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Action-sequence learning, habits and automaticity in obsessive-compulsive disorder

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Abstract

Enhanced habit formation, greater automaticity and impaired goal/habit arbitration in obsessive-compulsive disorder (OCD) are key hypotheses from the goal/habit imbalance theory of compulsion which have not been directly investigated. This article tests these hypotheses using a combination of newly developed behavioral tasks. First, we trained patients with OCD and healthy controls, using a novel smartphone app, to perform chunked action sequences, previously shown to engage habit brain circuitry. The motor training was daily over one month period. There was equivalent procedural learning and attainment of habitual performance (measured with an objective criteria of automaticity) in both groups, despite greater subjective habitual tendencies in patients with OCD, self-reported via a recently developed questionnaire. We then used a combination of follow-up behavioral tasks to further assess the arbitration between previous automatic and new goal-directed action sequences. We found no evidence for impairments of goal/habit arbitration in OCD following re-evaluation based on monetary feedback, although there was a greater preference for engaging in the trained habitual sequence under certain conditions which may have derived from its intrinsic value. These findings may lead to a reformulation of the goal/habit imbalance hypothesis in OCD. Finally, OCD patients with higher compulsivity scores and habitual tendencies showed more engagement with the motor habit-training app and reported symptom alleviation, with implications for its potential use as a form of habit reversal therapy.

eLife assessment

This study involves a **valuable** investigation of habit-learning in obsessive-compulsive disorder versus controls with participants engaging in a month of motor-sequence task practice administered via a smartphone app. Currently the results are **inadequate** to support the authors' key claims as not all of the criteria were met to establish that habit learning occurred.

Introduction

Considerable evidence has supported the concept of imbalanced cortico-striatal pathways mediating compulsive behavior in obsessive-compulsive disorder (OCD). This imbalance has been suggested to reflect a weaker goal-directed control and an excessive habitual control (Gillan et al., 2016). Dysfunctional goal-directed control in OCD has been strongly supported both behaviorally (Gillan et al., 2011; Vaghi et al., 2018) and in neural terms (Gillan et al., 2015a). However, enhanced (and potentially maladaptive) habit formation has hitherto mainly been inferred by the absence of goal-directed control, although there is recent evidence of greater self-reported habitual tendencies in OCD measured using the Self-Report Habit Index Scale (Ferreira et al., 2017). Problems with this "zero-sum" hypothesis (Robbins and Costa, 2017) (i.e., diminished goal directed control *thus* enhanced habitual control) have been underlined by recent findings linking stimulus-response strength (Zwosta et al., 2018) and goal devaluation (Gillan et al., 2015b) exclusively to a dysfunctional goal-directed neural system. There is thus a need to focus specifically on the habit component of the associative dual-process (i.e. goal/habit) model of behavior and test more directly the hypothesis of enhanced habit formation in OCD.

We have recently postulated that extensive training of sequential actions would more rapidly engage the 'habit system' as compared to single-action instrumental learning tasks typically used in the laboratory (Robbins et al., 2019). The rationale is that, on sequential actions (as it occurs during skilled routines), the performance of one action facilitates the next (via kinesthetic feedback, in a stimulus-response/automatic manner) and independent motor acts become integrated into a unified and coordinated sequence of actions (or "chunks") (Graybiel, 1998; Sakai et al., 2003), which can be quickly and more efficiently implemented. With practice and training, selection and execution of individual component actions become more efficient, stereotypical, requiring less cognitive effort, and performed with little variation, in a highly efficient manner (Diedrichsen and Kornysheva, 2015). Such features relate to the concept of *automaticity*, which captures many of the shared elements between habits and skills (Ashby et al., 2010). At a neural level, automaticity is associated with a shift in control from the anterior/associative (goal-directed) to the posterior/sensorimotor (habitual) striatal regions (Ashby et al., 2010; Graybiel and Grafton, 2015; Kupferschmidt et al., 2017), accompanied by a disengagement of cognitive control hubs in frontal and cingulate cortices (Bassett et al., 2015). In fact, within the skill learning literature, this progressive shift to posterior striatum has been linked to the gradually attained asymptotic performance of the skill (Bassett et al., 2015; Doyon et al., 2018, 2015; Lehericy et al., 2005). Hence chunked action sequences provide an opportunity to target the brain's goal-habit transition and study the relationships between automaticity, skills and habits (Dezfouli et al., 2014; Graybiel and Grafton, 2015; Robbins and Costa, 2017). This approach is relevant for OCD research as it mimics the sequences of motor events and routines observed in typical compulsions, which are often performed in a "just right"

manner (Hellriegel et al., 2017), akin to skill learning. Chunked action sequences also enable investigation of the relationships between hypothesized procedural learning deficits in OCD (Rauch et al., 1997) and automaticity.

Following this reasoning, we developed a smartphone motor sequence application with attractive sensory features in a game-like setting, to investigate automaticity and measure habit/skill formation within a naturalistic setting (at home). Our *Motor Sequencing App* is a self-instructed and self-paced app that enables subjects to learn and practice two sequences of finger movements, composed of chords and single presses (like a piano-based app). The task was specifically designed to focus on the positive features of habits, as suggested by Watson et al., 2022, and satisfies central criteria that define habits, according to a recent proposal by Balleine and Dezfouli, 2019: rapid execution, invariant response topography and action chunking. We also aimed to investigate within the same experiment three facets of automaticity which, according to Haith and Krakauer (2018), have rarely been measured together: habit, skill and cognitive load. Although there is no consensus on how exactly skills and habits interact (Robbins and Costa, 2017), it is generally agreed that both lead to automaticity with sufficient practice (Graybiel and Grafton, 2015) and that the autonomous nature of habits and the fluid proficiency of skills engage the same sensorimotor cortical-striatal 'loops' (the so-called 'habit circuitry') (Ashby et al., 2010; Graybiel and Grafton, 2015). By focusing more on the *automaticity* of the response per se (as reflecting the speed and stereotypy of over-trained movement sequences), rather than on the *autonomous* nature of the behavior (an action that continues after a state change, e.g. devaluation of the goal), we do not solely rely on the devaluation criterion used in previous studies of compulsive behavior. This is important because outcome devaluation insensitivity as a test of habit in humans is controversial (Watson et al., 2022) and may indeed be a more sensitive indicator of failures of goal-directed control rather than of habitual control per se (Balleine and Dezfouli, 2019; Robbins et al., 2019; Robbins and Costa, 2017).

While designing our app, we additionally took into consideration previous findings which defined training frequency, context stability, and reward contingencies as important features for increasing habit strength (Wood and Rünger, 2016). We used a period of 1-month's training to enable effective consolidation, required for habitual action control or skill retention to occur. This acknowledged previous studies showing that practice alone is insufficient for habit development as it also requires off-line consolidation computations, through longer periods of time (de Wit et al., 2018) and sleep (Nusbaum et al., 2018; Walker et al., 2003). Since previous research suggests that the speed to which habits are acquired depends on how predictable the reinforcers are (Bouton, 2021) we also employed two different schedules of reinforcement (continuous versus variable [probabilistic]) to assess its impact on habit formation amongst healthy volunteers (HV) and patients with OCD.

Outline

In this article, we applied, for the first time, a novel app-based behavioral training (experiment 1) to a sample of patients with OCD. We compared 32 patients (19 females) and 33 healthy controls (19 females), matched for age, gender, IQ and years of education in measures of motivation and app engagement (see Methods for participants' demographics and clinical characteristics). We also assessed to what extent performing such repetitive actions in one month impacted OCD symptomatology. In an *initial phase* (30 days), two action sequences were trained daily to produce habits/automatic actions (experiment 1). We continuously collected data online, in real time, thus enabling measurements of procedural learning as well as automaticity development. In a *second phase*, we administered two follow-up behavioral tasks (experiments 2 and 3) which allowed us to address two important questions relevant to the habit theory of OCD. The first research question explored the possibility that repeated performance of acquired motor sequences may develop implicit

rewarding properties, hence gaining value, and leading to compulsive-like behaviors (experiment 2). The hypothesis is that repeated performance of the motor sequences, initially driven by the goal of becoming proficient, may eventually become driven by their own implicit reward linked to their proprioceptive and kinesthetic feedback (for example, providing anxiety relief as well as skilled performance). Second, we examined whether a functional impairment in the mechanism of dynamic arbitration between automatic, habit-like actions and goal-directed behavior underlies OCD (experiment 3). This hypothesis has been previously proposed (Gruner et al., 2016), but to our knowledge, has not been rigorously tested so far. Finally, we administered a comprehensive set of self-reported clinical questionnaires, including a recently-developed questionnaire (Ersche et al., 2017) on aspects of habits such as routine and automatic tendencies to test: 1) whether patients with OCD exhibit more self-reported habits; 2) whether greater habitual tendencies expressed subjectively are predictive of enhanced procedural learning, automaticity development and an (in)ability to adjust to changing circumstances; and 3) whether habit reversal via app training produces any therapeutic benefit or and has any subjective sequelae in OCD.

Hypothesis

Following current theories related to implicit learning deficiency (Deckersbach et al., 2002; Kathmann et al., 2005; Rauch et al., 1997) and visuospatial and fine-motor skill difficulties in patients with OCD (Bloch et al., 2011), we anticipated that patients would display poorer procedural learning as compared to healthy volunteers. However, once learning is established, we predicted that OCD patients would attain automaticity faster than healthy volunteers, assuming a hypothetically greater tendency in OCD to form habitual/automatic actions (Gillan et al., 2016, 2014). We also hypothesized that the acquisition of learning and automaticity would differ between the two action sequences based on their associated rewarded schedule (continuous versus variable) and reward valence (positive or negative). This is based on previous research suggesting that habits may form more quickly when reinforcers are well-predicted and more slowly when uncertain (Bouton, 2021). We additionally examined differential effects of positive and negative feedback changes on performance to build on previous work demonstrating enhanced sensitivity to negative feedback in patients with OCD (Apergis-Schoute et al 2023, Becker et al., 2014; Kanen et al., 2019). Finally, we expected that OCD patients would generally report greater habits, as well as show enhanced habit attainment through a greater preference for performing familiar app sequences when given the choice to select any other, easier sequence. We also anticipated that patients would exhibit greater resistance to returning to a goal state.

Results

Self-reported habit tendencies

Participants completed self-reported questionnaires measuring various psychological constructs (see Methods). Highly relevant for the current topic is the Creature of Habit (COHS) Scale (Ersche et al., 2017), recently developed to measure individual differences in habitual routines and automatic tendencies in everyday life. This 27-item questionnaire incorporates two aspects of the general concept of habits: *routine* behavior and *automatic* responses. As compared to healthy controls, OCD patients reported significantly higher habitual tendencies both in the routine (t = -2.79, p = 0.01; HV:

$(t = -2.79, p = 0.01$; HV: $\overline{COHSroutine}$= 48.4 ± 9; OCD = $\overline{COHSroutine}$= 55.7 ± 11) and the automaticity (t = -3.15, p < 0.001; HV: $(t = -3.15, p < 0.001$; HV: $\overline{COHSautomaticity}$= 26.3 ± 8; OCD = $\overline{COHSautomaticity}$= 32.9 ± 9) subscales.

Phase A: Experiment 1

Motor Sequence Acquisition using the App

The task was a self-instructed and self-paced smartphone application (app) downloaded to participants' iPhones. It consisted of a motor practice program that participants committed to pursue daily, for a period of one month. An exhaustive description of the method has been previously published (Banca et al., 2020) but a succinct description can be found below, in Figure 1 and in the following video https://www.youtube.com/watch?v=XSYrBzD7ZpI.
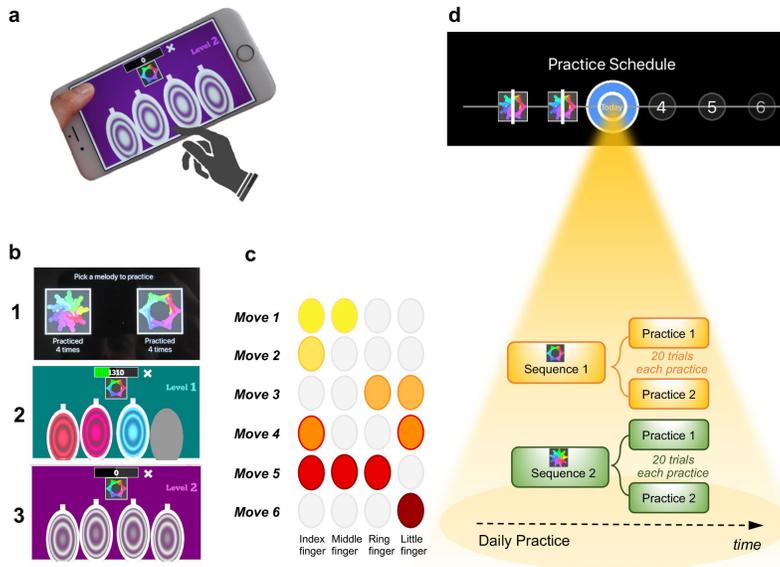
Figure 1.

Motor Sequencing App.

a) A trial starts with a static image depicting the abstract picture that identifies the sequence to be performed (or 'played') as well as the 4 keys that will need to be tapped. Participants use their dominant hand to play the required keys: excluding the thumb, the leftmost finger corresponds to the first circle and the rightmost finger corresponds to the last circle. **b)** Screenshot examples of the task design: (1) sequence selection panel, each sequence is identified by an abstract picture; (2) panel exemplifying visual cues that initially guide the sequence learning; (3) panel exemplifying the removal of the visual cues, when sequence learning is only guided by auditory cues. **c)** Example of a sequence performed with the right hand: 6-moves in length, each move can comprise multiple finger presses (2 or 3 simultaneous) or a single finger press. Each sequence comprises 3 single press moves, 2 two-finger moves, and 1 three-finger move. **d)** Short description of the daily practice schedule. Each day, participants are required to play *a minimum* of 2 practices per sequence. Each practice comprised 20 successful trials. Participants could play more if they wished and the order of the training practices was self-determined.

The training consisted of practicing two sequences of finger movements, composed of chords (two or three simultaneous finger presses) and single presses (one finger only). Each sequence comprised six moves and was performed using four fingers of the dominant hand (index, middle, ring and little finger). Participants received feedback on each sequence performance (trial). Successful trials (to which we later refer as sequence trial number, *n*) were followed by a positive ring tone and the unsuccessful ones by a negative ring tone. Every time a mistake occurred (irrespective of which move in the sequence it occurred), participants were prompted to restart the trial. Instructions were to respond swiftly and accurately. Participants were required to keep their fingers very close to the keys to minimize movement amplitude variation and to facilitate fast performance. To promote sequence memorization, exteroceptive cues (visual and auditory) were given in the first two days of training. These were then gradually removed (first visual and then auditory) to enable motoric independence and automaticity.

Each sequence, identified by a specific abstract image, was associated with a particular reward schedule. Points were calculated as a function of the time taken to complete a sequence trial. Accordingly, performance time was the instructed task-related dimension (i.e. associated with reward). In the *continuous reward schedule,* points were received for every successful trial whereas in the *variable reward schedule,* points were shown only on 37% of the trials. The rationale for having two distinct reward schedules was to assess their possible dissociable effect on the participants' development of automatic actions. For each rewarded trial, participants could see their achieved points on the trial. To promote motivation, the total points achieved on each daily training sessions were also shown, so participants could see how well they improved across days. The permanent accessibility of the app (given that most people carry their mobile phones everywhere) facilitated training frequency and enabled context stability.

Practice Schedule

All participants were presented with a calendar schedule and were asked to practice both sequences daily. They were instructed to practice as many times as they wish, whenever they wanted during the day and with the sequence order they would prefer. However, a minimum of 2 practices (*P*) per sequence was required every day; each practice comprised 20 successful sequence trials. If participants missed a day of practice, they were required to catch up on the training the following day, i.e. to complete the minimum training for the current and previous day.

A minimum of 30 days of training was required and all data were anonymously collected in real-time, through an online server. On the 21st day of practice, the rewards were removed (extinction) to ensure that the action sequences were more dependent on proprioceptive and kinesthetic, rather than on external, feedback.

