontal Cortex (10 %)	34	22	-7	0.016
5	736	Left Insula (90 %)	-34	16	2	0.025
		Left Frontal-Operculum Cortex (10 %)	-36	19	2	0.02

Table 2. *Experimental habits peaks coordinates in MNI152 space with region names from Harvard-Oxford atlas. Percentages of each brain region indicate how much activation from a cluster fall into such region. Coordinates of any activation comprising < 5% of its volume in a region are not shown for conciseness.*

Motor and associative segregation in life-long habits

We next tested whether the neural correlates of everyday-life habits varied between sensorimotor routines (walking or driving) and cognitive-associative ones (reading or writing). Clustered activation in motor tasks revealed a significant presence along the dorsal putamen compared with the associative tasks (Figure 3A). In addition, motor tasks extended the pattern of activation into more posterior sections of the right putamen, but only dorsally for the left putamen. This cluster was present across all the antero-posterior axes (Figure 3B).

In the case of habits acquired in everyday-life, we observed an activation pattern in ventral sections of the putamen bilaterally (Table 1). This effect showed significant bilateral

asymmetry favoring the left putamen where activation extended into more posterior regions. This was absent in the walking and driving tasks (Figure 3A).

Outside the striatum at the cortical level, the associative tasks acquired in everyday-life recruited premotor area and SMA. Activation was also observed in the cerebellum (Figure 3A). The same cortical regions were recruited during the walking and driving tasks, but none survived FWE-corrected thresholds.

To investigate further the failure of our thresholding procedures to detect activation in the caudate nucleus for any of the naturalistic habit categories, we included the distribution of all the foci that fell into the striatum in both categories of everyday-life habits (Figure 3C). This allowed activity in the right caudate to be observed (Figure 3C) in some associative studies, but not for the motor ones. For the left caudate nucleus, no foci were reported in any study, which confirms the absence of activity reported in the thresholded maps above.

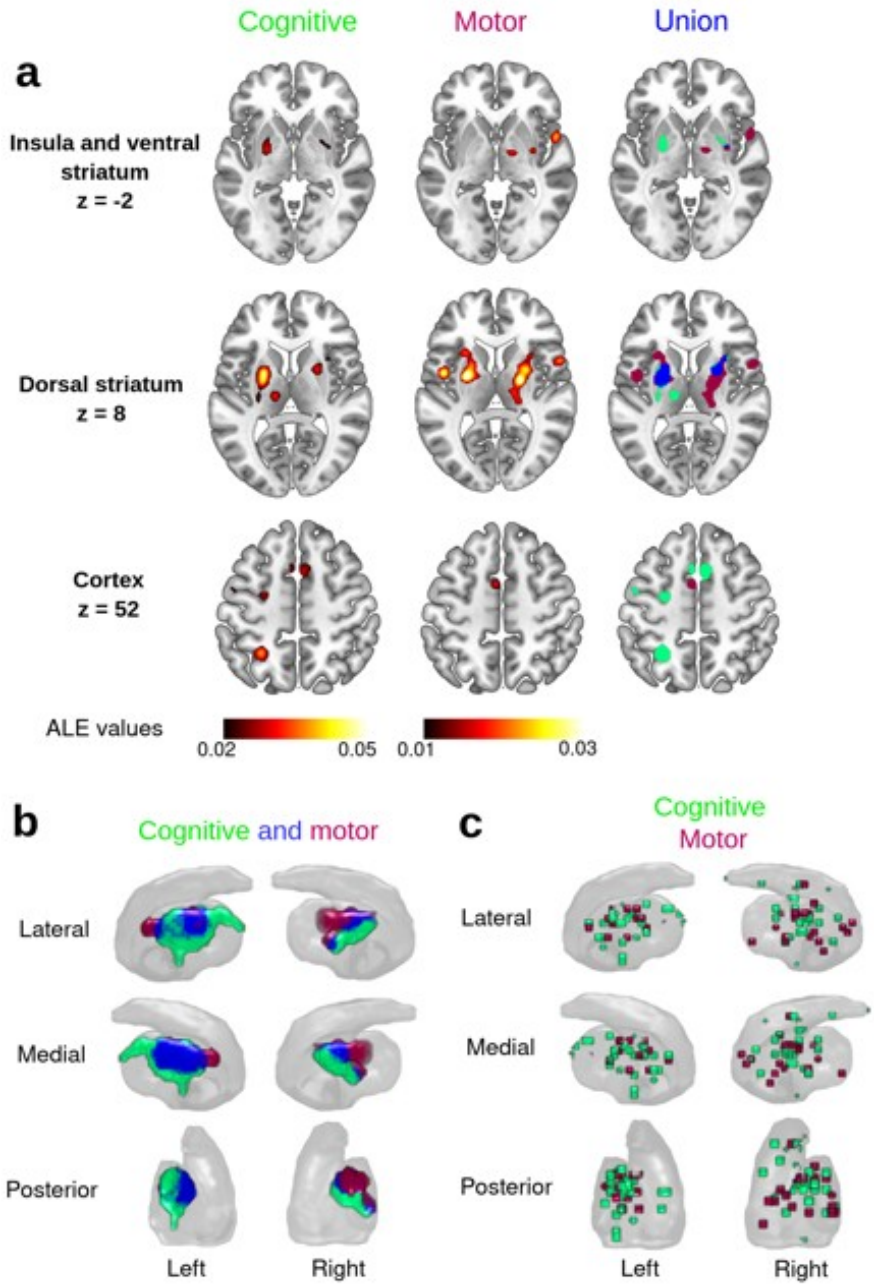


Figure 3. *Everyday-life cognitive-motor subcategories thresholded activation maps.* ***a)*** *Axial views for the main regions. Overlap regions at the right column are shown in blue.* ***b)*** *3D striatum reconstruction showing all the activation that falls inside it. Overlap regions at the right column are shown in blue.* ***c)*** *Foci distribution of all the studies that falls in the striatum. Note that some foci may correspond to the same study.*

