Internal Manipulation of Perceptual Representations in Human Flexible Cognition: A Computational Model

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Abstract

Executive functions represent a wide set of goal-directed cognitive processes that rely on integrated cortical-basal ganglia brain systems and are at the basis of human flexible behaviour. Several computational models have been proposed to study cognitive flexibility and the Wisconsin Card Sorting Test (WCST), an important neuropsychological test used for measuring such function. These models clarify important aspects of cognitive flexibility, in particular the processes concerning decision making, motor response, and feedback-dependent learning. However, several studies suggest that categorisation processes, as those involved in the solution of the WCST, also involve a fundamental category representation stage supporting the other processes. Surprisingly, all models of the WCST ignore such fundamental stage and propose that decision making directly triggers actions. Here we propose a novel hypothesis for which the key element of cognitive flexibility resides on the acquisition of suitable representations of percepts, and their top-down internal manipulation, to prepare effective actions. We also propose a neuro-inspired computational model to operationalise the hypothesis. The model is validated by systematically reproducing and interpreting the behaviour of healthy young and old adults, and of frontal and Parkinson pathological patients. The hypothesis and model also allow the proposal of a new version of the WCST that might be used to further investigate the important role of the internal manipulation of representations here proposed to be at the core of flexible goal-directed behaviour.

Keywords: Computational model, goal-directed behaviour, top-down representation manipulation, selective attention, cognitive flexibility.

1. Introduction

Executive functions are a set of high-order processes that allow the expression of flexible behaviour. Diamond (2013) describes executive functions as “a family of top-down mental processes needed when you have to concentrate and pay attention, when going on automatic or relying on instinct or intuition would be ill-advised, insufficient, or impossible”. This definition partially overlaps with the concept of *goal-directed behaviour* (GDB; Balleine and Dickinson, 1998; Daw et al., 2011; Berman et al., 1995; Mannella et al., 2013), referring to processes and mechanisms able to flexibly generate effective associations between perceptions and actions on the basis of goals. These contrast the processes underlying *habitual behaviour* (Yin and Knowlton, 2006; Gläscher et al., 2010) based on more direct and automatic associations between stimuli and responses.

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Here we focus on goal-directed processes that support *cognitive flexibility*, an executive function that allows the switching between different behavioural strategies depending on external and internal conditions. This executive function is commonly measured through the *Wisconsin Cards Sorting Test* (WCST), a neuropsychological test that exists in many forms for humans (Grant and Berg, 1948; Milner, 1963; Nelson, 1976; Heaton et al., 2000) and other species (Mansouri et al., 2006a; Brown and Bowman, 2002).

Several computational models, analysed in detail in Section 4, have been proposed to study cognitive flexibility and the WCST. These models focus on relevant issues concerning the WCST, such as its theoretical analysis (Dehaene and Changeux, 1991), its solution by psychiatric patients (Berdia and Metz, 1998), the variety of deficits it reveals (Kaplan et al., 2006), the neural working-memory dynamics involved in its solution (Rigotti et al., 2010), and the sequential learning processes it requires (Bishara et al., 2010; Ashby et al., 1998; Hélie et al., 2012). Other models focus on the brain mechanisms underlying the solution of the test, such as the selection processes relying on basal ganglia (Caso and Cooper, 2017) or the working memory processes relying on dopamine signals (Rougier et al., 2005; O'Reilly and Frank, 2006).

These models contribute to clarify relevant aspects of the goal-directed processes supporting the cognitive flexibility needed to solve the WCST, in particular they focus on the processes of decision-making, response selection, and feedback-dependent learning underlying the task solution. However, an extensive experimental and theoretical literature (e.g., Seger, 2008; Seger and Miller, 2010; Shankar and Kayser, 2017) suggests that categorisation tasks, of which the WCST is an instance, rely on multiple stages involving category representation, decision making, motor response, and feedback-dependent learning. Surprisingly, none of the current models of the WCST studies the early processes of learning and manipulation of categories notwithstanding the core aspect of the test requires the participants to flexibly switch the categories through which they process and react to the test stimuli.