Training engagement

Participants reliably committed to their regular training schedule, practicing consistently both sequences every day. Unexpectedly, OCD patients completed significantly more practices as compared with HV (*p* = 0.005) (Figure 2a). Descriptive statistics are as follows: HV: M$_P$ = 122, *IQR (Interquartile range)* = 7; OCD: M$_P$ = 130, *IQR* = 14. Note that main values are represented as median, and errors are reported as interquartile range unless otherwise stated, due to the non-Gaussian distribution of the datasets. When inspecting the weekly training pattern, we observed that the patients' commitment to training was consistently higher across the entire training period (Figure 2b). Daily, the approximately bimodal distribution observed by HV in Figure 2c, which depicts a tendency to practice mostly during early mornings (~8:00) and evenings (~19:00), is not followed by the patients, who had a somewhat more random pattern of daily practice, including engagement even during night times.
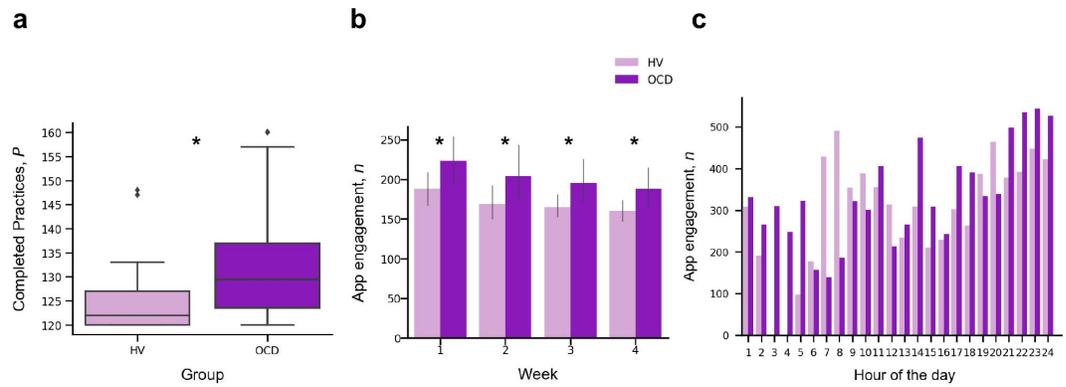
Figure 2.

Training Engagement.

a) Whole training overview. OCD patients engaged in significantly more training sessions than HV (* p = 0.005). The minimum required practices (P) were 120P. **b)** Weekly training pattern. OCD patients' greater commitment to training was consistent across the 4 weeks (* p < 0.005). App engagement (y-axis) is defined as the number of trials attempted, including successful and unsuccessful trials. **c)** Daily training pattern. OCD patients showed a more random pattern of daily practice, including engagement during the night-time, as opposed to HV who tended to practice mostly during early mornings (~ 8:00) and evenings (~ 19:00). The bar plots include the mean and confidence interval.

Learning

Learning was evaluated by the decrement in sequence duration throughout training. To follow the nomenclature of the motor control literature, we refer to sequence duration as movement time (*MT*), which is defined as

$$MT = t_6 - t_1, \tag{1}$$

where t_6 and t_1 are the time of the last (6th) and first key presses, respectively.

For each participant and sequence reward type (continuous and variable), we measured *MT* of a successful trial, as a function of the sequence trial number, n, across the whole training. Across trials, *MT* decreased exponentially (Figure 3a). The decrease in *MT* has been widely used to quantify learning in previous research (Crossman, 1959). A single exponential is viewed as the most statistically robust function to model such decrease (Heathcote et al., 2000). Accordingly, each participant's learning profile was modeled as follows:
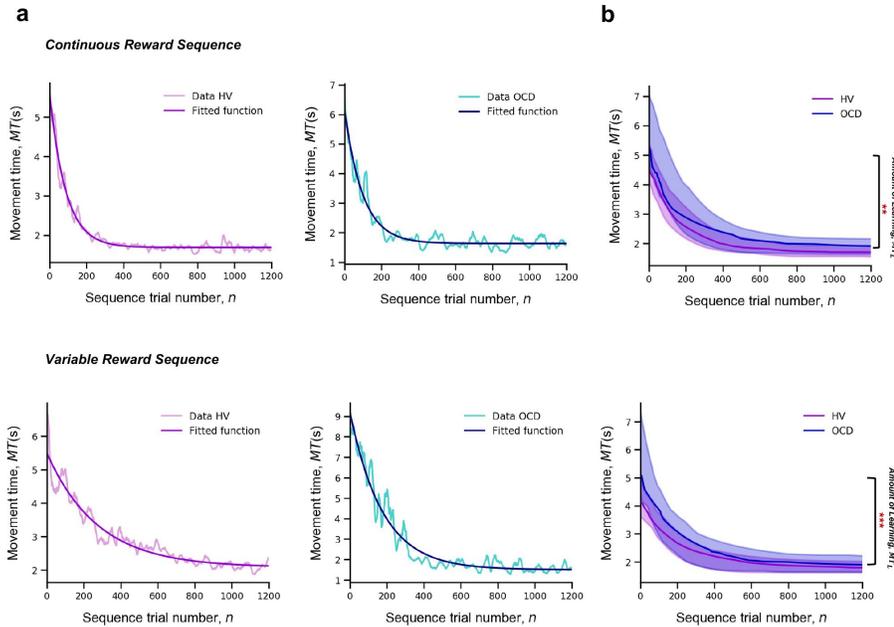
$$MT(n) = MT_0 + MT_L exp(-n/n_r), \tag{2}$$

Figure 3.

Learning.

Upper panel: Model fitting procedure conducted for the continuous reward sequence. **Lower panel:** Model fitting procedure conducted for the variable reward sequence. **a)** Individual plots exemplifying the time-course of MT as training progresses (lighter color) as well as the exponential decay fit modelling the learning profile of a single participant (darker color). Left panels depicts a HV and right panels a patient with OCD. **b)** Group comparison resulting from all individual exponential decays modelling the learning profile of each participant. Significant group difference on the amount of learning, MT_L, in both reward schedule conditions (continuous: $p = 0.009$; variable: $p < 0.001$). Solid lines: median (M); Transparent regions: interquartile range (IQR); Purple: healthy volunteers (HV); Blue: patients with obsessive-compulsive-disorder (OCD).

where n_r is the *learning rate* (measured in number of trials), which governs the rate of exponential decay. Parameter MT_0 is the movement time at *asymptote* (at the end of the training). Last, MT_L is the speed-up achieved over the course of the training (referred to as *amount of learning*) (Figure 3a). The larger the value of MT_L the bigger the decline in the movement time and thus the larger the improvement in the motor learning.

The individual fitting approach we used has the advantage of handling the different number of trials executed by each participant by modeling their behavior to a consolidated maximum value of n, $n_{max} = 1200$. We used a moving average of 20 trials to mitigate any effect of outlier trials. This analysis was conducted separately for continuous and variable reward schedules.

To statistically assess between-group differences in learning behavior, we pooled the relevant individual model parameters, MT_L and n_r conducted a Kruskal–Wallis H test to assess the effect of group (HV and OCD), reward type (continuous and variable) and their interaction on each parameter (Figure 3b).

There was a significant effect of group on the *amount of learning* parameter (MT_L $H = 16.5$, $p < 0.001$, but no reward ($p = 0.06$) or interaction effects ($p = 0.34$) (Figure 3c). Descriptive statistics: HV: M $MT_L = 3.1$ s, $IQR = 1.2$ s and OCD: M $MT_L = 3.9$ s, $IQR = 2.3$ s for the continuous reward sequence; HV: M $MT_L = 2.3$ s, $IQR = 1.2$ s and OCD: M $MT_L = 3.6$ s, $IQR = 2.5$ s for the variable reward sequence.

Regarding the *learning rate* (n_r) parameter, we found no significant main effects of group ($p = 0.79$), reward ($p = 0.47$) or interaction effects ($p = 0.46$). Descriptive statistics: sequence trials needed to asymptote HV: M$n_r = 176$, $IQR = 99$ and OCD: M$n_r = 200$, $IQR = 114$ for the continuous reward sequence; HV: M$n_r = 182$, $IQR = 123$ and OCD: M$n_r = 162$, $IQR = 141$ for the

variable reward sequence. These non-significant effects on the learning rate were further assessed with Bayes Factors (BF) for factorial designs (see Methods). This approach estimates the ratio between the full model, including main and interaction effects, and a restricted model that excludes a specific effect. The evidence for the lack of main effect of group was associated with a BF of 0.38, which is anecdotal evidence. We additionally obtained moderate evidence supporting the absence of a main effect of reward or a reward x group interaction (BF = 0.16 and 0.17 respectively).

Finally, there were no significant main or interaction effects on the asymptote parameter, MT_0 (group effect: p = 0.17; reward effect: p = 0.65 and interaction effect: p = 0.64). BF analysis provided anecdotal evidence supporting that there is no main effect of group (BF = 0.53), yet moderate evidence that reward and a reward x interaction factors do not modulate the performance time (BF = 0.12 and 0.17, respectively).

These results suggest that OCD patients have no learning deficits. Despite performing the action sequences significantly slower at the beginning of the training, patients demonstrated similar learning rates as compared to HV. Furthermore, both groups exhibited similar motor durations at asymptote which, which combined with the previous conclusion, indicates that OCD patients improved their motor learning more than controls, but to the same asymptote.

Automaticity

To assess automaticity, the ability to perform actions with low-level cognitive engagement, we examined the decline over time in the consistency of inter-keystroke interval (IKI) patterns trial to trial. We mathematically defined IKI consistency as the sum of the absolute value of the timelapses between finger presses from one sequence to the previous one

$$C = \sum_{k=1}^{5} \left| t_{k,n+1} - t_{k,n} \right|, \tag{3}$$

where n is the sequence trial number and k is the inter-keystroke response interval (Figure 4a). In other words, C quantifies how consistent/reproducible the press pattern is from trial to trial. The assumption here is that the more reproducible the sequences are *over time*, the more automatic the person's motor performance becomes.
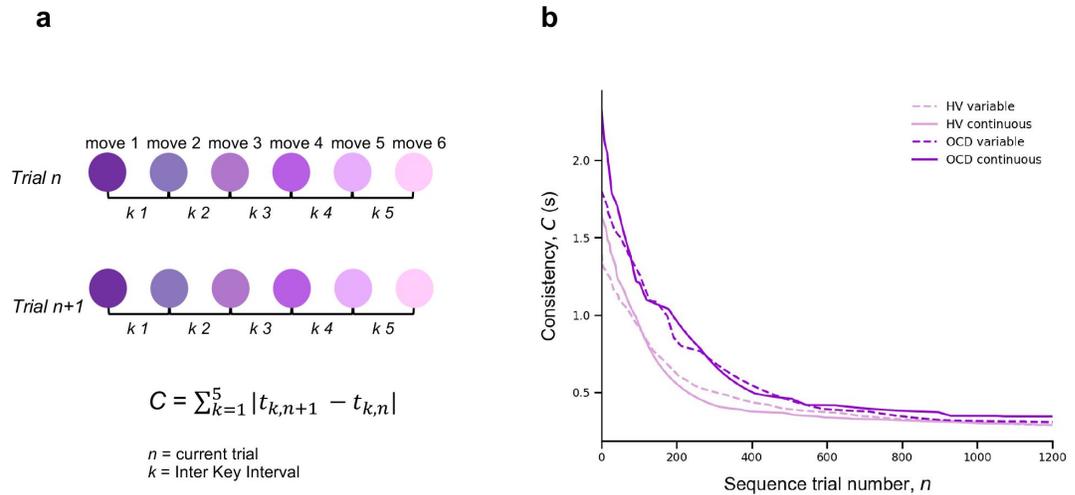
Figure. 4

Automaticity.

a) We mathematically defined trial-to-trial inter-keystroke-interval consistency (IKI consistency), denoted as C (in seconds), as the sum of the absolute values of the time lapses between finger presses across consecutive sequences. The variable n represents the sequence trial and k denotes the IKI. We evaluated automaticity by analyzing the decline in C over time, as it approached asymptotic levels. **b)** Group comparison resulting from all individual exponential decays modelling the automaticity profile (drop in C) of each participant. A significant group effect was found on the amount of automaticity gain, C_L (Kruskal–Wallis H = 11.1, $p < 0.001$) and on the automaticity constant, n_C (Kruskal– Wallis H = 4.61, $p < 0.03$). Solid and dashed lines are median values (M). Light purple: healthy volunteers (HV); Dark purple: patients with obsessive-compulsive-disorder (OCD); Solid lines: continuous reward condition; Dashed lines: variable reward condition.

For each participant and sequence reward type (continuous and variable), automaticity was assessed based on the decrement in C, as a function of n, across the entire training period. Since C decreased in an exponential fashion, we fitted the C data with an exponential decay function (following the same reasoning and procedure as MT) to model the automaticity profile of each participant,

$$C(n) = C_0 + C_L \exp\left(-\frac{n}{n_C}\right), \tag{4}$$

where n_c is the *automaticity rate* (measured in number of trials), C_0 is the sequence consistency at *asymptote* (by the end of the training) and C_L is the change in automaticity over the course of the training (which we refer to *amount of automation gain*). The model fitting procedure was conducted separately for continuous and variable reward schedules.

A Kruskal–Wallis H test was then conducted to assess the effect of group (OCD and HV) and reward type (continuous and variable) on each parameter resulting from the individual exponential fits (C_L, n_C and C_0).

There was a significant effect of group on the *amount of automation gain* (C_L: H = 11.1, p < 0.001) but no reward (p = 0.12) or interaction effects (p = 0.5) ([Figure 4b](#)). Descriptive statistics are as follows: HV: MD_L = 1.4 s, *IQR* = 0.7 s and OCD: MD_L = 1.9 s, *IQR* = 1.0 s for the continuous reward sequence; HV: MD_L = 1.1 s, *IQR* = 0.8 s and OCD: MD_L = 1.5 s, *IQR* = 1.1 s for the variable reward sequence.

There was also a significant group effect on the *automaticity rate* (n_C: H = 4.61, p < 0.03) but no reward (p = 0.42) or interaction (p = 0.12) effects. Descriptive statistics: sequence trials needed to asymptote HV: Mn_D = 142, *IQR* = 122 and OCD: Mn_D = 198, *IQR* = 162 for the continuous reward sequence; HV: Mn_D = 161, *IQR* = 104 and OCD: Mn_D = 191, *IQR* = 138 for the variable reward sequence.

At *asymptote*, no group (p = 0.1), reward (p = 0.9) or interaction (p = 0.45) effects were found. We found anecdotal evidence supporting that the group factor did not modulate the results (BF = 0.65). In addition, there was moderate evidence in favor of no main effects of reward or interaction (BF = 0.12 and 0.18 respectively).

Of note is the median difference in consecutive sequences achieved at asymptote: HV: MD_0 = 287 ms, *IQR* = 127 ms, OCD: MD_0 = 301 ms, *IQR* = 186 ms for the continuous reward sequence and HV: MD_0 = 288 ms, *IQR* = 110 ms, OCD: MD_0 = 300 ms, *IQR* = 114 ms for the variable reward sequence. These values of the C at asymptote are generally shorter than the normal reaction time for motor performance ([Kosinski, 2008](#)), reinforcing the idea that automaticity was reached by the end of the training.

In conclusion, patients were significantly slower, as compared to HV, at achieving a similar level of automaticity, in both types of reward sequences: they started slower, with a more irregular pace and had a slower progression rate to automaticity.

Sensitivity of sequence duration to reward

Our next goal was to investigate the sensitivity of performance improvements over time in our participant groups to changes in scores, either an increment or a decrease. To do this, we quantified the trial-by-trial behavioral changes in response to a decrement or increase in reward from the previous trial using the sequence duration (in ms), labeled as *MT* (movement time). Note that in our experimental design, *MT* was negatively correlated with the scores received. Following [Pekny et al., 2015](#), we represented the change from trial n to n + 1 in *MT* simply as:

$$\Delta MT^{(n+1)} = MT^{(n+1)} - MT^{(n)} \tag{5}$$

Reward (R) change at trial n was computed as:

$$\Delta R^{(n)} = R^{(n)} - R^{(n-1)} \tag{6}$$

Next, we analyzed separately ΔMT values that followed an increase in reward from trial n − *1* to n,$\Delta R+$, denoting a positive sign in ΔR; and those that followed a drop in reward, $\Delta R-$, indicating a negative sign in ΔR. Following [Pekny et al., 2015](#), we estimated for each participant the conditional probability distributions $p(\Delta T | \Delta R+)$ and $p(\Delta T | \Delta R-)$ (where T denotes a behavioral measure, *MT* in this section or *IKI* consistency in the next section) by fitting a Gaussian distribution to the histogram of each data sample (Figure S1). The standard deviation (σ) and the center μ of the resulting distributions were used for statistical analyses (Figure S1). Similar analyses were carried out on C index (defined above), which already reflected changes between consecutive trials.