Probabilistic learning and other tasks segregation in experimental habits

Finally, we aimed to replicate previous findings from laboratory conditions that linked the striatum to the learning and execution of new habits. Consistent striatal activity has been

reported when evaluating probabilistic or discriminative learning, 2-step learning and sequential tasks (Patterson and Knowlton, 2018). Here, the intention was to confirm and update these results with more recent findings by separating the studies involving trial-and-error probabilistic reward learning from those using different methodologies for stimulus learning. As predicted, both probabilistic learning and the other tasks showed common regions of striatal activation, with largest clusters in the nucleus accumbens and rostro-ventral sections of the caudate and putamen (Figure 4A). However, only the probabilistic tasks were associated with bilateral recruitment of the most anterior region of the putamen (Figure 4B). These results confirm the previous findings reported by Patterson and Knowlton, (2018). Similarly, the other experimental tasks differed with respect to the probabilistic ones by demonstrating unilateral recruitment of the left rostral caudate nucleus (Figure 4B). Outside the striatum, left insular cortex was activated in other tasks but not by the probabilistic ones (Figure 4A).

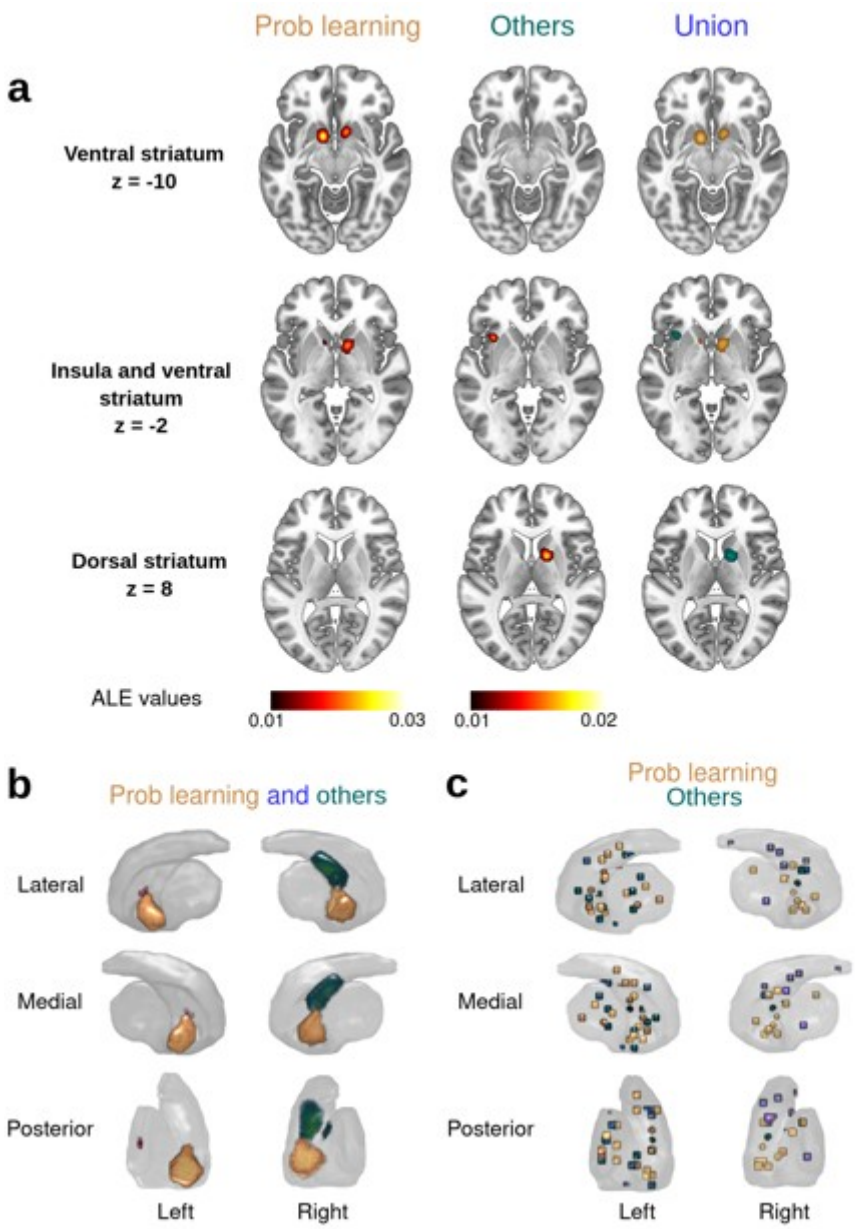


Figure 4. *Experimental subcategories thresholded activation maps.* ***a)*** *Axial views for the main regions. In this case there are no overlap regions at the right column.* ***b)*** *3D striatum reconstruction showing all the activation that fall inside it. In this case there are no overlap regions at the right column.* ***c)*** *Foci distribution of all the studies that fall in the striatum. Note that some foci may correspond to the same study.*

Between-study heterogeneity

The degree of heterogeneity was not strong (that is, a result not based on a reduced number of studies), as was also seen in the subgroup analyses for everyday-life and experimental results (Tables S3-S4).