In this work we face this problem by proposing three novel contributions that offer a new perspective on the processes supporting flexible cognition. The first contribution is the proposal of the hypothesis for which *the processes of top-down internal manipulation of representations, and their guidance of goal-directed embodied interactions with the environment, play a key role in flexible cognition*. This hypothesis builds on previous proposals on goal-directed selective attention processes (Miller and Cohen, 2001; Corbetta and Shulman, 2002; Gottlieb, 2007), claiming that goals drive the top-down selection of relevant parts of sensory input patterns, and on studies related to covert attention and imagination (Mechelli et al., 2004; Gazzaley and Nobre, 2012; Gazzaley et al., 2008; Kosslyn, 1999), claiming that the top-down activation of visual cortices can also support visual working memory and imagination processes in the absence of external stimuli. The hypothesis also linked to theories of *embodied cognition* that see cognitive processes and internal representations as strongly grounded on the interactions of the agents with the environment (Clark, 1997; Barsalou, 2008; Caligiore et al., 2010). Finally, the hypothesis is also driven by the recent progresses in machine learning that propose a parallelism between the internal functioning of *generative neural networks*, capable of producing ‘plausible’ images through internal processes (Hinton et al., 2006; Le Roux and Bengio, 2008; Hinton, 2012; Kingma and Welling, 2013; Goodfellow et al., 2014), and the interaction between frontal cortices and visual cortices in the brain considered above. Overall the hypothesis, described in detail in Section 2.2, attributes a fundamental role to the brain capacity of selecting categories and use them to internally re-code perceptual stimuli that then trigger the execution of suitable actions accomplishing the desired goals, for example to solve the WCST.

The second contribution is the proposal of a new computational model that operationalises the proposed hypothesis. The model includes some processes that are conceptually analogous to those used in previous models, in particular a mechanism for selecting the behavioural rule to follow and an error processing mechanism to correct such selection. However, the model also presents a fundamental novelty deriving from our hypothesis, namely a system that can manipulate internal representations for solving tasks such as the WCST. This system relies on three key components: (a) an *executive working memory* storing possible categorisation rules that are used to differentially interpret perceptual stimuli; (b) a *visual working memory* representing perceptual stimuli at different levels of abstraction; (c) an *internal manipulator* that selects the contents of the visual working memory on the basis of the categorisation rules stored in the executive working memory. The synergistic interaction between these components and sensorimotor processes allows the embodied model to interact with the environment and express flexible behaviour. This can lead to

the solution of the WCST based on the active switching of internal embodied representations of stimuli rather than of actions, as done by all previous models of the WCST. We validated the model proposed here by reproducing the data of different human groups who solved the WCST (early adults, old adults, frontal patients, and Parkinson’s patients). Moreover, we performed various ‘lesions’ of the model (based on the manipulation of key model parameters), reproducing specific alterations in the brain, to show the contribution of the different processes of the model to the production of different types of errors exhibited by humans performing the WCST.

The third contribution is a deeper study of the model core system performing the manipulation of the internal representations. In particular, we investigated how the visual working memory, biased by the executive working memory, might manage to maintain an internal representation of relevant object features during stimulus-response time delays during which the system perceives distracting stimuli. This allows the study of how the top-down bias on lower-level representations can counteract the disturbing effect of the distractors. Based on this latter study, we finally propose a new version of the WCST aimed to more directly test our hypothesis on the pivotal role played by the internal manipulation of representations for flexible goal-directed behaviour.

2. Methods

In this section we first illustrate the version of the WCST used here to test the model, then we present the architecture and functioning of the model, and finally we consider the techniques used to analyse the model.

2.1. The Wisconsin Card Sorting Test (WCST) and the brain processes involved in its solution

Materials and procedure. In the WCST (Figure 1, on top) the participants have to match a card drawn from a deck (called ‘response-card’ or ‘deck-card’) to one of four sample cards (called ‘stimulus-cards’ or ‘target-cards’).