As a general result, we expected that healthy participants would introduce larger behavioral changes (more pronounced reduction in *MT*, more negative *ΔMT*) following a decrease in scores, as shown previously (Chen et al., 2017; van Mastrigt et al., 2020). Accordingly, we predicted that the *p(ΔT/ΔR−)* distribution would be centered at more negative values than p(*Δ*T|*Δ*R+), corresponding to greater speeding following negative reward changes. Given previous suggestions of enhanced sensitivity to negative feedback in patients with OCD (Apergis-Schoute et al., 2023, Becker et al., 2014; Kanen et al., 2019), we predicted that the OCD group, as compared to the control group, would demonstrate greater trial-to-trial changes in movement time and a more negative center of the *p(ΔT/ΔR−)* distribution. Additionally, we examined whether OCD participants would exhibit more irregular changes to *Δ*R− and *Δ*R+ values, as reflected in a larger spread of the *p(ΔT/ΔR+)* and p(*ΔT/ΔR −*) distributions, compared to the control group.

The conditional probability distributions were separately fitted to subsamples of the data across *continuous* reward practices, splitting the total number of correct sequences into four bins. This analysis allowed us to assess changes in reward sensitivity and behavioral changes across bins of sequences (bins 1-4 by partitioning the total number of sequences, from the whole training, into four). We focused the analysis on the continuous reward schedule for two reasons: 1) changes in scores on this schedule are more obvious to the participants and 2) a larger number of trials in each subsample were available to fit the Gaussian distributions, due to feedback being provided on all trials.

We observed that participants speeded up their sequence duration more (negative changes in trial-wise *MT*) following a drop in scores, as expected (**Figure 5a**). Conducting a 3-way ANOVA with reward change (increase, decrease) and bin (1:4) as within-subject factors, and group as between-subject factor, we found a significant main effect of reward ($p = 1.53 \times 10^{-07}$), indicating that both groups reduced *MT* differently as a function of the change in reward. There was also a significant main effect of bin ($p = 1.30 \times 10^{-10}$), such that participants speeded up their sequence performance over practices. The main effects are illustrated in **Figure 5b**. In addition, there was a significant interaction between reward and bin in predicting the trial-to-trial changes in movement time ($p = 4.78 \times 10^{-09}$). This outcome suggested that the improvement in *MT* over sequences depended on whether the reward increased or decreased from the previous trial. To explore this interaction effect further, we conducted a dependent-sample pairwise t-test on *MT*, after collapsing the data across groups. In each sequence bin, participants speeded up *MT* more following a drop in scores than following an increment, as expected (corrected $p_{FDR} = 2 \times 10^{-16}$). On the other hand, assessing the effect of bins separately for each level of reward, we observed that the large sensitivity of *MT* changes to reward decrements was attenuated over bins of practices (corrected $p_{FDR} = 2 \times 10^{-16}$; dependent-sample t-tests between consecutive pairs of bins). By contrast, the sensitivity of *MT* changes to reward increments— consistently smaller—did not change over bins ($p_{FDR} = 0.88$). Overall, these findings indicate that both OCD and HV participants exhibited an acceleration in sequence performance following a decrease in scores (main effect). However, this sensitivity to score decrements was reduced as participants approached automaticity through repeated practice. Notably, the increased sensitivity to reward decrements relative to increments persisted throughout the practice sessions in both groups.
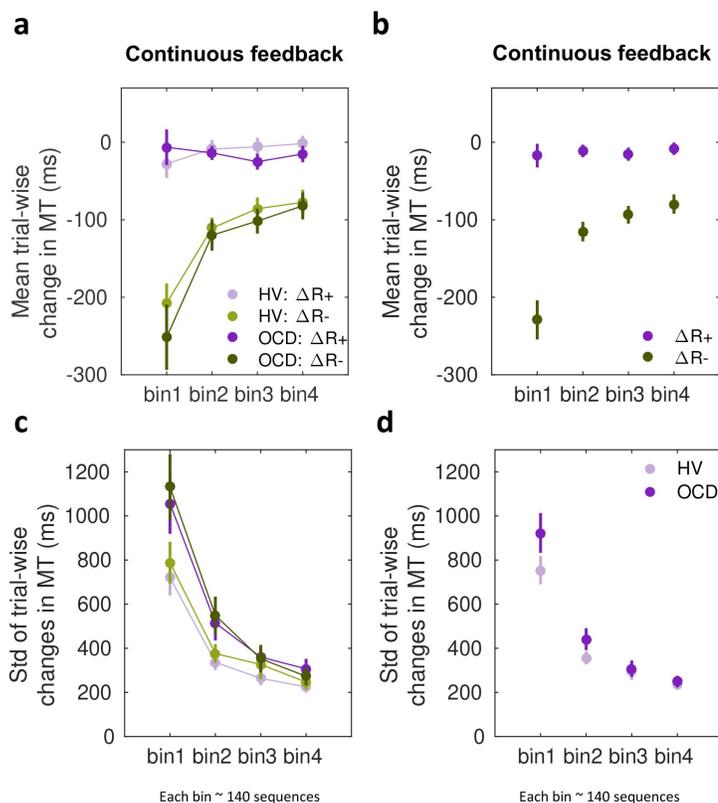
Figure 5.

Sensitivity of movement time to changes in reward in the continuous reward schedule.

a) Mean change in movement time (*MT*, ms) from trial *n* to *n+1* following an increment (*ΔR+*, in purple) or decrement (*ΔR-*, in green) in scores at *n*. The dots represent mean *MT* changes (error bars denote SEM) in each bin of correctly performed sequences, after partitioning all correct sequences into four subsets, and separately for OCD (dark colors), and HV (light colors). **b)** Both groups of participants speeded up their sequence performance more following a drop in scores (main effect of reward, $p = 1.53 \times 10^{-07}$; 2 × 4 reward x bin ANOVA); yet this acceleration was reduced over the course of practiced sequences (main bin effect, $p = 1.40 \times 10^{-10}$). **c)** Same as a) but for the spread (std, ms) of the *MT* change distribution. **d)** Illustration of the main effect of group on std ($p = 2.56 \times 10^{-07}$). Each bin depicted in the plots (x-axis) contains 140 correct sequences on average (further details in ***Supplementary Results: Sample size for the reward sensitivity analysis)***.

Assessment of the std (σ) of the Gaussian distributions $p\,(\Delta T/\Delta R-)$ and $p(\Delta T/\Delta R+)$ in the continuous reward condition (**Figure 5c**) with a similar 3-way ANOVA revealed a significant main effect of group ($p = 2.56 \times 10^{-07}$). As shown in **Figure 5d**, the std (σ) of the distribution of trial-to-trial *MT* changes was smaller in HV than in OCD. In addition, we observed a significant change over bins of sequences in (σ), and independently of the group or reward factors (main effect of bin, $p = 2 \times 10^{-16}$). This outcome reflected that over practices, both groups introduced less variable changes in MT over the course of training in response to both reward increments and decrements, in line with improvements in skill learning (Wolpert et al., 2011). No additional main or interaction effects were found. Control analyses demonstrated that the group, reward or bin effects were not confounded by differences in the size of the subsamples used for the Gaussian distribution fits (Supplementary Results).

Sensitivity of IKI consistency (C) to reward

To further explore the potential impact of reward changes on the previously reported group effects on automaticity, we quantified the trial-by-trial behavioral changes in IKI consistency (represented by *C*) in response to changes in reward scores relative to the previous trial. Note that a smaller C indicates a more reproducible IKI pattern trial to trial. During continuous reward practices, both patients and healthy controls exhibited an increased consistency of IKI patterns trial to trial across bins of correct sequences (decreased *C*, equation [3], **Figure 6a** and **6b**; main effect of bin on the center of the Gaussian distribution, $p = 2 \times 10^{-16}$; 3-way ANOVA). Performance in OCD and HV, however, differed with regards to how reproducible their timing patterns were (main effect of group, $p = 2.6 \times 10^{-05}$). Moreover, the IKI consistency improved more (smaller C) following reward increments than

after decrements, as shown in **Figure 6a** **and** **6b** (main reward effect, *p* = 0.002). No significant interaction effects between factors were found. Accordingly, although OCD participants exhibited an attenuated IKI consistency in their performance relative to HV, the main effects of reward and bins of sequences were independent of the group.
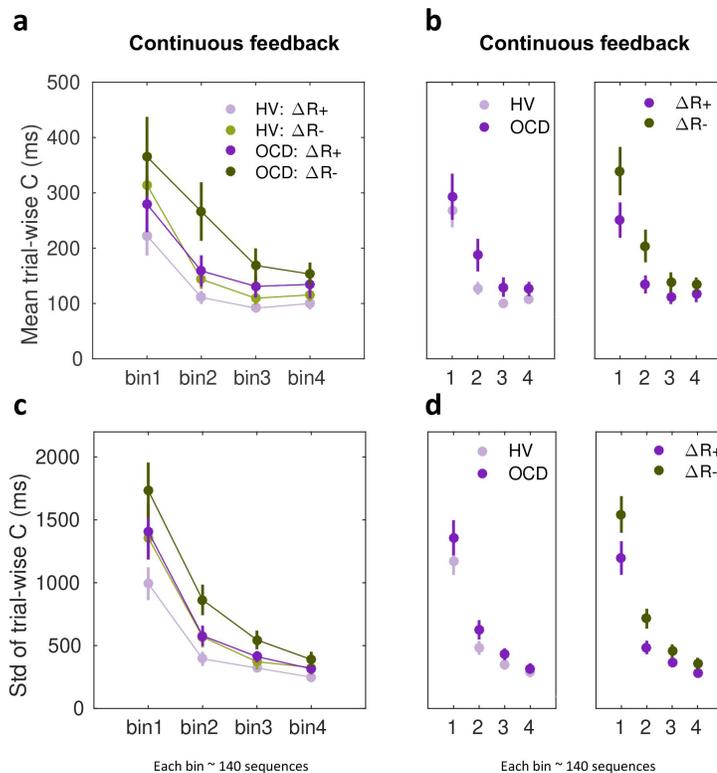

a Continuous feedback

b Continuous feedback

Sensitivity of IKI consistency (*C*) to reward changes in the continuous schedule.

a) The mean change in trial-to-trial IKI consistency (C) across bins of correct sequences is shown, separately for each group (OCD: dark colors; HV: light colors) and for reward increments (*ΔR+*, purple) and decrements (*ΔR-*, green). The dots represent the mean value, while the vertical bars denote SEM. **b)** Illustration of the main effect of group (left panel; *p* = 2.6 × 10^{-05}) and type of reward change (right panel; *p* = 0.002). **c)** Same as a) but for the std (in ms) of the distribution of IKI consistency changes, *C*. **d)** The left and right panels display the main effect of group (*p* = 2.56 × 10^{-07}) and increment/decrements in reward (*p* = 0.00145) on the std. Each bin depicted in the plots (x-axis) contains 140 correct sequences on average (See ***Supplementary Results***: ***Sample size for the reward sensitivity analysis)***.

c

d

Each bin ~ 140 sequences

Each bin ~ 140 sequences

Regarding the spread of the *p(ΔT |ΔR)* distributions, we found a significant main effect of the group (*p* = 2.56 × 10^{-07}), bin (*p* = 2 × 10^{-16}) and reward (*p* = 0.001) factors, but no significant interaction between the factors (**Figure 6c and 6d**). These outcomes suggest that the σ of the Gaussian distribution for *C* values differed between groups, such that OCD patients had a more variable distribution than healthy control participants, and independently of the reward or bin factor (**Figure 6c and 6d**). In addition, the *σ* was reduced across bins of practiced sequences. Last, the *C* values were more stable (smaller spread) following an increase in scores. The results highlight that over the course of training participants' IKI consistency values stabilized, but more so following reward gains. On a group level, the degree of IKI consistency was more irregular in the OCD sample. Similarly to the *MT* analyses, the sensitivity effects to reward changes were not accounted for by differences in the size of the subsamples used for the Gaussian distribution fits (Supplementary Results).

Phase B: Tests of action-sequence preference and goal/habit arbitration

Once the month-long training was completed, participants attended a laboratory session for follow-up behavioral tests aimed at assessing preference for familiar versus novel sequences (experiment 2 and 3) including a re-evaluation test to assess goal/habit arbitration (experiment 3 only). Below we briefly describe these two experiments and report the results. See Methods and **Table 3** for a more detailed description of the tasks.

Experiment 2

Preference for familiar versus novel action sequences

This experiment tests the hypothesis stated in the outline, that the trained action sequence gains intrinsic/rewarding properties or value. We used an *explicit preference task*, assessing participants' preferences for familiar (hypothetically habitual) sequences over goal-seeking sequences. We assume that if the trained sequences have acquired rewarding properties (for example, anxiety relief, or the inherent gratification of skilled performance or routine), participants would express a greater preference to select or 'play' them, even when given the option to play easier sequences (i.e., goal-seeking sequences).

After reporting which app sequence was their preferred, participants started the *explicit preference task*. On each trial, they were required to select and play 1 of 2 sequences. The 2 possible sequences were presented and identified using a corresponding image and participants had to choose which one they wanted to play. There were 3 conditions, each comprising a specific sequence pair: 1) app preferred sequence *versus* app non-preferred sequence (*control condition*) 2) app preferred sequence *versus* any 6-move sequence (*experimental condition 1*) ; 3) app preferred sequence *versus* any 3-move sequence (*experimental condition 2*). The app preferred sequence was their preferred putative habitual sequence and the 'any 6' or 'any 3'-move sequences were the goal-seeking sequences because they are supposedly easier for 2 reasons: 1) they could comprise any key press of participant's choice (for example the same single key press repeatedly 6 or 3 times respectively) and 2) they could have same or different key press combinations every time the 'any-sequence' needed to be input (i.e. not necessarily the same sequence on every trial). The conditions (15 trials each) were presented sequentially but counterbalanced among participants. See Methods and Figure 7a for further details.

Figure 7.

Preference for familiar versus novel action sequences. a) Explicit Preference Task.

Participants had to choose and play one of two given sequences. Once choice was made, the image correspondent to the selected sequence was highlighted in blue. Participants then played the sequence. While playing it, the bar on top registered each move progressively lighting up in green. There were 3 conditions, each comprising a specific sequence pair: 1) app preferred sequence *versus* app non-preferred sequence (*control condition*) 2) app preferred sequence *versus* any 6-move sequence of participant's choice (*experimental condition 1*); 3) app preferred sequence *versus* any 3-move sequence of participant's choice (*experimental condition 2*). **b)** No evidence for enhanced preference for the app sequence in either HV nor OCD patients. In fact, when an easier and shorter sequence is pitted against the app familiar sequence (right raincloud plot), both groups significantly preferred it (Kruskal-Wallis main effect of Condition H = 23.2, p < 0.001). Left raincloud plot: control condition; Middle raincloud plot: experimental condition 1; Right raincloud plot: experimental condition 2. Y-axis depicts the number of app-sequence choices (15 choice trials maximum). Connected lines depict mean values. **(c)** Exploratory analysis of the preference task following up unexpected findings on the mobile-app effect on symptomatology: re-analysis of the data conducting a Dunn's *post hoc* test splitting the OCD group into 2 subgroups based on their YBOCS change after the app training [14 patients with improved symptomatology (reduced YBOCS scores) and 18 patients who remained stable or felt worse (i.e. respectively, unchanged or increased YBOCS scores)]. Patients with reduced YBOCS scores after the app training had significantly higher preference to play the app sequence in both experimental conditions (left panel: p_{bonf} = 0.04*; right panel: p_{bonf} = 0.03*). The bar plots represent the sample mean and the vertical lines the confidence interval. Individual data points are included to show dispersion in the sample. Abbreviations: YBOCS = Yale-Brown obsessive-compulsive scale, HV = Healthy volunteers, OCD = patients with obsessive-compulsive disorder.