Discussion

By comparing long-established habits acquired in everyday-life with newly learned habits acquired under laboratory-controlled conditions, our meta-analysis identified two distinct types of habit-related mechanisms in the human striatum. Both common and distinct functional links between different sub-regions of the brain's habit-associated circuitry were identified. Differences in neural substrate were found with life-time habits showing enhanced activity in the dorsal posterior putamen, together with activity in the cerebellum and SMA, while laboratory habits engaged anterior sections of the putamen with activation extending into caudate nucleus and nucleus accumbens. Importantly, common regions of activation were found in posterior left and anterior right putamen. Ultimately, delineation of specific striatal contributions to motor-associative variables embedded in habits were responsible for shared anatomical patterns in everyday-life associative habits, such as reading and writing, that engaged rostral regions of the putamen.

The putamen function in everyday-life habits

The current findings provide direct evidence for bilateral putamen engagement in habits, long acquired and executed in everyday-life. Typically, we observed larger bilateral activity in studies of life-time habits compared with newly acquired experimental ones. This may implicate a broad putaminal role for the stimuli-rich sensorimotor computations required during complex everyday stimulus-response tasks. Consistent with this view, neuroimaging, lesioning and animal electrophysiological investigations all converge to pinpoint a role for the putamen in the expression of associations between specific stimuli and movement patterns to produce habitual behaviours with predicted outcomes (Bellebaum et al., 2008; Cromwell

and Schultz, 2003; Haruno and Kawato, 2006; Sommer and Pollmann, 2016; Yamada et al., 2004). Indeed, the neurophysiological properties of the putamen are supported by subpopulations of neurons that respond to sensory stimuli (Gardiner and Nelson, 1992), unifying actions sets for movement sequences (Cellini, 2017; Wymbs et al., 2012) and the integration of elementary units such as individual finger movements (Andersen et al., 2020). Moreover, putaminal activity is not solely dedicated to movement parameters, but is also present while learning without motor plans (Romero et al., 2008), increasing neural response magnitude to reinforced choices (Cohen et al., 2021), and for predicted well-learned and contextually-driven actions (Kimura, 1986; Kimura et al., 1990, 1984; Kunimatsu et al., 2019; Peters et al., 2021; Tunik et al., 2009). Hence, the diversity of sensorimotor-related and high-order reinforcement neurons in the putamen support it having a pivotal role at several levels in context-rich scenarios (sensorimotor control, predicted actions, object values) in the acquisition and expression of stimulus-response habits.

The role of the putamen in habitual behaviour is directly influenced by ascending dopaminergic system acting on cortical and thalamic inputs to this region (Haber et al., 2000). Afferent dopamine signals provide critical modulatory influences on striatal subregions whereby projections from substantia nigra pars compacta and the ventral tegmental area differentially target terminals in dorsal and ventral striatum respectively (Björklund and Dunnett, 2007). The main nigrostriatal projection is topographically organised with a medial to lateral gradient (Matsuda et al., 2009). Tonic firing within this system sustains, motivational, cognitive and action-specific decision making (Hikosaka et al., 2000; Redgrave et al., 1999), while sensory-evoked phasic patterns of dopaminergic activity provide a general mechanism for reinforcement learning associated with the acquisition of novel actions (Redgrave et al., 2008; Schultz, 2006). The large bilateral activity found in the striatum for the routines of everyday-life should be influenced by ascending dopaminergic fibers facilitating the selection of appropriate low-level stimulus-response associations required for writing or walking (proprioceptive and muscle sensorimotor control). Of interest,

the dorso-lateral caudal putamen was active for both cognitive (reading, writing) and motor operations (driving, walking), which corresponds with our understanding of parallel inter-related cortico-striatal functions (McFarland and Haber, 2002; Morris and Stein, 2017). The stimulus-response selection role of the putamen may well represent the low level sensorimotor selections necessary in all forms of habitual motor behaviour (Bromberg-Martin et al., 2010; Romero et al., 2008). Hence, the putamen will likely respond preferentially to the predictable sensorimotor contingences present in seemingly sophisticated behaviours that rely, in part, on low-level automatic stimulus-response associations for their execution, driving for example.

Cortical control over everyday-life habits

The substantial input that the striatum receives from cortical areas (Peters et al., 2021) permits this region to receive contextual, motivational and/or motor cues relevant to action selection (Haber and Knutson, 2009; Redgrave et al., 1999). Several cortical areas represent potentially competing behavioural options that can be expressed under habitual control, including ventral premotor (de Wit et al., 2012b; Ohbayashi et al., 2016), extraestriate visual cortex (Luque et al., 2017) and bilateral insula or precentral gyrus (Eryilmaz et al., 2017). In addition, premotor cortex has been shown to interact directly with the posterior putamen during the acquisition of habits (de Wit et al., 2012b).

In the present study we found that SMA activity was an essential component of the habitual circuitry engaged by the everyday-life tasks. The SMA represents one of the important junctions between cortical-subcortical motor and cognitive circuits (Nachev et al., 2008), with projections to the dorso-lateral striatum and posterior putamen (Leh et al., 2007). The SMA has been shown to be involved in learning stimulus-response contingencies (Chen and Wise, 1995; Nachev et al., 2008) and model-free (habitual) tasks (Morris et al., 2016). Yet, the SMA is not represented in most studies involving new learning of actions. Probably, the multi-dimensional components required while learning to walk or drive (somatosensory, visuo-spatial, prediction, motor planning, etc) will be mediated via other cortical inputs (likely

SMA integration function) to the putamen (Haber and Knutson, 2009; Leisman et al., 2016). When bolted together, serial selections in such complicated but eventually predictable tasks can be viewed as coherent sequences of habitual behaviour. For example, the sophisticated set of movements required to change gear when engine revs go above a certain level, and the precise flow of hand movements required to write individual letters, with repetition, can be expressed under automatic stimulus-response control. The absence of SMA activity in experimental tasks included in the present, and previous investigations, attests to the importance of multi-dimensional computations when cognitive and motor functions are integrated to develop habitual sequences of behaviour in everyday-life. Such automatic sequences are likely to recruit medial cortical motor areas including the SMA as a mechanism to boost expected motor and associative computations that, with subcortical structures, including putamen (Cunnington et al., 2002; Smittenaar et al., 2013) represent a looped architecture that can select an appropriate sequences of sensory-driven movements that implement predictable task components.