Figure 1: A schema of the typical elements of the Wisconsin Card Sorting Test. Bottom: a schema of the sequence of cognitive processes required to pass a single trial of WCST

Each card contains coloured items having a unique combination of features. These features are differentiated in three categories, each involving four attributes: (1) colour: red, green, blue, or yellow; (2) form: stars, triangles, circles, or crosses; (3) number: one, two, three, or four elements. The participant is requested to bring the deck card close to one of the target cards by trying to match them in terms of either

the colour, form, or number. A first key element of the test is that the correct rule for matching the cards is not told to the participant: after each action, an operator furnishes a ‘correct’ or ‘incorrect’ feedback based on the current matching rule and on this basis the participant has to infer the correct rule. A second key challenge of the test, probing in particular cognitive flexibility, is that the correct matching rule changes after a certain number of uninterrupted correct actions, so the participant has to search and switch to the new rule based on the sole information from the feedback. To pass the test the participant has to complete a certain number of uninterrupted card sequences each involving a different rule.

There are many versions of the WCST differing in the test procedure or the performance score. We used the Heaton’s version of the test (Heaton et al., 2000) having these specific features: (a) participants can use up to two decks of 64 cards; (b) completing a category set requires ten correct matches in sequence; (c) after completion of a category set the sorting rule changes without the participant being told; (d) to pass the test the participant has to complete a series involving six different correct matching rules: colour, form, number, colour, form, number; (e) if the participant uses both decks without completing the series of categories, the test is considered ‘failed’.

The WCST is similar to another test, the *match-to-sample task*, used to probe working memory (e.g., Smeets et al., 2000; Sidener and Michael, 2006). The classic match-to-sample task requires to remember a cue on the basis of which the participant has to select, after a short time delay, one of two items where only one of the two is equal or related to the cue. Also the WCST puts a strong demand on working memory but in addition it also requires to actively manipulate its contents, in particular the information related to the possible correct matching rule to use next.

The WCST also involves many processes shared with classical categorisation tasks, in which a participant has to classify an input respect a specific rule (e.g., Seger and Miller, 2010). Differently from categorisation tasks, in the WCST the categorisation rule dynamically changes based on both the participant’s actions and a prefixed order, and this requires a higher cognitive load.

Scoring and types of errors. For the test scoring we followed the official documentation of the test (Heaton et al., 2000), in particular we used five principal indices giving a full profile of the participants’ performance (see the documentation for a thorough explanation of the indices):

- *Completed Categories (CC)*: this index, ranging in (0, 6), indicates the number of successfully completed categories; the index scores the global performance.
- *Total Errors (TE)*: total incorrect responses, including both PE and NPE (see below); this index scores the level of global deficit.
- *Perseverative Errors (PE)*: cards sorted with the same incorrect rule after a negative feedback error; the index indicates a perseverative behaviour.
- *Non Perseverative Errors (NPE)*: errors not included in PE; these errors occur in different situations and they could suggest an attentional failure or an incorrect inferential reasoning.
- *Failure to Maintain Set (FMS)*: whatever errors occurring after five consecutive correct matches.

Neural correlates of the behaviour exhibited during the WCST solution. The model we present here is biologically inspired in that it reproduces some important functions and mechanisms commonly ascribed to relevant brain systems. This section briefly mentions the literature we considered to design the model. Notice that for its scope, focused on the system-level operationalisation of the internal representation manipulation hypothesis, the model reproduces the relevant functions and lesions of the brain areas discussed here mostly at a functional level, in particular without reproducing the specific features of the underlying anatomy and physiology of the brain.