A Kruskal-Wallis H test indicated a main effect of Condition (H = 23.2, p < 0.001) but no Group (p = 0.36) or interaction effects (p = 0.72) (Figure 7b). Dunn's *post hoc* pairwise comparisons revealed that *experimental condition 2 (app sequence versus any 3 sequence)* was significantly different from *control condition* (p_{bonf} < 0.001) and from *experimental condition 1 (app sequence versus any 6 sequence)* (p_{bonf} = 0.006). No differences were found between the latter two conditions (p_{bonf} = 0.08). Bayesian analysis further provided moderate evidence in support of the absence of main effects of group (BF = 0.129) and interaction (BF = 0.054). These results denote that both groups evaluate the trained app sequences as being equally attractive as the alternative novel-but-easier sequence when of the same length (Figure 7b, middle plot). However, when given the option to play an easier-but-shorter sequence (in *experimental condition 2*), both groups significantly preferred it over the app familiar sequence (Figure 7b, right plot). A positive correlation between COHS and the app sequence choice (*Pearson r* = 0.36, p = 0.005) further showed that those participants with greater habitual tendencies had a greater propensity to prefer the trained app sequence under this condition.

Given the high variance of participants' choices on this preference task, particularly in the experimental conditions, and the findings reported below related to the mobile-app performance effect on symptomatology, we further conducted an exploratory Dunn's *post hoc* test splitting the OCD group into 2 subgroups based on their YBOCS score changes after the app training: 14 patients with improved symptomatology (reduction in YBOCS scores) and 18 patients who remained stable or felt worse (i.e. respectively, same or increase in YBOCS scores). Patients with lowered YBOCS scores after the app training had significantly greater preference for the app trained sequence in both experimental conditions as compared to patients with same or increased YBOCS scores after the app training: *experimental condition 1* (p_{bonf} = 0.04, Figure 7c, *left*) and *experimental condition 2* (p_{bonf} = 0.03, Figure 7c, *right*). In conclusion, most participants prefer to play shorter and easier alternative sequences, thus not showing a bias towards the trained/familiar app sequences. Contradicting our hypothesis, OCD patients followed the same behavioral pattern. However, some participants still preferred the app sequence, specifically those with greater habitual tendencies, including patients who considered the app training beneficial. Such preference presumably arose because some intrinsic value may have been attributed to the trained action sequence.

Experiment 3

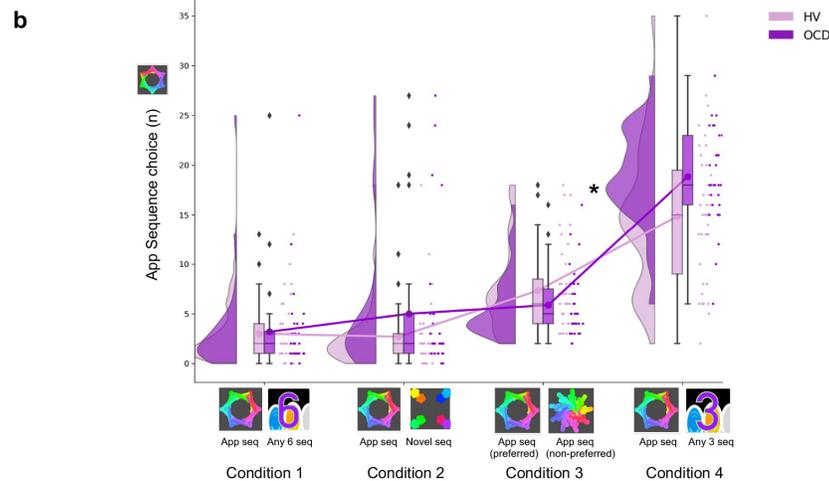### Test of goal/habit arbitration: re-evaluation of the learned action sequence

A *2-choice appetitive learning task* was used to test participants' ability to switch to a different behavior. By providing more value to alternative action sequences, participants were required to re-evaluate their options and act accordingly. The task was conducted in a new context, which has been shown to promote re-engagement of the goal system (Bouton, 2021).

On each trial, participants were required to choose between two 'chests' based on their associated reward value. Each chest depicted an image identifying the sequence that needed to be completed to be opened. After choosing which chest they wanted, participants had to play the specific correct sequence to open it. Their task was to learn by trial and error which chest would give them more rewards (gems), which by the end of the experiment would be converted into real monetary reward. There was no penalty for incorrectly keyed sequences because behavior was assessed based on participants' choice regardless of the sequence accuracy.

Four chest-pairs (conditions, 40 trials each) were tested (see Figure 8a and methods for detailed description of each condition): three conditions pitted the trained/familiar app sequence against alternative sequences of higher monetary outcomes (given by variable amount of reward that did not overlap [deterministic]). The fourth condition kept the monetary value equivalent for the two options (thus rendering a probabilistic rather than deterministic contingency) but provided a much easier/shorter alternative sequence, and thus pitted the intrinsic value of the familiar sequence against a motorically less effortful sequence. The conditions were presented sequentially but counterbalanced among participants.

Goal / habit arbitration

a

	Condition	Monetary Reward	Effort	Research question
1	App sequence *vs* Any-6 sequence	Higher	Same	Are OCD patients able to re-evaluate options and re-engage the goal system as function of reward value?
2	App sequence *vs* Novel sequence	Higher	Higher	Is a goal-directed response explored even if it involves a much bigger effort?
3	App preferred *vs* Non-preferred	Higher	Same	Does any failure of OCD patients to re-engage the goal-directed system arise from an insensitivity to reward revaluation or avoidance of unfamiliar actions
4	App sequence *vs* Any-3 sequence	Same	Lower	Are OCD patients able to re-evaluate options and re-engage the goal system as function of effort?

b

Figure 8.

Re-evaluation procedure: 2-choice appetitive learning task.

a) shows the task design. We tested 4 conditions, with chest-pairs corresponding to the following motor sequences: 1) app preferred sequence *versus* any 6-move sequence; 2) app preferred sequence *versus* novel (difficult) sequence; 3) app preferred sequence *versus* app non-preferred sequence; 4) app preferred sequence *versus* any 3-move sequence. The 'any 6-move' or 'any 3-move' sequences could comprise any key press of the participant's choice and could be played by different key press combinations on each trial. The 'novel sequence' (in 2) was a 6-move sequence of similar complexity and difficulty as the app sequences, but only learned on the test day (therefore, not overtrained). In conditions 1, 2 and 3, the preferred app sequence was pitted against alternative sequences of higher monetary value. In condition 4, the intrinsic value of the preferred app sequence was pitted against a motorically less effortful sequence (i.e. a shorter/easier sequence). Each condition addressed specific research questions, which are detailed in the right column of the table. **b)** demonstrates the task performance per group and over the 4 conditions. Both groups were able to switch from previous automatic to new goal-directed action sequences as a function of monetary re-evaluation. When re-evaluation involved an effort manipulation, OCD patients chose the app sequence significantly more than HV (* = *p* < 0.05) (condition 4). Y-axis depicts the number of app-sequence chests chosen (40 trials maximum) and connected lines depict mean values.

Both groups were highly sensitive to the re-evaluation procedure based on monetary feedback, choosing more often the non-app sequence, irrespective of the novelty of that sequence (Figure 8b, no group effects (*p* = 0.210 and BF = 0.742, anecdotal evidence). However, when re-evaluation involved motoric effort (condition 4), participants did not choose the alternative, 'any 3', the lower motoric effort sequence as readily (Kruskal-Wallis

main effect of condition: H = 151.1 p < 0.001) and OCD patients persisted significantly more than HV with the trained app sequence (*post hoc* group x condition 4 comparison: p = 0.04). In conclusion, after the month's training, both groups demonstrated ability to arbitrate between previous automatic and new goal-directed action sequences as a function of monetary re-evaluation. However, OCD patients nevertheless chose the familiar sequence when an easier and shorter (thus motorically less effortful) alternative was available.

Mobile-app performance effect on symptomatology: exploratory analyses

In a debriefing questionnaire, participants were asked to give feedback about their app training experience and how it interfered with their routine: a) how stressful/relaxing the training was (rated on a scale from -100% highly stressful to 100% very relaxing); b) how much it impacted their life quality (Q) (rated on a scale from -100% maximum decrease to 100% maximum increase in life quality). Supplementary Table S4 and Figure S2 depicts participants' qualitative and quantitative feedback. Of the 33 HV, 30 reported the app was neutral and did not impact their lives, neither positively nor negatively. The remaining 3 reported it as being a positive experience, with an improvement in their life quality (rating their life quality increase as 10%, 15% and 60%). Of the 32 patients assessed, 14 unexpectedly showed improvement (I) in their OCD symptoms during the month as measured by the YBOCS difference, in percentage terms, pre-post training ($\bar{I}$= 20 ± 9%), 5 felt worse ($\bar{I}$= -19 ± 9%) and 13 remained stable during the month (all errors are standard deviations). Of the 14 who felt better, 10 directly related their OCD improvement to the app training (life quality increase: Q= 43 ± 24%). Nobody rated the app negatively. Of note, the symptom improvement was positively correlated with patients' habitual tendencies reported in the Creature of Habits questionnaire, particularly with the routine subscale (Pearson r = 0.45, p = 0.01) (Figure 9a, left). A three-way ANOVA test showed that patients who reported less obsessions and compulsions after the month training were the ones with more pronounced habit routines (Group effect: F = 13.7, p < 0.001, Figure 9a, right). A strong positive correlation was also found between the OCD improvement reported subjectively as direct consequence of the app training and the OCI scores and reported habit tendencies (Pearson r = 0.8, p = 0.008; Pearson r = 0.77, p < 0.01, respectively) (Figure 9b): i.e., patients who considered the app somewhat beneficial were the ones with higher compulsivity scores and higher habitual tendencies. In HV, participants who also had greater tendency for automatic behaviors, regarded the app as more relaxing (Pearson r = 0.44, p < 0.01). However, such correlation between the self-reported relaxation measure attributed to the app and the COHS automaticity subscale was not observed in OCD (p = 0.1). Additionally, there was no correlation between patients' symptom improvement and how relaxing they considered the app training (p = 0.1).
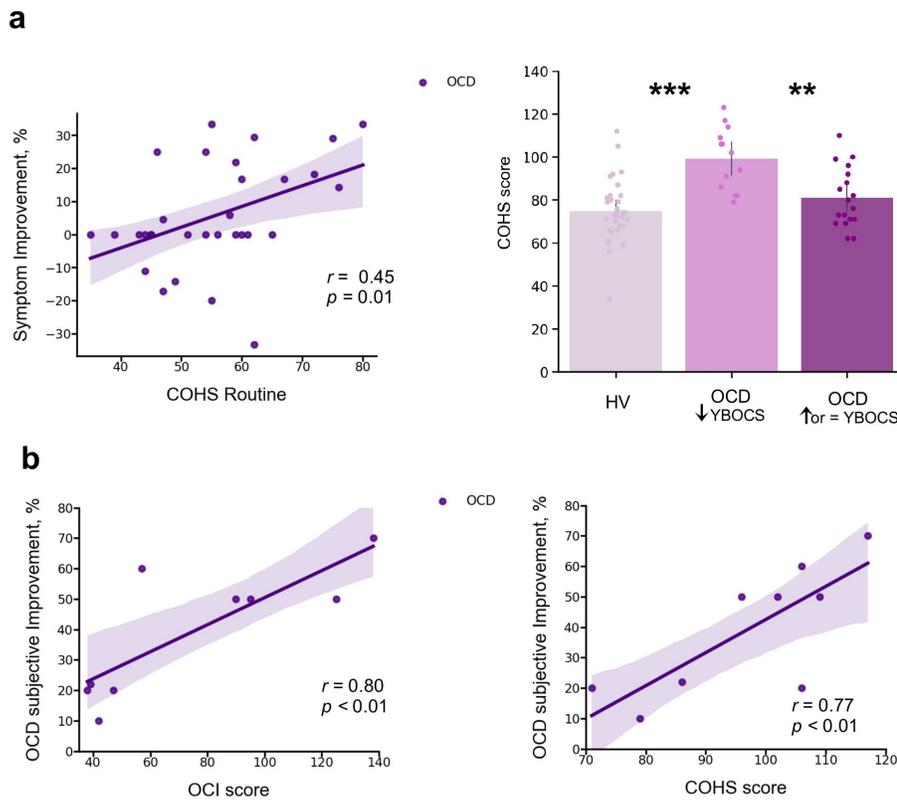
Mobile-app effect on symptomatology.

a) *Left:* positive correlation between patients' routine tendencies reported in the Creature of Habits (COHS) questionnaire and the symptom improvement (Pearson $r = 0.45$, $p = 0.01$). Symptom improvement was measured by the difference in YBOCS scale before and after app training. *Right*: Patients with greater improvement in their symptoms after the one month app training had greater habitual tendencies as compared to HV ($p < 0.001$) and to patients who did not improve post-app training ($p = 0.002$). The bar plot represents the sample means and the vertical lines the confidence interval. Individual data points are included to show dispersion in the sample. **b)** OCD patients who related their symptom improvement directly to the app training were the ones with higher compulsivity scores on the OCI (Pearson $r = 0.8$, $p = 0.008$) (*left*) and higher habitual tendencies on the COHS (Pearson $r = 0.77$, $p < 0.01$) (**right**). Note that b) has one missing patient because he did not complete the OCI and COHS scales.

Abbreviations: OCI = Obsessive-Compulsive Inventory, COHS = Creature of Habits Scale, YBOCS = Yale-Brown obsessive-compulsive scale, HV = Healthy volunteers, OCD = patients with obsessive-compulsive disorder.

Other self-reported symptoms

In addition to the Creature of Habit findings, of the remaining self-reported questionnaires assessed (see Methods), OCD patients also reported enhanced intolerance of uncertainty, elevated motivation to avoid aversive outcomes and higher perfectionism, worries and perceived stress, as compared to healthy controls (see Table 1 for statistical results and Figure 10 in the Methods section for overall summary).

Table 1.