Our results also showed a consistent activation of the inferior frontal gyrus. but only by everyday-life habits. It is known that this region is part of the mirror neuron system related to action observation and execution (Kilner et al., 2009; Molenberghs et al., 2012). A possible interpretation of this activation would be that mirror neurons encode behaviour at the level of actions, rather than as individual movements comprising complex behaviour. Consequently, only when an action representation is established and well-practiced would a mirror system be expected to respond accordingly. Perhaps recent, laboratory-acquired stimulus-response associations are not sufficiently well embedded.

Everyday-life vs experimental scenarios to study habits

Our analyses may also have implications for understanding previous studies that investigated novel stimulus-response habits learned in experimental laboratories

(probabilistic or discriminative learning, 2-step learning or sequential tasks), and which also report significant striatal activations (de Wit et al., 2012b; Eryilmaz et al., 2017; Huang et al., 2020; Jankowski et al., 2009; Lehéricy et al., 2005b; Liljeholm et al., 2015a; Morris and Stein, 2017; Patterson and Knowlton, 2018; Tricomi et al., 2009). Specifically, our analyses show stimulus-responses behaviour acquired both in everyday-life and under laboratory conditions showed common striatal activity in the right anterior putamen and left posterior putamen. The everyday-life tasks included long established sensorimotor responses triggered by sensory cues in the absence of new associative learning. In contrast, laboratory learned habits typically involved relatively minor motor components (finger key presses), but novel cue-response associations driven by reinforcement learning. In line with a previous meta-analysis on basal ganglia activation across multiple motor disciplines (Arsalidou et al., 2013), left lateralized putaminal activity was prominent in motor operations (such as eye movements and body motion), has a larger volume in right-handed participants (Peterson et al., 1993), and is critical in behaviours guided by stimulus-response mappings (Liljeholm et al., 2015a; Patterson and Knowlton, 2018). Hence, our observation of left posterior putamen activation by both long-established and novel habits suggests this region is critical for aspects of automatic stimulus-response processing that are present in a wide range of habitual behaviours.

In contrast, activation of the anterior putamen would accord well with neural patterns associated with initial learning of stimulus-response associations in experimental settings (Jankowski et al., 2009). Activity in key regions of the circuitry associated with goal-directed behavioural control (caudate and nucleus accumbens) were also present in laboratory studies of habits. These findings match those of several fMRI studies using various reinforcement learning tasks. When encoding the value of predicted reward outcome linked to new actions activation of the ventro-medial prefrontal cortex, insula and anterior striatum has been widely reported (Grabenhorst and Rolls, 2011; Parkes et al., 2015; Tanaka et al., 2008). An issue here could be that in some of these studies behaviours established in the

laboratory that are presumed to be habits fail to meet formal requirements. For example, several recent human experimental studies failed to demonstrate an effect of training duration on insensitivity to outcome-devaluation test (de Wit et al., 2018; Pool et al., n.d.; Watson and de Wit, 2018). In such studies it is possible that more trials may be needed to establish stimulus-response associations that are fully automatic and can persist after devalued outcome challenges. In the case of every-day habits, independence of outcome value is typically demonstrated in cases of action slips. That is, when a long established habitual response produces an undesired outcome, such as taking the elevator to the floor of an old office. Last, there is the possibility that some differences between everyday-life and laboratory-developed habits, such as activation of the nucleus accumbens, may be due to the explicit rewards component present in some laboratory paradigms rather than any fundamental difference in the habitual network.

Dysfunctional habits: inability to exploit stimulus-response habits

Insofar as the caudal putamen has been identified as a critical node in the neural substrate responsible for automatic habitual behaviour, malfunctioning of this region should be associated with deficits in habitual performance. A notable instance of this would be the differential loss of dopamine neurotransmission from this region in Parkinson's disease (Redgrave et al., 2010a). The causes of this selective loss is not known, however given the high metabolic cost of dopaminergic neurotransmission Hernandez et al., (2019) suggested it could reflect an over-reliance throughout life on automatic habitual control. The particular problems Parkinson's disease patients have with stimulus-response behaviours e.g. walking and writing (Bannard et al., 2019; Peterson and Horak, 2016; Wu et al., 2016), and their inability to demonstrate novel associations in the laboratory (de Wit et al., 2010; Wu et al., 2015), can be seen as an inability of Parkinson's patients to enact established habits and acquire new ones. In contrast, other neuropsychiatric conditions, such as the addictions, patients exhibit an excessive cue-dependent use of certain rewards linked to increased

posterior putamen activity (Everitt et al., 2008; Sjoerds et al., 2013). In the light of this work, an important future question would be whether the limbic and associative territories of the basal ganglia (Alexander and Crutcher, 1990) can operate in a similar habitual mode as has been established for stimulus-response motor habits in the sensorimotor territories. If so, this would move towards a reconceptualization of stimulus evoked motivations (e.g. drug craving), stimulus-evoked cognitions (e.g. prejudices), and stimulus-evoked motor responses (motor habits) as part of a general mode of model-free stimulus-response behavioural control. Were this to be the case, one might speculate there would likely be a general mechanism of neural implementation across all territories of the basal ganglia.