The literature proposes various partially-overlapping interpretations on the neural correlates of the behaviour exhibited by WCST participants. Figure 2 represents both a schematic brain overview of highly activated areas during the WCST, and lesions sites related to specific errors occurring during the test. To build the diagram, we analysed the works reported in the meta-review of Nyhus and Barcelò (2009), focusing

in particular on data having a spatial resolution at the level of specific cortical areas for the activations and the indication of the specific sites of the lesions (Table S1 in Supplementary Materials illustrates the specific lesions considered and the literature supporting them).

Figure 2: Left: The brain areas that are highly active during the WCST performance. The colour and size of circles indicates the number of papers we considered that found a specific activation site (small/green: < 3 ; large/orange ≥ 3). Right: Sites of lesions that cause specific errors during the WCST. The colour intensity of the bolt arrows suggests the specificity of lesions (transparent: distributed lesions; dark: focused lesions). For both graphs, see Table S1 in Supplementary Materials for the literature supporting this overview.

This analysis indicates that the brain areas that are highly involved in the WCST performance are the fronto-parietal cortices, supporting goal-directed perception and attention (Vossel et al., 2014; Parks and Madden, 2013), sub-cortical structures (in particular basal ganglia), supporting the processing of reward (Yin et al., 2008), frontal structures such as the orbital cortex and the ventro-medial prefrontal cortex, supporting emotional processing, and the anterior cingulate cortex, supporting error detection (Stuss et al., 2000; Zald and Andreotti, 2010). Several studies (e.g., Goldman-Rakic, 1996; Hoffmann, 2013) indicate that these frontal, parietal and sub-cortical systems form an integrated network of systems underpinning cognitive flexibility and other executive cognitive functions.

Figure 2 also summarises the relation between errors occurring during the WCST performance and different lesion sites. In this respect, coherently with the functional interpretation of the active areas seen in healthy participants and discussed above, the neuropsychological literature highlights: (a) a correlation between perseverative errors and both sub-cortical and medial cortex impaired sites; (b) a correlation between most types of errors and superior frontal lesion sites. In particular, PE are considered an indicator of flexibility impairment related to the incapacity to change a behavioural rule that has been successful up to a certain time (e.g., Dehaene and Changeux, 1991; Nelson, 1976). Alongside these classical interpretations focused on PE, some studies articulate the meaning of the NPE and FMS errors. Among these, Li (2004) suggests that NPE are related to attentional or reasoning failures, while Barceló and Knight (2002) link them to attention and working memory dysfunctions. Figueroa and Youmans (2013) focus on FMS errors suggesting that they reflect distractibility rather than a cognitive flexibility deficit.

2.2. A three-component hypothesis on the flexible manipulation of internal representations

In this section we propose a theoretical hypothesis of the brain internal manipulation of perceptual representations underlying the solution of the WCST. The top-down modulation of the activation of internal representations is a brain mechanism based on the application of an activation bias to information flows exchanged by cortex (Cisek and Kalaska, 2010). Many studies (e.g., Kosslyn, 1999; Mechelli et al., 2004; Gazzaley and Nobre, 2012; Fuster and Bressler, 2015; Baldauf and Desimone, 2014) suggest that this mechanism supports the extraction of external input features, the top-down biased selection of relevant information (selective attention), the internal persistent maintenance of information in the absence of external input (imagination) for example related to goals and anticipated action outcomes. We propose that all these processes rely on the interplay of three fundamental systems (Figure 3; cf. Wolters and Raffone, 2008; Miller and Cohen, 2001; Fuster and Bressler, 2015; Baldassarre et al., 2013; Corbetta and Shulman, 2002; Gottlieb, 2007): (a) a system storing goals and behavioural rules; (b) a system extracting and storing perceptual representations; (c) a system manipulating perceptual representations on the basis of goals and behavioural rules. We now consider the interplay of these three systems, operationalised in the computational model, and for concreteness we exemplify how they might work while performing the WCST.

Figure 3: Schema showing the three-component hypothesis supporting the internal manipulation of representations. The colour gradient (red to blue) indicates a gradual change of computational functions from those encoding goals and behavioural rules (red; fronto-striatal areas) to those encoding percepts (blue; dorso-caudal areas).