Self-reported measures on various scales measuring impulsiveness, compulsiveness, habitual tendencies, self-control, behavioral inhibition and activation, intolerance of uncertainty, perfectionism, stress and the trait of worry.

| | HV | OCD | Statistics | | |
	(n= 33)	(n= 32)	t	df	p
CPAS	5.9 (4.0)	14.2 (5.0)	-7.37	62	<0.001***
COHS routine	48.4 (9.4)	55.7 (11.1)	-2.79	62	0.01*
COHS automaticity	26.3 (8.2)	32.9 (8.5)	-3.15	62	<0.001***
COHS total	74.8 (14.4)	88.7 (16.7)	-3.56	62	<0.001***
HSCQ	50.7 (7.3)	42.5 (8.5)	4.17	62	<0.001***
BIS	17.5 (3.5)	24.4 (2.7)	-8.81	61	<0.001***
BAS reward responsibility	15.9 (2.2)	15.1 (2.5)	1.25	61	0.22
BAS drive	10.0 (2.4)	9.6 (2.6)	0.66	61	0.51
BAS fun seeking	11.1 (1.9)	9.7 (2.4)	2.60	61	0.01*
Barratt total	58.8 (8.4)	65.0 (10.1)	-2.68	61	0.01*
Barratt attentional	14.6 (4.1)	19.8 (4.7)	-4.74	61	<0.001***
Barratt motor	21.2 (2.6)	21.4 (3.2)	-0.23	61	0.82
Barratt non-planning	23.7 (3.3)	24.6 (4.5)	-0.96	61	0.34
IUS	41.9 (10.0)	87.3 (20.2)	-11.23	61	<0.001***
SCS	118.5 (21.4)	118.3 (17.2)	0.04	62	0.97
FMPS	70.3 (21.0)	95.4 (21.4)	-4.73	62	<0.001***
PSS	13.7 (4.7)	22.9 (5.1)	-7.51	62	<0.001***
PSWQ	37.9 (11.7)	64.0 (11.0)	-9.20	62	<0.001***

Abbreviations: HV, Healthy Volunteers; OCD, Patients with Obsessive-Compulsive Disorder; CPAS, Compulsive Personality Assessment Scale; COHS, Creature of Habit Scale; HSCQ, Habitual Self Control Questionnaire; BIS, Behavioral Inhibition System; BAS, Behavioral Activation System; Barratt, Barratt Impulsiveness Scale; IUS, Intolerance of Uncertainty Scale; SCS, Self-Control Scale; FMPS, Frost Multidimensional Perfectionism Scale; PSS, Perceived Stress Scale; PSWQ, Penn State Worry Questionnaire. Standard deviations are in parentheses: mean (std). One patient and one healthy control missed a few questionnaires. * = $p < 0.05$ level, *** = $p < 0.001$ level (2-tailed).
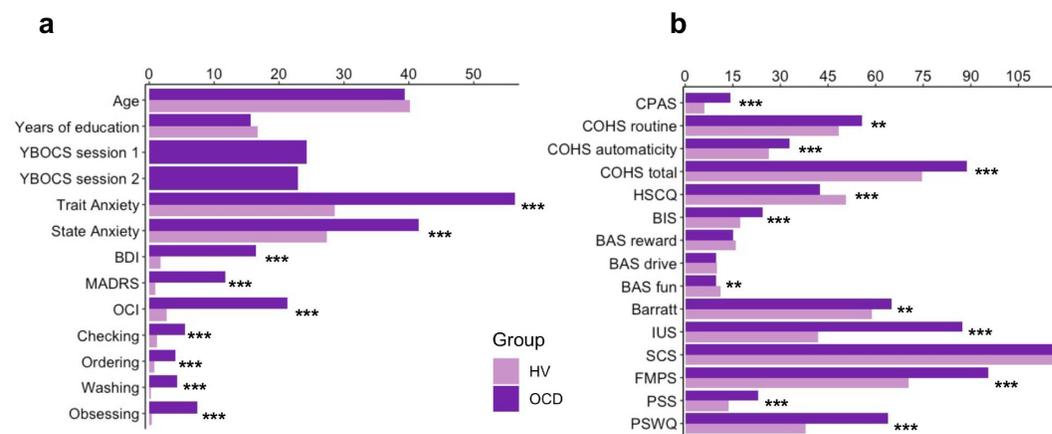

Figure 10.

a) Participants' demographics and clinical characteristics. **b)** Between group results from the self-reported questionnaires. **Abbreviations**: HV, Healthy Volunteers; OCD, Patients with Obsessive-Compulsive Disorder; Y-BOCS, Yale-Brown obsessive-compulsive scale; MADRS, Montgomery-Asberg Depression Rating Scale; STAI, The State-Trait Anxiety Inventory; BDI, Beck Depression Inventory; OCI, Obsessive-Compulsive Inventory; CPAS, Compulsive Personality Assessment Scale; COHS, Creature of Habit Scale; HSCQ, Habitual Self Control

Questionnaire; BIS, Behavioral Inhibition System; BAS, Behavioral Activation System; Barratt, Barratt Impulsiveness Scale; IUS, Intolerance of Uncertainty Scale; SCS, Self-Control Scale; FMPS, Frost Multidimensional Perfectionism Scale; PSS, Perceived Stress Scale; PSWQ, Penn State Worry Questionnaire. ** = p < 0.01, *** = p <0.001.

Discussion

This study investigated the possible roles of habits, including their automaticity, and impaired goal/habit arbitration as explanations of compulsive OCD symptoms. We focused specifically on the habit component of the associative dual-process (i.e. goal/habit) model of behavior as applied to OCD, and described in the Introduction. First, we provide evidence, via a recently developed self-report questionnaire (Ersche et al., 2017), of greater subjective habitual tendencies in patients with OCD as compared to controls, in terms of both factors of 'routine' and 'automaticity'. Then, using a novel smartphone tool, we studied in real life the acquisition of two putative habits (6-element action sequences) for the first time in patients with OCD during their everyday schedule and home environment, while continuously collecting 30 days of real-time data. We found that OCD patients engaged more with the app training than healthy volunteers: patients enjoyed performing the sequences and practiced them significantly more, even though we did not request additional training. Despite performing the action sequences slower and at a more irregular speed at the beginning of training, OCD patients reached the same asymptotic level of automaticity (objectively determined) as healthy controls and exhibited equivalent evidence of 'chunking' (Smith and Graybiel, 2016). There was no evidence of procedural learning deficits *per se* in patients, but they attained automaticity significantly more slowly than controls. In subsequent, second phase testing conducted in a new context, we confirmed that both groups successfully transferred both trained action sequences to their corresponding discriminative stimuli (i.e., visual icons). Both groups also demonstrated successful arbitration between their previous automatic and new goal-directed action sequences in that they preferred the monetarily more valuable sequences. Nevertheless, OCD patients disadvantageously preferred the previously trained/familiar action sequence under certain conditions. First, exploratory analysis revealed that those patients with higher habitual tendencies and compulsivity scores significantly preferred the familiar sequence. Second, when required to choose between the familiar and a novel, less effortful sequence, the OCD group preferred the previously trained option. In both cases, this preference for the familiar sequence in OCD patients presumably arose because of its intrinsic value. These results are relevant to the theory of goal-direction/habit imbalance in OCD (Gillan et al., 2016) by suggesting the predominance of habits in certain contexts where such habits may have acquired intrinsic value. One possible source of such value is symptom relief. This would be consistent with follow-up findings that many of the patients found the app to be beneficial, improving their symptomatology after the month training (as measured by the Y-BOCS scale difference pre-post training, as well as individual feedback).

Implications for the dual associative theory of habitual and goal-directed control

Rapid execution, invariant response topography, action chunking and low cognitive load, have all been considered essential criteria for the definition of habits (Balleine and Dezfouli, 2019; Haith and Krakauer, 2018). We have successfully achieved all of these elements with our app using the criteria of extensive training and context stability, both previously shown

to be essential to enhance formation and strengthening of habits (Haith and Krakauer, 2018; Verplanken and Wood, 2006). *Context stability* was provided by the tactile, visual and auditory stimulation associated with the phone itself, which establishes a strong and similar context for all participants, regardless of their concurrent circumstances. *Overtraining* has been one of the most important criteria for habit development, and used by many as an operational definition on how to form a habit (Dickinson et al., 1995; Haith and Krakauer, 2018; Tricomi et al., 2009) (for a review see Balleine and O'Doherty, 2010), despite current controversies raised by de Wit et al., 2018 on its use as an objective test of habits. A recent study has demonstrated though that even short overtraining (1 day only) is effective at producing habitual behavior in participants high in affective stress (Pool et al., 2022), confirming previous suggestions for the key role of anxiety and stress on the behavioral expression of habits (Dias-Ferreira et al., 2009; Hartogsveld et al., 2020; Schwabe and Wolf, 2009). Here we have trained a clinical population with moderately high baseline levels of stress and anxiety, with training sessions of a higher order of magnitude than in previous studies (de Wit et al., 2018, 2018; Gera et al., 2022) (30 days instead of 3 days). By all accounts our overtraining is valid: to our knowledge the longest overtraining in human studies achieved so far. Both OCD patients and healthy controls attained automaticity in this study, exhibiting similar and stable asymptotic performance, both in terms of speed and the invariance in the kinematics of the motor movement.

We succeeded in achieving automaticity - which at a neural level is known to reliably engage the brain's habitual circuitry (Ashby et al., 2010; Bassett et al., 2015; Graybiel and Grafton, 2015; Lehericy et al., 2005) - and fulfilled three of the four criteria for the definition of habits according to Balleine and Dezfouli 2019 (Balleine and Dezfouli, 2019) (rapid execution, invariant topography and chunked action sequences). We were not, however, able to test the fourth criterion, of resistance to devaluation. Therefore, we are unable to firmly conclude that the action sequences are habits rather than, for example, goal-directed skills. According to a very recent study, also employing an app to study habitual behavior, the criterion of devaluation resistance was shown to apply to a simple 2-element sequence with less training (Gera et al., 2022). Thus, it remains possible that the overtraining of our 6-element sequence might have achieved behavioral autonomy from the goal in addition to behavioral automaticity.

Regardless of whether the trained action sequences can be defined as habits or goal-directed motor skills, it has to be considered why OCD patients chose the familiar sequences in certain conditions, even when it was superficially maladaptive to do so (i.e. effort condition). This leads us to postulate that action sequences may be motivated by more than one explicit goal (i.e. money in such patients), especially given the apparent therapeutic (intrinsic) value of their performance, and therefore the difficulty of allocating specific, single goals to human action sequences. One implication of this analysis may be to consider that behavior in general is 'goal-directed' but may vary in the balance of control by extrinsic and intrinsic goals. This may be consistent with motor control theories that refer to the successful completion of a motor action itself, in the spatio-temporal sense, as being 'goal-related'. For any action sequences there may thus exist an hierarchy of goals underpinning performance, ranging for example from explicit monetary feedback to intrinsic relief from an endogenous state (e.g. anxiety or boredom). Therefore, the dual associative process account of behavioral control may be reconstrued in terms of the relative balance of extrinsic to intrinsic outcomes. Another possible formulation is that habits, which depend initially on cached or historically acquired rewarding action values may not necessarily lose current value, but instead acquire alternative sources of value (O'Doherty, 2014).

Implications for understanding OCD symptoms

We observed a slower and greater irregularity of performance in patients with OCD as compared to controls at the beginning of the training. This was expected given previous reports of visuospatial and fine-motor skill difficulties in patients with OCD (Bloch et al., 2011). However, despite this initial slowness, no procedural learning deficits were found in patients. Such a finding is inconsistent with other implicit learning deficits previously reported in OCD using the serial reaction time (SRT) paradigm (Deckersbach et al., 2002; Joel et al., 2005; Kathmann et al., 2005; Rauch et al., 2001, 1997). However, it is in line with recent studies demonstrating successful learning both in patients with OCD (Soref et al., 2018) and healthy individuals with subclinical OCD symptoms (Barzilay et al., 2022) when instructions are given explicitly and participants intentionally search for the underlying sequence structure. In fact, our task does not tap into memory processes as strongly as SRT tasks because we explicitly demonstrate the sequence to participants before they begin their 30-day training, which likely decreases demands on procedural learning.

The quantification of trial-to-trial behavioral changes as function of a drop or increase in reward further revealed that the slower automaticity progression observed in OCD patients was mainly driven by a reduced sensitivity to changes in feedback scores in this group relative to healthy participants. Both groups, however, reproduced the IKI patterns more consistently following reward increments. This outcome contrasts with the more pronounced acceleration of *MT* in both samples in response to negative reward changes. Greater sensitivity to negative feedback has been reported previously (Becker et al., 2014). Here we show it has a dissociable effect on sequence duration and IKI consistency. In particular, we observed that the reduction in feedback scores interfered with automatization, despite a general beneficial effect on movement speed. The enhanced sensitivity to negative feedback is in line with recent studies showing higher response switching followed negative feedback (Marzuki et al., 2021), hyperactive monitoring system, increased prediction errors (Hauser et al., 2017) and enhanced error-related negativity amplitudes in OCD, the latter currently considered a biomarker for the disorder (Endrass and Ullsperger, 2014; Gehring et al., 2000; Riesel, 2019).

Considering the hypothetically greater tendency in OCD to form habitual/automatic actions described earlier (Gillan et al., 2014; Voon et al., 2015), we predicted that OCD patients would attain automaticity faster than healthy controls. This was not the case. In fact, the opposite was found. Since this was the first study to our knowledge assessing action sequence automatization in OCD, our contrary findings may confirm recent suggestions that previous studies were tapping into goal-directed behavior rather than habitual control per se (Gillan et al., 2015b; Vaghi et al., 2018; Zwosta et al., 2018) and may therefore have inferred enhanced habit formation in OCD as a defaulting consequence of impaired goal-directed responding. On the other hand, we are describing here two potential sources of evidence in favor of enhanced habit formation in OCD. First, OCD patients show a bias towards the previously trained, apparently disadvantageous, action sequences. In terms of the discussion above, this could possibly be reinterpreted as a narrowing of goals in OCD (Robbins et al., 2019) underlying compulsive behavior, in favor of its intrinsic outcomes. Secondly, OCD patients self-reported greater habitual tendencies in both the 'routine' and 'automaticity' subscales. Previous studies have reported that subjective habitual tendencies are associated with compulsive traits (Ersche et al., 2019; Wuensch et al., 2022) and act, in addition to cognitive inflexibility, as a predictor of subclinical OCD symptomatology in healthy populations (Ramakrishnan et al., 2022). There is an apparent discrepancy between self-reported 'automaticity' and the objective measure of automaticity we provided. This may result from a possible mis-labelling of this factor in the Creature of Habit questionnaire, where many of the relevant items indicate automatic S-R elicitation by situational triggering

stimuli rather than motor topographic features of the behavior (e.g. '*when walking past a plate of sweets or biscuits, I can't resist taking one*').

Finally, we also expected that OCD patients would show a functional impairment in arbitrating between actions, represented by a greater resistance than controls to redirect themselves to a goal state. By testing goal/habit arbitration using a re-evaluation task that applied a contextual change, which has previously been shown to recall attention and reengage the goal circuitry (Bouton, 2021; Vandaele and Ahmed, 2021), we found that the dynamic arbitration between previous automatic, and new goal-directed, action sequences observed in OCD patients was different from healthy volunteers, being driven hypothetically by the intrinsic value associated with the automatic sequences.

Possible beneficial effect of action sequence training on OCD symptoms as habit reversal therapy

OCD patients engaged significantly more with the motor sequencing app and enjoyed it more than healthy volunteers. Additionally, those patients more prone to routine habits and with higher OCI scores found use of the app beneficial, showing symptomatic improvement based on the YBOCS scale. One hypothesis for the therapeutic potential of this motor sequencing training is that the trained action sequences may disrupt OCD compulsions either via 'distraction' or habit 'replacement' by engaging the same neural 'habit circuitry'. This habit 'replacement' hypothesis is in line with successful interventions in Tourette Syndrome (Hwang et al., 2012), Tic disorders and Trichotillomania (Morris et al., 2013).

Limitations

As mentioned above, we were unable to employ the often-mooted 'gold standard' criterion of resistance to devaluation because it would have invalidated the goal/habit arbitration test. This meant that we were unable to conclusively define the trained action sequences as habitual, although they satisfied other important criteria such as automatic execution, invariant response topography and action chunking and low cognitive load. Nevertheless, the utility of the devaluation criterion has been questioned especially when applied to human studies of habit learning because devaluation can be difficult to achieve given that human behavior has multiple goals some of which may be implicit, and thus difficult to control experimentally, as well as being subject to great individual variation.

Although we found a significant preference for the trained action sequence in OCD patients in the condition where it was pitted against a simpler and shorter motor sequence, as compared to the monetary discounting condition, the reason for this difference is not immediately obvious. However, it may have arisen because of the nature of the contingencies inherent in these choice tests. Specifically, the 'monetary discounting' condition involved a simple deterministic choice between the two alternatives, which should readily be resolved in favor of the option associated with the greater, non-overlapping, range of rewards provided (e.g. 1-7 versus 8-15 gems). In contrast, in the 'effort discounting' condition, the reward ranges for the two options were equivalent (e.g. 1-7 gems), which raised uncertainty concerning which of the chosen sequences was optimal. The probabilistic constraint over this choice may therefore account for the greater sensitivity of the task in highlighting preference in OCD, given the greater susceptibility of such patients to uncertainty (Pushkarskaya et al., 2015).

Finally, some of the conclusions relating to the effects of OCD diagnosis on sequence preference without feedback were based only on a *post hoc* exploratory analysis. Specifically, only those patients with higher compulsivity (OCI) and Creature Of Habit (COHS)

scores exhibited this preference, therefore consistent with the hypothesis described above of the importance of intrinsic value of the habitual sequence to the development of compulsions. Evidence of this intrinsic value was provided by the greater engagement with, and therapeutic findings for, the app training in these patients. However, the latter effect needs to be confirmed in a registered clinical NHS trial in a controlled manner, which is ongoing.