Limitations & strengths

Despite the clear positive findings of the present investigation, certain limitations must be acknowledged. First, the ALE analysis can cause some parameters, such as voxel peaks, to be overlooked. Ideally, exploring the statistical activity maps of each study individually would be of great value. Unfortunately, most studies did not have full imaging datasets so this would be precluded.

Second, some studies using RPE contrasts combined mixed regressors of choice and outcome thereby rendering it difficult to make separations between habitual stimulus-response components. To avoid this, we explored our principal findings without these studies and found similar patterns of striatal activation (anterior putamen; Figure 4A). Moreover, our heterogeneity analysis showed a reduced number of RPE studies (6/25 studies for left putamen; 4/20 studies for right putamen) that contributed to the significant activity of such clusters (as displayed in Table S4 for experimental studies). Consequently, the putamen clusters we report are not mainly driven by the RPE studies

Third, as stimulus-response habits are driven by specific conjunctions of sensory stimuli, the heterogeneity of every-day and laboratory tasks included in our analysis means

the stimuli driving brain responses necessarily will have differed. Moreover, the laboratory studies included have minor motor components compared with the typical motor-sophistication of habits established over a lifetime. To control for this possibility, and following imaging meta-analysis best practice (Müller et al., 2018), as different stimuli and task-related activities were collected, general and specific sub-analysis were conducted. Last, due to the difficulty of performing some behaviours in the MRI scanner, necessarily we had to restrict our selection to everyday-life behaviours where scanning was possible. This could restrict the generalisation of our findings to other activities prevalent in every-day life.

The main strengths of the work point to the possible generalizability and external validity of lab-developed habits, as well as proposing novel methodological procedures to investigate human habitual behaviour. The heterogeneity of tasks necessarily means there was a diverse range of both stimuli and behavioural responses deployed in the studies included in our analyses. It is therefore remarkable we were able to pull out common patterns of neural activation associated with stimulus-response control.

A further strength of our investigation was that we were able to find significant striatal activation in tasks with high levels of stimulus-response behaviour in studies that were not originally designed to study habits. This was despite the behaviours of interest not having been formally identified as habitual using outcome devaluation or other tests. That we find common neural maps with widely different means for testing habits lends support to this idea.

Future research and conclusions

Recently, a range of procedures have been developed to establish and test the expression of newly acquired habits in the experimental laboratory, including reversal of learned actions after overtraining (Luque et al., 2020), overloading goal-directed top-down control while measuring execution of learned stimulus-response associations (Hardwick et

al., 2019) or biasing movement kinematics (Wong et al., 2017). Interestingly, pre-existing categorical associations established in everyday-life (i.e. color associations or prejudice) have a clear advantage on measuring automatic processing (Amodio, 2014; Ceceli et al., 2020). Further methodological options for studying long established habits acquired in everyday-life include assessing the motor performance of expert musicians (Vaquero et al., 2016), tennis players (Cacioppo et al., 2014) and expert shooters (Kim et al., 2014). Hence, getting subjects to bring their everyday-life stimulus-response associations into the laboratory under controlled conditions is an important option for studying the neural substrates underlying habitual behaviour in humans. Although there is less control of the independent variables in such studies, by selecting subjects with different amounts of everyday-life experience it is possible to relate the amount of practice with habit strength.

In conclusion, the present study points to a fundamental functional role for the posterior putamen in the expression of habits acquired in everyday-life. Importantly, a critical dissociation was established between different brain regions whose contributions to motor-cognitive representations of habits have, thus far, been largely indistinguishable. Conversely, the engagement of the anterior putamen was shown to be associated more with habits newly learned in experimental laboratories. Careful experimental protocols must be designed to identify those chunks of complex behaviour that are under automatic stimulus-response control and can occur independently of outcome value or response contingency. This is true both for newly acquired associations in the laboratory and long-standing habits established in everyday-life. Finally, the present study highlights the importance and value of having subjects bring life-long habits into the laboratory to be investigated and compared with recently acquired stimulus-response associations. This meta-analysis provides strong evidence for a striatal role in everyday-life and lab-developed habits giving a novel contribution to the literature on the general neural footprint of human habits.

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Author Contributions

P.G. design, data collection, writing; M.M. design, data collection, analysis, writing; P.R. writing; D.L. design, data collection, writing; I.O. design, data collection, writing;

Competing Interests statement

The authors declare no competing interest.

Figure Legends and Tables

Figure 1. Hypothetical diagram on striatal role in both everyday-life and experimental habits. Activities with strong stimulus-response components such as writing, reading, walking or driving were selected as everyday-life habits (see Box 1 for task measurements and details). Striatal activations elicited by these activities can be compared to those evoked by stimulus-response paradigms commonly used to investigate habits in the cognitive science literature.

Figure 2. Everyday-life and experimental thresholded activation maps. **a)** Axial views for the main regions. Overlap regions at the right column are shown in blue. Note activation in the cerebellar cortex for everyday-life studies, but it is omitted here for brevity. Z=52 view for the experimental studies is shown as an unthresholded map for comparison (ALE value ≈ 0.01) **b)** 3D striatum reconstruction showing all the activation that fall inside it. Overlap regions at the right column are shown in blue. **c)** 3D striatum reconstruction showing the differential activation of the Everyday -life > Experimental contrast (in green) and the Experimental > Everyday-life contrast (in red).