Conclusion

We used a combination of behavioral tasks that addressed two key hypotheses from the goal/habit imbalance theory of compulsion relating to greater automaticity and impaired goal habit arbitration in OCD. In the initial phase, a novel app-based procedure for measuring action sequence learning and performance revealed evidence of equivalent procedural learning and attainment of objective automatization criteria of habitual performance in healthy volunteers and patients with OCD. A second phase found evidence for no impaired goal/habit arbitration in OCD following re-evaluation based on monetary feedback although there was greater preference for the trained action sequence under certain conditions. These findings may lead to a reformulation of the goal/habit imbalance hypothesis in OCD.

Finally, OCD patients with higher compulsivity scores and habitual tendencies showed more engagement with the motor training app and reported symptom alleviation, with implications for its potential use as a form of habit reversal therapy.

Materials and Methods Participants

We recruited 33 OCD patients and 34 healthy individuals, matched for age, gender, IQ and years of education. Two participants (1 HV and 1 OCD) were excluded because they did not perform the minimum required training (i.e. 2 daily practices for a period of 30 days). Therefore, a total of 32 OCD patients (19 females) and 33 healthy controls (19 females) were included in the analysis. Most participants were right-handed (left-handed: 4 OCD and 6 HV). Participants' demographics and clinical characteristics are presented in Table 2 and Figure 10.

Table 2.

Demographic and clinical characteristics of OCD patients and matched healthy controls

	HV	OCD	Statistics		
	(n= 33)	(n= 32)	t	df	p
Gender ratio (male/female)	14/19	13/19			
Age	40.2 (11.7)	39.3 (12.5)	0.29	63	0.77
Years of education	16.8 (3.4)	15.6 (3.5)	1.33	63	0.19
Predicted verbal IQ	117.8 (5.6)	118.4 (4.6)	-0.43	63	0.67
YBOCS session 1	0.0	24.3 (5.7)	-	-	-
YBOCS Obsessions session1	0.0	12.2 (3.0)	-	-	-
YBOCS Compulsions session1	0.0	11.8 (3.7)	-	-	-
YBOCS session 2	0.0	22.9 (6.6)	-	-	-
YBOCS Obsessions session2	0.0	11.6 (3.1)	-	-	-
YBOCS Compulsions session2	0.0	11.1 (4.2)	-	-	-
Trait Anxiety (STAI-T)	28.6 (5.9)	56.4 (8.6)	-15.11	63	<0.001***
State Anxiety (STAI-S)	28.6 (5.9)	56.4 (8.6)	-15.2	63	<0.001***
BDI	1.7 (2.3)	16.5 (9.4)	-8.72	62	<0.001***
MADRS	0.9 (1.5)	11.8 (6.2)	-9.88	63	<0.001***
OCI	7.3 (9.1)	68.4 (30.9)	-10.83	62	<0.001***
Checking	0.9(1.9)	11.7 (9.4)	-6.5	62	<0.001***
Ordering	0.7 (1.6)	5.8 (3.3)	-7.92	62	<0.001***
Washing	7.3 (9.2)	66.0 (28.6)	-11.18	62	<0.001***
Doubting	1.9 (2.7)	13.6 (7.5)	-8.37	62	<0.001***
Obsessing	1.1 (1.8)	7.9 (4.0)	-8.82	62	<0.001***

Abbreviations: OCD, patients with obsessive-compulsive disorder; HV, Healthy volunteers; Y-BOCS, Yale-Brown obsessive-compulsive scale; MADRS, Montgomery-Asberg Depression Rating Scale; STAI, The State-Trait Anxiety Inventory; BDI, Beck Depression Inventory; OCI, Obsessive-Compulsive Inventory. Standard deviations are in parentheses: mean (std). One patient missed the BDI and the OCI questionnaires. *** = $p < 0.001$ level (2-tailed)

Healthy individuals were recruited from the community, were all in good health, unmedicated and had no history of neurological or psychiatric conditions. Patients with OCD were recruited through an approved advertisement on the OCD action website (www.ocdaction.org.uk) and local support groups and via clinicians in East Anglia. All patients were screened by a qualified psychiatrist of our team, using the Mini International Neuropsychiatric Inventory (MINI) to confirm the OCD diagnosis and the absence of any comorbid psychiatric conditions. Patients with hoarding symptoms were excluded. Our patient sample comprised 6 unmedicated patients, 20 taking selective serotonin reuptake inhibitors (SSRIs) and 6 on a combined therapy (SSRIs + antipsychotic). OCD symptom severity and characteristics were measured using the Y-BOCS scale (Goodman, 1989), mood status was assessed using the Montgomery-Asberg Depression Rating Scale (MADRS) (Montgomery and Asberg, 1979) and Beck Depression Inventory (BDI) (Beck et al., 1961), anxiety levels were evaluated using the State-Trait Anxiety Inventory (STAI) (Spielberger et al., 1983), and verbal IQ was quantified using the National Adult Reading Test (NART) (Nelson and Willison, 1982). All patients included suffered from OCD and scored > 16 on the Y-BOCS, indicating at least moderate severity. They were also free from any additional axis-I disorders. General exclusion criteria for both groups were substance dependence, current depression indexed by scores exceeding 16 on the MADRS, serious neurological or medical illnesses or head injury. All participants completed additional self-report questionnaires measuring:

1. impulsiveness: Barratt Impulsiveness Scale (Barratt, 1994)

2. compulsiveness: Obsessive Compulsive Inventory (Foa et al., 1998) and Compulsive Personality Assessment Scale (Fineberg et al., 2007)

3. habitual tendencies: Creature of Habit Scale (Ersche et al., 2017)

4. self-control: Habitual Self-Control Questionnaire (Schroder et al., 2013) and Self-Control Scale (Tangney et al., 2004)

5. behavioral inhibition and activation: BIS/BAS Scale (Carver and White, 1994)

6. intolerance of uncertainty (Buhr and Dugas, 2002)

7. perfectionism: Frost Multidimensional Perfectionism Scale (Frost and Marten, 1990)

8. stress: Perceived Stress Scale (Cohen et al., 1983)

9. trait of worry: Penn State Worry Questionnaire (Meyer et al., 1990).

All participants gave written informed consent prior to participation, in accordance with the Declaration of Helsinki, and were financially compensated for their participation. This study was approved by the East of England - Cambridge South Research Ethics Committee (16/EE/0465).

Phase B: Tests of action-sequence preference and goal/habit arbitration

After completing the month-long app training, participants attended a laboratory session to conduct additional behavioral tests aiming at assessing preference for familiar versus novel sequences (experiment 2 and 3) including a re-evaluation test to assess goal/habit arbitration (experiment 3 only). The description of the tasks is below and instructions to the participants are presented in Table 3. Since these follow-up tests required observing additional stimuli *while* performing the action sequences, it was impractical to use participant's individual iPhones to simultaneously present the task stimuli and be an interface to play the action sequences. We therefore used a 'makey-makey' device which enabled connecting the testing laptop (presenting the task stimuli) to four keys made of playdough arranged on a table (used as an interface for the action sequences input). This device allowed for accurate registration of input keys as well as their timings. The playdough keys were built with the same size as the keys shown in the screens of the individual iPhones used for the one month training. Participants were asked to practice the action sequences trained at home within the new context for several minutes, until they became familiar and comfortable with it. Hence, the transition to a non-mobile/laboratory context was conducted with great care.

Table 3.

Follow up task instructions

Explicit Preference Task

You will be given 2 sequences to choose from.

You can play either of them and switch as you go.

Select the sequences using the left and right pads and then play it

Two-choice Appetitive Instrumental Task

In the following task, you will need to choose between 2 chests. Pick a chest using the left and right pads and play the matching sequence to open it. Open any chest you want. One of the chests may reward you more than the other. The more gems you get, the more money you will earn at the end of the task. Try to win as much as you can! You will receive your winnings at the end of the study.

Experiment 2: explicit preference task

Participants observed, on each trial, 2 sequences identified by a corresponding image, and were asked to choose which one they wanted to play. Once choice was made, the image correspondent to the selected sequence was highlighted in blue. Participants then played the sequence. The task included 3 conditions (15 trials each). Each condition comprised a specific sequence pair: 2 experimental conditions pairing the app preferred sequence (putative habit) with a goal-seeking sequence and 1 control condition pairing both app sequences trained at home. The conditions were as follows: 1) app preferred sequence *versus* app non-preferred sequence (*control condition*) 2) app preferred sequence *versus* any 6-move sequence (*experimental condition 1*); 3) app preferred sequence *versus* any 3-move sequence (*experimental condition 2*). The app preferred sequence was the putative habitual sequence and the 'any 6' or 'any 3'-move sequences were the goal-seeking sequences because they are supposedly easier: they could comprise any key press of participant's choice (for example the same single key press repeatedly 6 or 3 times respectively) and they could have same or different key press combinations every time the 'any-sequence' needed to be input. The conditions (15 trials each) were presented sequentially but counterbalanced among participants. Figure 7a for illustration of the task.

Experiment 3: two-choice appetitive learning task

On each trial, participants were presented with two 'chests', each containing an image identifying the sequence that needed to be completed to be able to open the chest. Participants had to choose which chest to open and play the correct sequence to open it. Their task was to learn by trial and error which chest would give them more rewards 'gems', which by the end of the experiment would be converted into real monetary reward. If mistakes were made inputting the sequences, participants could simply repeat the moves until they were correct, without any penalty. Behavior was assessed based on participants' choice, regardless of the accuracy of the sequence. The task included 4 conditions (40 trials each), with chest-pairs correspondent to the following motor sequences (see also figure 8 for illustration of each condition):

- *condition 1*: app preferred sequence *versus* any 6-move sequence

- *condition 2*: app preferred sequence *versus* a novel (difficult) sequence

- *condition 3*: app preferred sequence *versus* app non-preferred sequence

- *cndition 4*: app preferred sequence *versus* any 3-move sequence

As in the preference task described above, the 'any 6-move' or 'any 3-move' sequences could comprise any key press of participant's choice (for example the same single key press repeatedly 6 or 3 times respectively) and could be played by different key press combinations on each trial. The novel sequence (in condition 3) was a 6-move sequence of similar complexity and difficulty as the app sequences, but only learned on the day, before starting this task (therefore, not overtrained). In conditions 1, 2 and 3, higher monetary outcomes were given to the alternative sequences. To remove the uncertainty confound commonly linked to probabilistic tasks, conditions 1, 2 and 3 followed a deterministic nature: in all trials, the choice for the preferred app sequence was rewarded with smaller monetary outcomes (sampled from a random distribution between 1-7 gems) whereas the alternative option always provided higher monetary outcomes (sampled from a random distribution between 8-15 gems). Therefore, variable amount of reward that did not overlap was given (deterministic). Condition 4, on the other hand, kept the monetary value equivalent for the two options (thus rendering a probabilistic rather than deterministic contingency) but provided a much easier/shorter alternative sequence, and thus pitted the intrinsic value of the familiar sequence against a motorically less effortful sequence. The conditions were presented sequentially but counterbalanced among participants.

Statistical analyses

Participant's characteristics and self-reported questionnaires were analyzed with χ^2 and independent t-tests respectively. The Motor Sequencing App automatically uploaded the data to a cloud-based database. This task enabled us to compare patients with OCD and healthy volunteers in the following measures: training engagement (which included as primary output measures of the *total number of practices completed* and *app engagement* as defined as the number of sequences attempted, including both correct and incorrect sequences); procedural learning, automaticity development, sensitivity to reward (see definitions and description of data analyses in results section) and training effects on symptomatology as measured by the YBOCS difference pre-post training. The Phase B experiments enabled further investigation of preference and goal/habit arbitration. The primary outcome was the number of choices.

Between-group analyses were conducted using Kruskal-Wallis H tests when the normality assumption was violated. Parametric factorial analyses were carried out with analyses of variance (ANOVA). Our alpha level of significance was 0.05. On the descriptive statistics, main values are represented as median, and errors are reported as interquartile range unless otherwise stated, due to the non-Gaussian distribution of the datasets. When conducting several tests related to the same hypothesis, or when running several post-hoc tests following factorial effects, we controlled the FDR at level q = 0.05. Significant values after FDR control are denoted by p_{FDR}. For the Dunn's *post hoc* pairwise comparisons we have used Bonferroni correction denoted by p_{bonf}. Analysis were performed using Python version 3.7.6 and JASP version 0.14.1.0.

In the case of non-significant effects in the factorial analyses, we assessed the evidence in favor or against the full factorial model relative to the reduced model with Bayes Factors (BF: ratio BFfull/BFrestricted) using the bayesFactor toolbox (https://github.com/klabhub /bayesFactor) in MATLAB®. This toolbox implements tests that are based on multivariate generalizations of Cauchy priors on standardized effects(Rouder et al., 2012) (Rouder et al.,

2012). As recommended by Rouder and colleagues (2012), we defined the restricted models as the full factorial model without one specific main or interaction effect. The ratio BFfull/BFrestricted represents the ratio between the probability of the data being observed under the full model and the probability of the same data under the restricted model. BF values were interpreted following(Andraszewicz et al., 2015). The relationship between primary outcomes and clinical measures was calculated using a Pearson correlation.

Data Availability

The source data for all figures and analyses are provided with this paper. They are available in the Open Science Framework, in the following link: https://osf.io/9xrdz/

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Reviewer #1 (Public Review):

It is known that aberrant habit formation is a characteristic of obsessive-compulsive disorder (OCD). Habits can be defined according to the following features (Balleine and Dezfouli, 2019): rapid execution, invariant response topography and action 'chunking'. The extent to which OCD behavior is derived from enhanced habit formation relative to deficits in goal-directed behavior is a topic of debate in the current literature. This study examined habit-learning specifically (cf. deficits in goal-directed behavior) by regularly presenting, via smartphone, sequential learning tasks to patients with OCD and healthy controls. Participants engaged in the tasks every day over the course of a month. Automaticity, including the extent to which individual actions in the sequence become part of a unified 'chunk', was an important outcome variable. Following the 30 days of training, in-laboratory tasks were then administered to examine 1) if performing the learned sequences themselves had become rewarding 2) differences in goal-directed vs. habitual behavior.

Several hypotheses were tested, including:
Patients would have impaired procedural learning vs. healthy volunteers (this was not supported, possibly because there were fewer demands on memory in the task used here)
Once the task had been learned, patients would display automaticity faster (unexpectedly, patients were slower to display automaticity)
Habits would form faster under a continuous (vs. variable) reinforcement schedule

Exploratory analyses were also conducted: an interesting finding was that OCD patients with higher self-reported symptoms voluntarily completed more sessions with the habit-training app and reported a reduction in symptoms.

Strengths

This paper is well situated theoretically within the habit learning/OCD literature. Daily training in a motor-learning task, delivered via smartphone, was innovative, ecologically valid and more likely to assay habitual behaviors specifically. Daily training is also more similar to studies with non-humans, making a better link with that literature. The use of a sequential-learning task (cf. tasks that require a single response) is also more ecologically valid.

The in-laboratory tests (after the 1 month of training) allowed the researchers to test if the OCD group preferred familiar, but more difficult, sequences over newer, simpler sequences.

Weaknesses

The sample size was relatively small. Some potentially interesting individual differences within the OCD group could have been examined more thoroughly with a bigger sample (e.g., preference for familiar sequences). A larger sample may have allowed the statistical testing of any effects due to medication status.

The authors were not able to test one criterion of habits, namely resistance to devaluation, due to the nature of the task

The authors achieved their aims in that two groups of participants (patients with OCD and controls) engaged with the task over the course of 30 days. The repeated nature of the task meant that 'overtraining' was almost certainly established, and automaticity was demonstrated. This allowed the authors to test their hypotheses about habit learning. The results are supportive of the author's conclusions.

This article is likely to be impactful -- the delivery of a task across 30 days to a patient group is innovative and represents a new approach for the study of habit learning that is superior to an in-laboratory approach.

An interesting aspect of this manuscript is that it prompts a comparison with previous studies of goal-directed/habitual responding in OCD that used devaluation protocols, and which may have had their effects due to deficits in goal-directed behavior and not enhanced habit learning per se.

Reviewer #2 (Public Review):

In this study, the researchers employed a recently developed smartphone application to provide 30 days of training on action sequences to both OCD patients and healthy volunteers. The study tested learning and automaticity-related measures and investigated the effects of several factors on these measures. Upon training completion, the researchers conducted two preference tests comparing a learned and unlearned action sequences under different conditions. While the study provides some interesting findings, I have a few substantial concerns:

1. Throughout the entire paper, the authors' interpretations and claims revolve around the domain of habits and goal-directed behavior, despite the methods and evidence clearly focusing on motor sequence learning/procedural learning/skill learning. There is no evidence to support this framing and interpretation and thus I find them overreaching and hyperbolic, and I think they should be avoided. Although skills and habits share many characteristics, they are meaningfully distinguishable and should not be conflated or mixed up. Furthermore, if anything, the evidence in this study suggests that participants attained procedural learning, but these actions did not become habitual, as they remained deliberate actions that were not chosen to be performed when they were not in line with participants' current goals.

2. Some methodological aspects need more detail and clarification.
3. There are concerns regarding some of the analyses, which require addressing.

Please see details below, ordered by the paper sections.

Introduction:
It is stated that "extensive training of sequential actions would more rapidly engage the 'habit system' as compared to single-action instrumental learning". In an attempt to describe the rationale for this statement the authors describe the concept of action chunking, its benefits and relevance to habits but there is no explanation for why sequential actions would engage the habit system more rapidly than a single-action. Clarifying this would be helpful.

In the Hypothesis section the authors state: "we expected that OCD patients... show enhanced habit attainment through a greater preference for performing familiar app sequences when given the choice to select any other, easier sequence." I find it particularly difficult to interpret preference for familiar sequences as enhanced habit attainment.

A few notes on the task description and other task components:
It would be useful to give more details on the task. This includes more details on the time/condition of the gradual removal of visual and auditory stimuli and also on the within practice dynamic structure (i.e., different levels appear in the video).

Some more information on engagement-related exclusion criteria would be useful (what happened if participants did not use the app for more than one day, how many times were allowed to skip a day etc.).

According to the (very useful) video demonstrating the task and the paper describing the task in detail (Banca et al., 2020), the task seems to include other relevant components that were not mentioned in this paper. I refer to the daily speed test, the daily random switch test, and daily ratings of each sequence's enjoyment and confidence of knowledge.
If these components were not included in this procedure, then the deviations from the procedure described in the video and Banca al. (2020) should be explicitly mentioned. If these components were included, at least some of them may be relevant, at least in part, to automaticity, habitual action control, formulation of participants' enjoyment from the app etc. I think these components should be mentioned and analyzed (or at least provide an explanation for why it has been decided not to analyze them).
This is also true for the reward removal (extinction) from the 21st day onwards which is potentially of particular relevance for the research questions.

Training engagement analysis:
I find referring to the number of trials including successful and unsuccessful trials as representing participants "commitment to training" (e.g. in Figure legend 2b) potentially inadequate. Given that participants need at least 20 successful trials to complete each practice, more errors would lead to more trials. Therefore, I think this measure may mostly represent weaker performance (of the OCD patients as shown in Figure 2b). Therefore, I find the number of performed practice runs, as used in Figure 2a (which should be perfectly aligned with the number of successful trials), a "clean" and proper measure of engagement/commitment to training.

Also, to provide stronger support for the claim about different diurnal training patterns (as presented in Figure 2c and the text) between patients and healthy individuals, it would be beneficial to conduct a statistical test comparing the two distributions. If the results of this test are not significant, I suggest emphasizing that this is a descriptive finding.

Learning results:
When describing the Learning results (p10) I think it would be useful to provide the descriptive stats for the MT0 parameter (as done above for the other two parameters).

Sensitivity of sequence duration and IKI consistency (C) to reward:
I think it is important to add details on how incorrect trials were handled when calculating ΔMT (or C) and ΔR, specifically in cases where the trial preceding a successful trial was unsuccessful. If incorrect trials were simply ignored, this may not adequately represent trial-by-trial changes, particularly when testing the effect of a trial's outcome on performance change in the next trial.

I have a serious concern with respect to how the sensitivity of sequence duration to reward is framed and analyzed. Since reward is proportional to performance, a reduction in reward essentially indicates a trial with poor performance, and thus even regression to the mean (along with a floor effect in performance [asymptote]) could explain the observed effects. It is possible that even occasional poor performance could lead to a participant demonstrating this effect, potentially regardless of the reward. Accordingly, the reduced improvement in performance following a reward decrease as a function of training length described in Figure 5b legend may reflect training-induced increased performance that leaves less room for improvement after poor trials, which are no longer as poor as before. To address this concern, controlling for performance (e.g., by taking into consideration the baseline MT for the previous trial) may be helpful. If the authors can conduct such an analysis and still show the observed effect, it would establish the validity of their findings."
Another way to support the claim of reward change directionality effects on performance (rather than performance on performance), at least to some extent, would be to analyze the data from the last 10 days of the training, during which no rewards were given (pretending for analysis purposes that the reward was calculated and presented to participants). If the effect persists, it is less unlikely that the effect in question can be attributed to the reward dynamics.
This concern is also relevant and should be considered with respect to the Sensitivity of IKI consistency (C) to reward (even though the relationship between previous reward/performance and future performance in terms of C is of a different structure).
This concern is also relevant and should be considered with respect to the sensitivity of IKI consistency (C) to reward. While the relationship between previous reward/performance and future performance in terms of C is of a different structure, the similar potential confounding effects could still be present.

Another related question (which is also of general interest) is whether the preferred app sequence (as indicated by the participants for Phase B) was consistently the one that yielded more reward? Was the continuous sequence the preferred one? This might tell something about the effectiveness of the reward in the task.

Regarding both experiments 2 and 3:
The change in context in experiment 2 and 3 is substantial and include many different components. These changes should be mentioned in more detail in the Results section before describing the results of experiments 2 and 3.

Experiment 2:
In Experiment 2, the authors sometimes refer to the "explicit preference task" as testing for habitual and goal-seeking sequences. However, I do not think there is any justification for interpreting it as such. The other framings used by the authors - testing whether trained action sequences gain intrinsic/rewarding properties or value, and preference for familiar versus novel action sequences - are more suitable and justified. In support of the point I raised here, assigning intrinsic rewarding properties to the learned sequences and thereby

preferring these sequences can be conceptually aligned with goal-directed behavior just as much as it could be with habit.

Experiment 3:
Similar to Experiment 2, I find the framing of arbitration between goal-directed/habitual behavior in Experiment 3 inadequate and unjustified. The results of the experiment suggest that participants were primarily goal-directed and there is no evidence to support the idea that this re-evaluation led participants to switch from habitual to goal-directed behavior. Also, given the explicit choice of the sequence to perform participants had to make prior to performing it, it is reasonable to assume that this experiment mainly tested bias towards familiar sequence/stimulus and/or towards intrinsic reward associated with the sequence in value-based decision making.

Mobile-app performance effect on symptomatology: exploratory analyses:
Maybe it would be worth testing if the patients with improved symptomatology (that contribute some of their symptom improvement to the app) also chose to play more during the training stage.

Discussion:
Based on my earlier comments highlighting the inadequacy and mis-framing of the work in terms of habit and goal-directed behavior, I suggest that the discussion section be substantially revised to reflect these concerns.

In the sentence "Nevertheless, OCD patients disadvantageously preferred the previously trained/familiar action sequence under certain conditions" the term "disadvantageously" is not necessarily accurate. While there was potentially more effort required, considering the possible presence of intrinsic reward and chunking, this preference may not necessarily be disadvantageous. Therefore, a more cautious and accurate phrasing that better reflects the associated results would be useful.

Materials and Methods:
The authors mention: "The novel sequence (in condition 3) was a 6-move sequence of similar complexity and difficulty as the app sequences, but only learned on the day, before starting this task (therefore, not overtrained)." - for the sake of completeness, more details on the pre-training done on that day would be useful.

Minor comments:
In the section discussing the sensitivity of sequence duration to reward, the authors state that they only analyzed continuous reward trials because "a larger number of trials in each subsample were available to fit the Gaussian distributions, due to feedback being provided on all trials." However, feedback was also provided on all trials in the variable reward condition, even though the reward was not necessarily aligned with participants' performance. Therefore, it may be beneficial to rephrase this statement for clarity.

With regard to experiment 2 (Preference for familiar versus novel action sequences) in the following statement "A positive correlation between COHS and the app sequence choice (Pearson r = 0.36, p = 0.005) further showed that those participants with greater habitual tendencies had a greater propensity to prefer the trained app sequence under this condition." I find the use of the word "further" here potentially misleading.

Author Response

We truly appreciate the positive assessment of referee 1, particularly the consideration that our study is theoretically strong and that 'the results are supportive of the authors' conclusions'. This is an important external endorsement of our conclusions, contrasting somewhat with the views of referee 2.

We agree with the reviewer that the proof of principle established in our study opens new avenues for research into the psychological and behavioral determinants of the heterogeneity of this clinical population. However, considering the study timeline and the pandemic constraints, a bigger sample was not possible. Our sample can indeed be considered small if one compares it with current online studies, which do not require in-person/laboratory testing, thus being much easier to recruit and conduct. However, given the nature of our protocol (with 2 demanding test phases, 1-month engagement per participant and the inclusion of OCD patients without comorbidities only) and the fact that this study also involved laboratory testing, we consider our sample size reasonable and comparable to other laboratory studies (typically comprising on average between 30-50 participants in each group).

Thank you for acknowledging the impact of our study, in particular the unique ability of our task to interrogate the habit system.

Reviewer #2 (Public Review):

In this study, the researchers employed a recently developed smartphone application to provide 30 days of training on action sequences to both OCD patients and healthy volunteers. The study tested learning and automaticity-related measures and investigated the effects of several factors on these measures. Upon training completion, the researchers conducted two preference tests comparing a learned and unlearned action sequences under different conditions. While the study provides some interesting findings, I have a few substantial concerns:

> 1. *Throughout the entire paper, the authors' interpretations and claims revolve around the domain of habits and goal-directed behavior, despite the methods and evidence clearly focusing on motor sequence learning/procedural learning/skill learning. There is no evidence to support this framing and interpretation and thus I find them overreaching and hyperbolic, and I think they should be avoided. Although skills and habits share many characteristics, they are meaningfully distinguishable and should not be conflated or mixed up. Furthermore, if anything, the evidence in this study suggests that participants attained procedural learning, but these actions did not become habitual, as they remained deliberate actions that were not chosen to be performed when they were not in line with participants' current goals.*

We acknowledge that the research on habit learning is a topic of current controversy, especially when it comes to how to induce and measure habits in humans. Therefore, within this context referee's 2 criticism could be expected. Across disQnct fields of research, different methodologies have been used to measure habits, which represent relaQvely stereotyped and autonomous behavioral sequences enacted in response to a specific sQmulus without consideraQon, at the Qme of iniQaQon of the sequence, of the value of the outcome or any representaQon of the relaQonship that exists between the response and the outcome. Hence these are sQmulus-bound responses which may or may not require the implementaQon of a skill during subsequent performance. Behavioral neuroscienQsts define habits similarly, as sQmulus-response associaQons which are independent of reward or outcome, and use devaluaQon or conQngency degradaQon strategies to probe habits (Dickinson and Weiskrantz, 1985; Tricomi et al., 2009). Others conceptualize habits as a form of procedural memory, along with skills, and use motor sequence learning paradigms to invesQgate and dissect different components of habit learning such as acQon selecQon, execuQon and consolidaQon (Abrahamse et al., 2013; Doyon et al., 2003; Squire et al., 1993). It is also generally agreed that the autonomous nature of habits and the fluid proficiency of skills are both usually achieved with many hours of training or pracQce, respecQvely (Haith and Krakauer, 2018).

We consider that Balleine and Dezfouli (2019) made an excellent attempt to bring all these different criteria within a single framework, which we have followed. We also consider that our discussion in fact followed a rather cautious approach to interpretation solely in terms of goaldirected versus habitual control.

Referee 2 does not actually specify criteria by which they define habits and skills, except for asserting that skilled behavior is goal-directed, without mentioning what the actual goal of the implantation of such skill is in the present study: the fulfillment of a habit? We assume that their definition of habit hinges on the effects of devaluation, as a single criterion of habit, but which according to Balleine and Dezfouli (2019) is only 1 of their 4 listed criteria. We carefully addressed this specific criterion in our manuscript: "We were not, however, able to test the fourth criterion, of resistance to devaluation. Therefore, we are unable to firmly

conclude that the action sequences are habits rather than, for example, goal-directed skills. Regardless of whether the trained action sequences can be defined as habits or goal-directed motor skills, it has to be considered...". Therefore, we took due care in our conclusions concerning habits and thus found the referee's comment misleading and unfair.

We note that our trained motor sequences did in fact fulfil the other 3 criteria listed by Balleine and Dezfouli (2019), unlike many studies employing only devaluation (e.g. Tricomi et al 2009; Gillan et al 2011). Moreover, we cited a recent study using very similar methodology where the devaluation test was applied and shown to support the habit hypothesis (Gera et al., 2022).

Whether the initiation of the trained motor sequences in experiment 3 (arbitration) are underpinned by an action-outcome association (or not) has no bearing on whether those sequences were under stimulus-response control after training (experiment 1). Transitions between habitual and goal-directed control over behavior are quite well established in the experimental literature, especially when choice opportunities become available (Bouton et al (2021), Frölich et al (2023), or a new goal-directed schemata is recruited to fulfill a habit (Fouyssac et al, 2022). This switching between habits and goal-directed responding may reflect the coordination of these systems in producing effective behavior in the real world.

- Fouyssac M, Peña-Oliver Y, Puaud M, Lim NTY, Giuliano C, Everitt BJ, Belin D. (2021).Negative Urgency Exacerbates Relapse to Cocaine Seeking After Abstinence. Biological Psychiatry. doi: 10.1016/j.biopsych.2021.10.009

- Frölich S, Esmeyer M, Endrass T, Smolka MN and Kiebel SJ (2023) Interaction between habits as action sequences and goal-directed behavior under time pressure. Front. Neurosci. 16:996957. doi: 10.3389/fnins.2022.996957

- Bouton ME. 2021. Context, attention, and the switch between habit and goal-direction in behavior. Learn Behav 49:349– 362. doi:10.3758/s13420-021-00488-z

1. Some methodological aspects need more detail and clarification.

1. There are concerns regarding some of the analyses, which require addressing.

We thank referee 2 for their detailed review of the methods and analyses of our study and for the helpful feedback, which clearly helps improve our manuscript. We will clarify the methodological aspects in detail and conduct the suggested analysis. Please see below our answers to the specific points raised.

Introduction:

1. It is stated that "extensive training of sequential actions would more rapidly engage the 'habit system' as compared to single-action instrumental learning". In an attempt to describe the rationale for this statement the authors describe the concept of action chunking, its benefits and relevance to habits but there is no explanation for why sequential actions would engage the habit system more rapidly than a single-action. Clarifying this would be helpful.

We agree that there is no evidence that action sequences become habitual more readily than single actions, although action sequences clearly allow 'chunking' and thus likely engage neural networks including the putamen which are implicated in habit learning as well as skill. In our revised manuscript we will instead state: "we have recently postulated that extensive training of sequential actions could be a means for rapidly engaging the 'habit system' (Robbins et al., 2019)]"

> 1. In the Hypothesis section the authors state: "we expected that OCD patients… show enhanced habit attainment through a greater preference for performing familiar app sequences when given the choice to select any other, easier sequence". I find it particularly difficult to interpret preference for familiar sequences as enhanced habit attainment.

We agree that choice of the familiar response sequence should not be a necessary criterion for habitual control although choice for a familiar sequence is, in fact, not inconsistent with this hypothesis. In a recent study, Zmigrod et al (2022) found that 'aversion to novelty' was a relevant factor in the subjective measurement of habitual tendencies. It should also be noted that this preference was present in patients with OCD. If one assumes instead, like the referee, that the familiar sequence is goal-directed, then it contravenes the well-known 'egodystonia' of OCD which suggests that such tendencies are not goal-directed.

To clarify our hypothesis, we will amend the sentence to the following: "Finally, we expected that OCD patients would generally report greater habits, as well as attribute higher intrinsic value to the familiar app sequences manifested by a greater preference for performing them when given the choice to select any other, easier sequence".