Figure 3. Everyday-life cognitive-motor subcategories thresholded activation maps. **a)** Axial views for the main regions. Overlap regions at the right column are shown in blue. **b)** 3D striatum reconstruction showing all the activation that fall inside it. Overlap regions at the right column are shown in blue. **c)** Foci distribution of all the studies that fall in the striatum. Note that some foci may come from the same study.

Figure 4. Experimental subcategories thresholded activation maps. **a)** Axial views for the main regions. In this case there are no overlap regions in the right column. **b)** 3D striatum reconstruction showing all the activation that fall inside it. In this case there are no overlap regions in the right column. **c)** Foci distribution of all the studies that fall in the striatum. Note that some foci may come from the same study.

Table 1. Activation by everyday-life habits. Percentages of each brain region indicate how much activation from a cluster fall into that region. Coordinates of any activation comprising < 5% of its volume in a region are not shown for brevity. Activity peak coordinates reported based on MNI152 space with region names from Harvard-Oxford atlas.

Table 2. Activation by experimental. Percentages of each brain region indicate how much activation from a cluster fall into that region. Coordinates of any activation comprising < 5% of its volume in a region are not shown for brevity. Activity peak coordinates reported based on MNI152 space with region names from Harvard-Oxford atlas.

Supplementary material

An fMRI meta-analysis of the role of the striatum in everyday-life vs laboratory-developed habits

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Methods

The complete set of search terms were as follows:

1. Search on PubMed

   Everyday-life habits:

   (walking[MeSH Terms] OR walking[Title/Abstract]) OR (Driving behaviour[MeSH Terms] OR Driving behaviour[Title/Abstract]) OR (Driving behavior[MeSH Terms] OR Driving behavior[Title/Abstract]) OR (car driving[MeSH Terms] OR Car driving[Title/Abstract]) OR (writing[MeSH Terms] OR writing[Title/Abstract]) OR (handwriting[MeSH Terms] OR handwriting[Title/Abstract]) OR

(reading[Title/Abstract] OR reading[MeSH Terms) AND (functional magnetic resonance imaging[MeSH Terms] OR fMRI[Title/Abstract]) AND ((basal ganglia[Title/Abstract] OR caudate[Title/Abstract] OR putamen[Title/Abstract] OR striatum[Title/Abstract]) OR (basal ganglia[MeSH Terms] OR caudate nucleus[MeSH Terms] OR putamen[MeSH Terms] OR striatum[MeSH Terms]))

Experimental habits:
(“habit” OR “habits” OR “probabilistic classification” OR “weather prediction” OR “response learning” OR “instrumental conditioning” OR “instrumental learning” OR “reinforcement learning” OR “outcome devaluation” OR “sequential decision” OR “two step” OR “2 step”) AND (“basal ganglia” OR “caudate” OR “putamen” OR “striatum”) AND (“fMRI” OR “functional magnetic resonance imaging” OR “functional MRI”) AND ("2017/06/22"[PDAT] : "3000/12/31"[PDAT])

2. Search on Web of Science

Everyday-life habits:
TI=(((driving) OR (car driving) OR (walking) OR (writing) OR (handwriting) OR (reading)) AND ((functional magnetic resonance imaging OR fMRI)) AND (((basal ganglia OR caudate OR putamen OR striatum)))) OR AB=(((driving) OR (car driving) OR (walking) OR (writing) OR (handwriting) OR (reading)) AND ((functional magnetic resonance imaging OR fMRI)) AND (((basal ganglia OR caudate OR putamen OR striatum))))

Experimental habits:
(TI=((habit OR habits OR probabilistic classification OR weather prediction OR response learning OR instrumental conditioning OR instrumental learning OR reinforcement learning OR outcome devaluation OR sequential decision OR two step OR 2 step) AND (basal ganglia OR caudate OR putamen OR striatum) AND (fMRI

OR functional magnetic resonance imaging OR functional MRI))) OR AB=((habit OR habits OR probabilistic classification OR weather prediction OR response learning OR instrumental conditioning OR instrumental learning OR reinforcement learning OR outcome devaluation OR sequential decision OR two step OR 2 step) AND (basal ganglia OR caudate OR putamen OR striatum) AND (fMRI OR functional magnetic resonance imaging OR functional MRI))

Supplementary Material Figure Legends and Tables

Figure S1. PRISMA chart describing the steps followed for the selection of studies.

Table S1. Studies with everyday-life habits included in the meta-analysis.

Table S2. Studies with experimental habits included in the meta-analysis.

Table S3. Additional diagnostics used to check the heterogeneity for everyday-life studies. The list details which studies have any foci contributing to the significant clusters in the ALE meta-analysis for everyday-life studies.

(IN CSV)

Table S4. Additional diagnostics to check the heterogeneity for experimental studies. The list details which studies have any foci contributing to the significant clusters in the ALE meta-analysis for experimental studies.

(IN CSV)

Figure S1. PRISMA chart describing the steps followed for the selection of studies.