> A few notes on the task description and other task components:

> 1. It would be useful to give more details on the task. This includes more details on the time/condition of the gradual removal of visual and auditory stimuli and also on the within practice dynamic structure (i.e., different levels appear in the video).

These details will be included in the revised manuscript. Thank you for pointing out the need for further clarification of the task design.

> 1. Some more information on engagement-related exclusion criteria would be useful (what happened if participants did not use the app for more than one day, how many times were allowed to skip a day etc.).

This additional information will be added to the revised manuscript. If participants omitted to train for more than 2 days, the researcher would send a reminder to the participant to request to catch up. If the participant would not react accordingly and a third day would be skipped, then the researcher would call to understand the reasons for the lack of engagement and gauge motivation. The participant would be excluded if more than 5 sequential days of training were missed. Only 2 participants were excluded given their lack of engagement.

> 1. According to the (very useful) video demonstrating the task and the paper describing the task in detail (Banca et al., 2020), the task seems to include other relevant components that were not mentioned in this paper. I refer to the daily speed test, the daily random switch test, and daily ratings of each sequence's enjoyment and confidence of knowledge.

> If these components were not included in this procedure, then the deviations from the procedure described in the video and Banca al. (2020) should be explicitly mentioned. If these components were included, at least some of them may be relevant, at least in part, to automaticity, habitual action control, formulation of participants' enjoyment from the app etc. I think these components should be mentioned and analyzed (or at least provide an explanation for why it has been decided not to analyze them).

> This is also true for the reward removal (extinction) from the 21st day onwards which is potentially of particular relevance for the research questions.

The task procedure was indeed the same as detailed in Banca et al., 2020. We did not include these extra components in this current manuscript for reasons of succinctness and because

the manuscript was already rather longer than a common research article, given that we present three different, though highly inter-dependent, experiments in order to answer key interrelated questions in an optimal manner. However, since referee 2 considers this additional analysis to be important, we will be happy to include it in the supplementary material of the revised manuscript.

> *Training engagement analysis:*

> *9) I find referring to the number of trials including successful and unsuccessful trials as representing participants "commitment to training" (e.g. in Figure legend 2b) potentially inadequate. Given that participants need at least 20 successful trials to complete each practice, more errors would lead to more trials. Therefore, I think this measure may mostly represent weaker performance (of the OCD patients as shown in Figure 2b). Therefore, I find the number of performed practice runs, as used in Figure 2a (which should be perfectly aligned with the number of successful trials), a "clean" and proper measure of engagement/commitment to training.*

We acknowledge referee's concern on this matter and agree to replace the y-axis variable of Figure 2b to the number of performed practices (thus aligning with Figure 2a). This amendment will remove any potential effect of weaker performance on the engagement measurement and will provide clearer results.

> 1. *Also, to provide stronger support for the claim about different diurnal training patterns (as presented in Figure 2c and the text) between patients and healthy individuals, it would be beneficial to conduct a statistical test comparing the two distributions. If the results of this test are not significant, I suggest emphasizing that this is a descriptive finding.*

We will conduct the statistical test and report accordingly.

> *Learning results:*

> 1. *When describing the Learning results (p10) I think it would be useful to provide the descriptive stats for the MT0 parameter (as done above for the other two parameters).*

Thank you for pointing this out. The descriptive stats for MT0 will be added to the revised version of the manuscript.

> 1. *Sensitivity of sequence duration and IKI consistency (C) to reward:*

> *I think it is important to add details on how incorrect trials were handled when calculating ΔMT (or C) and ΔR, specifically in cases where the trial preceding a successful trial was unsuccessful. If incorrect trials were simply ignored, this may not adequately represent trial-by-trial changes, particularly when testing the effect of a trial's outcome on performance change in the next trial.*

This is an important question. Our analysis protocol was designed to ensure that incorrect trials do not contaminate or confound the results. To estimate the trial-to-trial difference in ΔMT (or C) and ΔR, we exclusively included pairs of contiguous trials where participants achieved correct performance and received feedback scores for both trials. For example, if a participant made a performance error on trial 23, we did not include ΔR or ΔMT estimates for the pairs of trials 23-22 and 24-23. Instead of excluding incorrect trials from our analyses, we retained them in our time series but assigned them a NaN (not a number) value in Matlab. As a result, ΔR and ΔMT was not defined for those two pairs of trials. Similarly for C. This approach ensured that our analyses are not confounded by incremental or decremental feedback scores between noncontiguous trials. In the past, when assessing the timing of correct actions during skilled sequence performance, we also considered events that were preceded and followed by correct actions. This excluded effects such as post-error slowing from contaminating our results (Herrojo Ruiz et al., 2009, 2019). Therefore, we do not believe that any further reanalysis is required.

- Ruiz MH, Jabusch HC, Altenmüller E. Detecting wrong notes in advance: neuronal correlates of error monitoring in pianists. Cerebral cortex. 2009 Nov 1;19(11):2625-39.

- Bury G, García-Huéscar M, Bhattacharya J, Ruiz MH. Cardiac afferent activity modulates early neural signature of error detection during skilled performance. NeuroImage. 2019 Oct 1;199:704-17.

> *1. I have a serious concern with respect to how the sensitivity of sequence duration to reward is framed and analyzed. Since reward is proportional to performance, a reduction in reward essentially indicates a trial with poor performance, and thus even regression to the mean (along with a floor effect in performance [asymptote]) could explain the observed effects. It is possible that even occasional poor performance could lead to a participant demonstrating this effect, potentially regardless of the reward. Accordingly, the reduced improvement in performance following a reward decrease as a function of training length described in Figure 5b legend may reflect training-induced increased performance that leaves less room for improvement after poor trials, which are no longer as poor as before. To address this concern, controlling for performance (e.g., by taking into consideration the baseline MT for the previous trial) may be helpful. If the authors can conduct such an analysis and still show the observed effect, it would establish the validity of their findings."*

Thank you for raising this point. Figure 5b illustrates two distinct effects of reward changes on behavioral adaptation, which are expected based on previous research.

I. Practice effects: Firstly, we observe that as participants progress across bins of practice, the degree of improvement in behavior (reflected by faster movement time, MT) following a decrease in reward (ΔR−) diminishes, consistent with our expectations based on previous work. Conversely, we found that ΔMT does not change across bins of practices following an increase in reward (ΔR+). We appreciate the reviewer's suggestion regarding controlling for the reference movement time (MT) in the previous trial when examining the practice effect in the p(ΔT|ΔR−) and p(ΔT|ΔR+) distributions. In the revised manuscript, we will conduct the proposed control analysis to better understand whether the sensitivity of MT to score decrements changes across practice when normalising MT to the reference level on each trial. But see below for a preliminary control analysis.

II. Asymmetry of the effect of ΔR− and ΔR+ on performance: Figure 5b also depicts the distinct impact of score increments and decrements on behavioural changes. When aggregating data across practice bins, we consistently observed that the centre of the p(ΔT|ΔR−) distribution was smaller (more negative) than that of p(ΔT|ΔR+). This suggests that participants exhibited a greater acceleration following a drop in scores compared to a relative score increase, and this effect persisted throughout the practice sessions. Importantly, this enhanced sensitivity to losses or negative feedback (or relative drops in scores) aligns with previous research findings (Galea et al., 2015; Pekny et al., 2014; van Mastrigt et al., 2020).

We have conducted a preliminary control analysis to exclude the potential impact that reference movement time (MT) values could have on our analysis. We have assessed the asymmetry between behavioural responses to ΔR− and ΔR+ using the following analysis: We estimated the proportion of trials in which participants exhibited speed-up (ΔT < 0) or slow-down (ΔT > 0) behaviour following ΔR− and ΔR+ across different practice bins (bins 1 to 4). By discretising the series of behavioural changes (ΔT) into binary values (+1 for slowing down, -1 for speeding up), we can assess the type of changes (speed-up, slow-down) without the absolute ΔT or T values contributing to our results. We obtained several key findings:

• Consistent with expectations (sanity check), participants exhibited more instances of speeding up than slowing down across all reward conditions.

• Participants demonstrated a higher frequency of speeding up following ΔR− compared to ΔR+, and this asymmetry persisted throughout the practice sessions (greater proportion of -1 events than +1 events). 53% events were speed-up events in the in the p(ΔT|ΔR+) distribution for the first bin of practices, and 55% for the last bin. Regarding p(ΔT|ΔR-), there were 63% speed-up events throughout each bin of practices, with this proportion exhibiting no change over time.

• Accordingly, the asymmetry of reward changes on behavioural adaptations, as revealed by this analysis, remained consistent across the practice bins.

Thus, these preliminary findings provide an initial response to referee 2 and offer valuable insights into the asymmetrical effects of positive/negative reward changes on behavioural adaptations. We plan to include these results in the revised manuscript, as well as the full control analysis suggested by the referee. We will further expand upon their interpretation and implications.

> 1. *Another way to support the claim of reward change directionality effects on performance (rather than performance on performance), at least to some extent, would be to analyze the data from the last 10 days of the training, during which no rewards were given (pretending for analysis purposes that the reward was calculated and presented to participants). If the effect persists, it is less unlikely that the effect in question can be attributed to the reward dynamics.*

The reviewer's concern is addressed in the previous quesQon. Also, this analysis would not be possible because our Gaussian fit analyses use the Qme series of conQnuous reward scores, in which ΔR− or ΔR+ are embedded. These events cannot be analyzed once reward feedback is removed because we do not have behavioral events following ΔR− or ΔR+ anymore.

> 1. *This concern is also relevant and should be considered with respect to the sensitivity of IKI consistency (C) to reward. While the relationship between previous reward/performance and future performance in terms of C is of a different structure, the similar potential confounding effects could still be present.*

We will conduct this analysis for the revised manuscript, similarly to the control analysis suggested by referee 2 on MT. Our preliminary control analysis, as explained above, suggests that the fundamental asymmetry in the effect of ΔR+ and ΔR+ on behavioral changes persists when excluding the impact of reference performance values in our Gaussian fit analysis.

> 1. *Another related question (which is also of general interest) is whether the preferred app sequence (as indicated by the participants for Phase B) was consistently the one that yielded more reward? Was the continuous sequence the preferred one? This might tell something about the effectiveness of the reward in the task.*

We have now conducted this analysis. There is in fact no evidence to conclude that the continuously rewarded sequence was the preferred one. The result shows that 54.5% of HV and 29% of the OCD sample considered the continuous sequence to be their preferred one. Of note, this preference may not necessarily be linked to the trial-by-trial reward sensitive analysis. The latter assesses how learning may be affected by reward. The overall preference may be influenced by many other factors, such as, for example, the aesthetic appeal of particular combinations of finger movements.

> *Regarding both experiments 2 and 3:*

> 1. *The change in context in experiment 2 and 3 is substantial and include many different components. These changes should be mentioned in more detail in the Results section before describing the results of experiments 2 and 3.*

Following referee's advice, we will move these details (currently written in the Methods section) to the Results section, when we introduce Phase B and before describing the results of experiments 2 and 3.

> *Experiment 2:*
>
>> 1. *In Experiment 2, the authors sometimes refer to the "explicit preference task" as testing for habitual and goal-seeking sequences. However, I do not think there is any justification for interpreting it as such. The other framings used by the authors - testing whether trained action sequences gain intrinsic/rewarding properties or value, and preference for familiar versus novel action sequences - are more suitable and justified. In support of the point I raised here, assigning intrinsic rewarding properties to the learned sequences and thereby preferring these sequences can be conceptually aligned with goal-directed behavior just as much as it could be with habit.*

We clearly defined the theoretical framing of experiment 2 as a test of whether trained action sequences gain intrinsic value and we are pleased to hear that the referee agrees with this framing. If the referee is referring to the paragraph below (in the Discussion), we actually do acknowledge within this paragraph that a preference for the trained sequences can either be conceptually aligned with a habit OR a goal-directed behavior.

"On the other hand, we are describing here two potential sources of evidence in favor of enhanced habit formation in OCD. First, OCD patients show a bias towards the previously trained, apparently disadvantageous, action sequences. In terms of the discussion above, this could possibly be reinterpreted as a narrowing of goals in OCD (Robbins et al., 2019) underlying compulsive behavior, in favor of its intrinsic outcomes"

This narrowing of goals model of OCD refers to a hypothetically transiQonal stage of compulsion development driven by behavior having an abnormally strong, goal-directed nature, typically linked to specific values and concerns.

If the referee is referring to the penulQmate sentence of hypothesis secQon, this has been amended in response to Q5. We cannot find any other possible instances in this manuscript stating that experiment 2 is a test of habitual or goal-directed behavior.

> *Experiment 3:*
>
>> 1. *Similar to Experiment 2, I find the framing of arbitration between goal-directed/habitual behavior in Experiment 3 inadequate and unjustified. The results of the experiment suggest that participants were primarily goal-directed and there is no evidence to support the idea that this reevaluation led participants to switch from habitual to goal-directed behavior.*
>
> *Also, given the explicit choice of the sequence to perform participants had to make prior to performing it, it is reasonable to assume that this experiment mainly tested bias towards familiar sequence/stimulus and/or towards intrinsic reward associated with the sequence in value-based decision making.*

This comment is aligned with (and follows) the referee's criticism of experiment 1 not achieving automatic and habitual actions. We have addressed this matter above, in response 1 to Referee 2.

> *Mobile-app performance effect on symptomatology: exploratory analyses:*

> *1. Maybe it would be worth testing if the patients with improved symptomatology (that contribute some of their symptom improvement to the app) also chose to play more during the training stage.*

We have conducted analysis to address this relevant question. There is no correlation between the YBOCS score change and the number of total practices, meaning that the patients who improved symptomatology post training did not necessarily chose to play the app more during the training stage (rs = 0.25, p = 0.15). Additionally, we have statistically compared the improvers (patients with reduced YBOCS scores post-training) and the non-improvers (patients with unchanged or increased YBOCS scores post-training) in their number of app completed practices during the training phase and no differences were observed (U = 169, p = 0.19).

> *Discussion:*

> *1. Based on my earlier comments highlighting the inadequacy and mis-framing of the work in terms of habit and goal-directed behavior, I suggest that the discussion section be substantially revised to reflect these concerns.*

We do not agree that the work is either "inadequate or mis-framed" and will not therefore be substantially revising the Discussion. We will however clarify further the interpretation we have made and make explicit the alternative viewpoint of the referee. For example, we will retitle experiment 3 as "Re-evaluation of the learned action sequence: possible test of goal/habit arbitration" to acknowledge the referee's viewpoint as well as our own interpretation.

> *1. In the sentence "Nevertheless, OCD patients disadvantageously preferred the previously trained/familiar action sequence under certain conditions" the term "disadvantageously" is not necessarily accurate. While there was potentially more effort required, considering the possible presence of intrinsic reward and chunking, this preference may not necessarily be disadvantageous. Therefore, a more cautious and accurate phrasing that better reflects the associated results would be useful.*

We recognize that the term "disadvantageously" may be semantically ambiguous for some readers and therefore we will remove it.

> *Materials and Methods:*

> *1. The authors mention: "The novel sequence (in condition 3) was a 6-move sequence of similar complexity and difficulty as the app sequences, but only learned on the day, before starting this task (therefore, not overtrained)." - for the sake of completeness, more details on the pre-training done on that day would be useful.*

Details of the learning procedure of the novel sequence (in condition 3, experiment 3) will be provided in the methods of the revised version of the manuscript.

> *Minor comments:*

> *1. In the section discussing the sensitivity of sequence duration to reward, the authors state that they only analyzed continuous reward trials because "a larger number of trials in each subsample were available to fit the Gaussian distributions, due to feedback being provided on all trials." However, feedback was also provided on all trials in the variable reward condition, even though the reward was not necessarily aligned with participants' performance. Therefore, it may be beneficial to rephrase this statement for clarity.*

We will follow this referee's advice and will rephrase the sentence for clarity.

1. *With regard to experiment 2 (Preference for familiar versus novel action sequences) in the following statement "A positive correlation between COHS and the app sequence choice (Pearson r = 0.36, p = 0.005) further showed that those participants with greater habitual tendencies had a greater propensity to prefer the trained app sequence under this condition." I find the use of the word "further" here potentially misleading.*

The word "further" will be removed.