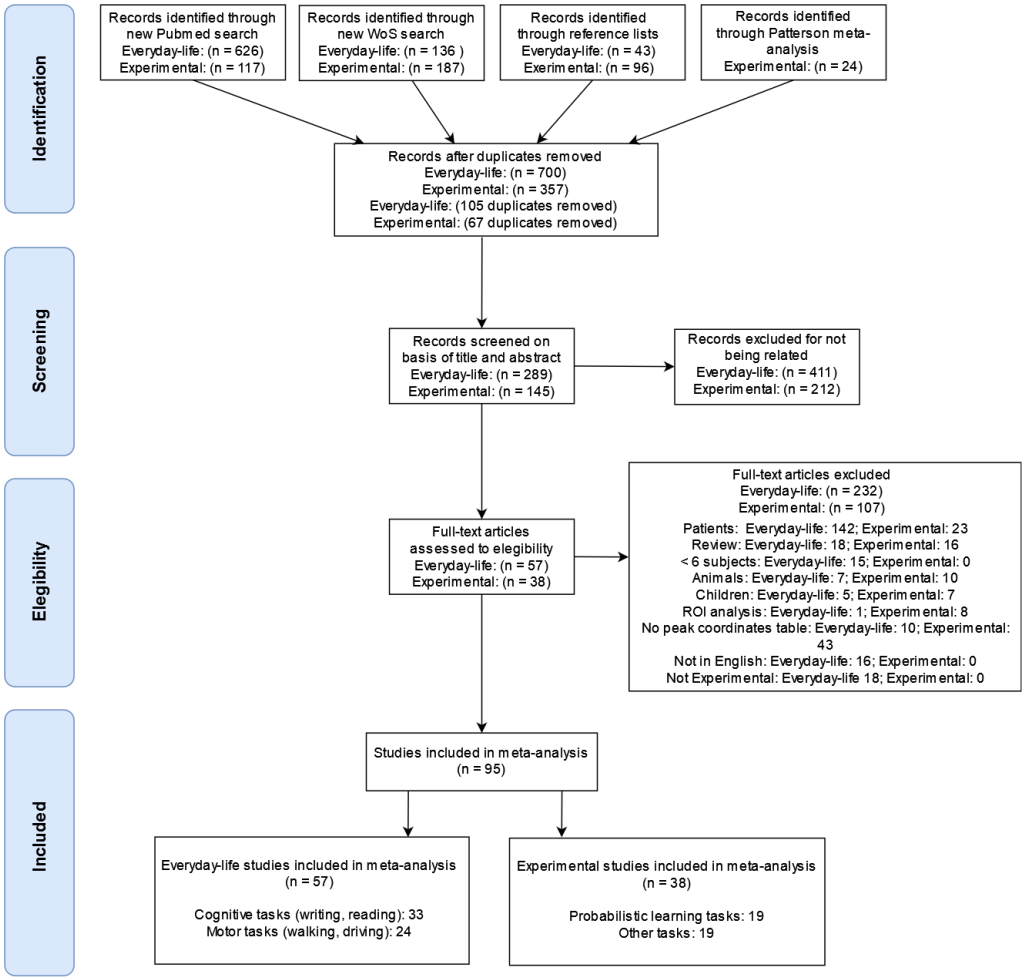

Table S1. Studies with everyday-life habits included in the meta-analysis.

Study by domain	n = 1536	Foci	Task	Contrast	Statistical threshold
Writing					
Katanoda et al., (2001)	17	19	Write a name of an object or naming the object	Writing > naming	p < 0.001 voxel-level & p < 0.05 cluster-level corrected
Nakamura et al., (2002)	9	10	Upon auditory presentation subjects wrote kanji word.	Writing > Rest	p < 0.05 corrected for multiple comparison
Beeson et al., (2003)	12	29	Writing words or drawing circles	Writing words > drawing circles	p < 0.001 uncorrected
Hu et al., (2006)	10	11	Writing with a pencil	Main Effect of Writing with a pencil	p < 0.0001 uncorrected
Segal & Petrides, (2012)	9	19	Writing or naming pictures of objects and drawing one loop per syllable of the object's name	Writing > naming plus loops	p < 0.05 corrected
Horovitz et al., (2013)	13	5	Writing, tapping, and zigzagging with each limb	Right-handwriting > other tasks	p < 0.001 FWE corrected
Erhard et al., (2014)	20	13	Creative writing	Main effects of creative writing in expert writers	p < 0.05 FWE corrected
Longcamp et al., (2014)	18	13	Writing of letters or digits	Writing > holding the pen still	p < 0.05 voxel-level FWE corrected
Potgieser et al., (2015)	16	21	Write a sentence or hand tapping	Right-handwriting > right-hand tapping	p < 0.001 voxel-level & p < 0.05 cluster-level FWE corrected & k≥8
Bisio et al., (2017)	7	25	Writing sentences	Writing > resting	p < 0.05 FWE corrected
Karimpoor et al., (2018)	12	38	Copying grocery lists, phone numbers or sentences	All handwriting tasks > resting	p < 0.05 FDR corrected
Yang et al., (2018)	34	29	Copying chinese characters	Writing high frequency > writing low frequency	p < 0.05 FDR corrected
Swett et al., (2010)	12	11	Learning Chinese word characters	Late learning > baseline	p < 0.05 uncorrected
Reading					
Bookheimer et al., (1995)	16	33	Reading words or naming objects	Main effect of read aloud	p < 0.001 corrected
Moore & Price, (1999)	8	7	Reading/naming	Main effect of reading words	p < 0.001 uncorrected
Mechelli et al., (2003)	20	10	Early/late reading processing	Early reading > Fixation	p < 0.05 corrected
Buchsbaum et al., (2005)	17	15	Reading/Hearing	Reading > Control	z > 2.33 & p < 0.01 cluster-corrected
Vigneau et al., (2005)	23	39	Reading words/ non reading letters	Read > Cross fixation	p < 0.001 uncorrected
Meschyan & Hernandez, (2006)	12	12	Reading different languages	Reading > Resting	p < 0.001 uncorrected & p < 0.05 corrected spatial extent threshold
Binder et al., (2006)	30	31	Non-word reading	Reading > Fixation	p < 0.00001 uncorrected & p < 0.05 corrected
Carreiras et al., (2007)	36	32	Reading/Lexical decision	Reading > Baseline	p < 0.05 corrected
Church et al., (2008)	50	37	Reading/Repeat	Reading > Repeat	p < 0.05 corrected with k≥24 voxels

Table S2. Studies with experimental habits included in the meta-analysis.

Study by domain	n = 938	Foci	Task	Contrast (short)	Statistical threshold
Probabilistic learning					
Poldrack et al., (1999)	8	15	Probabilistic learning task	Task > control (perceptual-motor)	p < 0.05 corrected with Gaussian Random Field Theory
Poldrack et al., (2001)	13	25	Probabilistic learning task	Task > control (perceptual-motor)	p < 0.005 uncorrected & k≥5 voxels
Aron et al., (2004)	15	9	Probabilistic learning task	Task > baseline	p < 0.05 FDR corrected
Delgado et al., (2005)	17	2	Probabilistic learning task	Condition and time interaction	p < 0.0001 uncorrected & k≥5 voxels
Fera et al., (2005)	18	5	Probabilistic learning task	Task > control (perceptual-motor)	p < 0.05 uncorrected
Aron et al., (2006)	8	9	Probabilistic learning task	Task > control (perceptual-motor)	z > 2.3 voxel-level & p < 0.01 cluster-level corrected with Gaussian Random Field Theory
Foerde et al., (2006)	14	2	Probabilistic learning task	Modulation by performance (accuracy)	p < 0.05 corrected with Gaussian Random Field Theory
Gläscher et al., (2010)	18	1	2-step probabilistic learning task	RPE	p < 0.006 corrected & k≥10
Celone et al., (2011)	19	8	Probabilistic learning task	Task > control (perceptual-motor)	p < 0.01 voxel-level & p < 0.05 cluster-level corrected
Wunderlich et al., (2012)	21	17	2-step probabilistic learning task	Trained > Planning (RPE)	p < 0.05 FWE corrected & k≥5
Soares et al., (2012)	12	10	Probabilistic learning task	Stress > control	p < 0.05 FWE corrected
Schwabe et al., (2013)	75	14	Probabilistic learning task	Task > control (perceptual-motor)	p < 0.05 FWE corrected & k≥5
Wan Lee et al., (2014)	22	5	2-step probabilistic learning task	RPE	p < 0.05 FWE corrected
Deserno et al., (2015)	29	7	2-step probabilistic learning task	Model-free component	p < 0.05 corrected
Doll et al., (2015)	20	5	2-step probabilistic learning task	RPE	p ≤ 0.0005 cluster-level FWE corrected
Oh-Descher et al., (2017)	25	3	Probabilistic learning task	High time pressure > low time pressure Positive subjective sum of evidence)	p < 0.005 voxel-level & p < 0.05 cluster-level corrected
Nebe et al., (2018)	146	35	2-step probabilistic learning task	RPE	p < 0.05 FWE corrected

Erdeniz & Done, (2019)	19	15	Probabilistic learning task	CS familiar > CS novel	p < 0.005 uncorrected
Mas-Herrero et al., (2019)	20	2	2-step probabilistic learning task	RPE pseudofeedback)	p < 0.001 corrected
Others					
Gottfried et al., (2003)	13	7	Associative learning	Outcome devaluation	p < 0.001 uncorrected
Iaria et al., (2003)	7	5	Maze navigation	Task > control perceptual-motor)	p < 0.05 corrected
Lehéricy et al., (2005)	14	3	Motor sequence learning	Modulation by task experience	p < 0.0001 voxel-level & p < 0.05 cluster-level corrected
Forstmann et al., (2008)	19	3	Moving dots task	Speed > accuracy	p < 0.001 corrected
Fernández-Seara et al., (2009)	14	30	Motor sequence learning	Late > early	p < 0.01 uncorrected
Tricomi et al., (2009)	15	4	Discriminative learning	Late > early	p < 0.001 uncorrected & k≥5
Steele & Penhune, (2010)	15	14	Motor sequence learning	Late > early	p < 0.001 uncorrected & k≥100
Brovelli et al., (2011)	14	3	Discriminative learning	P correct | past observations) > P correct by chance)	P < 0.05 FWE corrected
Beierholm et al., (2011)	23	11	Sequential choice	Model-free component	p < 0.001 uncorrected & k≥5
de Wit et al., (2012)	24	3	Discriminative learning	Negative predictors of goal-directed action outcome devaluation)	p < 0.005 uncorrected & k≥20
Etchamendy et al., (2012)	15	3	Maze navigation	Q-signal, learners	p < 0.05 corrected
Liljeholm & O'doherty, (2012)	15	4	Sequential choice	Decreased activity in the R-O but not int the S-R	p < 0.05 corrected with cluster size thresholding
Liljeholm et al., (2015)	19	13	Sequential choice	Modulation by devaluation insensitivity	p < 0.05 cluster-level corrected
Fermin et al., (2016)	18	9	Grid-Sailing	Previous S-R learning – Model-based conditions	p < 0.0001 uncorrected
Eryilmaz et al., (2017)	72	5	Discriminative learning	Incongruent > standard cue	p < 0.001 voxel-level & p < 0.05 cluster-level corrected
van Steenbergen et al., (2017)	19	5	Discriminative learning	Cue-driven > Value-driven action control	p < 0.001 uncorrected & k≥15
Zwosta et al., (2018)	53	29	Discriminative learning	Decrease reward and no reward Contingency degradation)	p < 0.001 voxel-level & p < 0.05 cluster-level corrected
Watson et al., (2018)	23	8	Discriminative learning	Slip of action trials > still-valued	p < 0.05 corrected

				responses	
Anggraini et al., (2018)	27	16	Maze navigation	Model-free component	$p < 0.001$ voxel-level & $p < 0.05$ cluster-level corrected

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