The more abstract amodal *executive working memory* (Hartley and Speer, 2000; Braver and Bongiolatti, 2002), relying on fronto-striatal networks, selects and stores, on the basis of motivational drives, the overall goal to pursue (e.g., obtaining a positive feedback in the WCST) and the possible sub-goals to accomplish it (e.g., the behavioural rules linked to the card features to match). Such high-level goals and sub-goals are encoded as perceptual representations resulting from the abstraction processes of perceptual cortical hierarchies.

The *fronto-parietal cortical system*, based on perceptual attentional processes (Vossel et al., 2014; Parks and Madden, 2013) supported by basal-ganglia selection mechanisms (Redgrave et al., 1999; Seger, 2008; Chelazzi et al., 2013; Pessoa, 2015), furnishes a top-down bias to the lower-level competition processes taking place within sensory cortices. This bias is driven by the behavioural rules stored in the executive working memory and is led by them to support the selection of alternative contents within the perceptual cortical system (e.g., the colour rather than the shape of the elements in the card).

The *perceptual cortical system* transmits sensory information to the higher-level cognitive systems. This perceptual system (Rizzolatti and Matelli, 2003; Gazzaley and Nobre, 2012), excited by the top-down biases, also implements a perceptual working memory storing input selected features. In particular, the top-down

bias leads the system to encode in a stronger way perceptual representations that are relevant to accomplish the pursued goal (e.g., specific features of cards based on different possible card sorting rules).

Figure 4 highlights how the three systems encompassed by the hypothesis interplay to support the processes underlying the solution of the WCST. In particular, it shows how the sub-goals (behavioural rules linked to specific categories) stored in executive working memory fuel a selection process that leads to choosing specific contents of the perceptual working memory. Under this bias, the perceptual working memory generates a representation of the deck card suitable to compare it with a target card with respect to the chosen category, and thus to guide downstream motor processes.

Our hypothesis and model agree with empirical evidence on the brain macro architecture showing how prefrontal cortex is strongly connected with parietal cortex as much as, or even more, than with motor areas; the parietal cortex in turn exerts a strong control on motor areas (Rizzolatti and Craighero, 2004; Passingham and Wise, 2012). Functionally, the parietal cortex plays a key role in controlling action on the basis of the representation of the features of objects, such as their position and size, relevant to interact with them (Jeannerod et al., 1995; Thill et al., 2013): these representations are thus said to encode *affordances* (Gibson, 1979; Norman, 1988; an action affordance can be intended as an agent’s activated internal representation of the preconditions necessary for the successful accomplishment of the action, Fagg and Arbib, 1998; Thill et al., 2013; Baldassarre et al., 2019). Our proposal contrasts the hypothesis, summarised in Figure 4, that emerges from previous models of the WCST. According to these models, the high-level selection of the category rule directly biases the selection of the motor responses rather than the lower-level perceptual representations.

Figure 4: Top: Key elements of the hypothesis proposed here on the processes that might underlie flexible cognition and the solution of the WCST. Bottom: Hypothesis that emerges from other models of the WCST.

2.3. Overview of the functioning of the model components and their biological underpinnings

This section illustrates the architecture of the model, in particular the functioning of its components, the information flow between them, and their biological underpinnings. The model architecture operationalises the three-fold hypothesis related to the manipulation of perceptual representations illustrated in the previous section, and also encompasses auxiliary components needed to have an agent able to interact with the environment and form realistic representations of the cards. The model architecture and components are summarised in Figure 5 and are now explained in detail.

Figure 5: A schema of the model components and functions, the flows of information between the components, and the interaction loops the agent engages with the environment (red: attentional loop; green: object-displacement loop; blue: feedback-manipulation loop).

Visual sensor. This component corresponds to the eye retina. The sensor is actuated and so that it can focus on one card at a time (see below). The sensor returns a visual image of the cards: the sensor is large enough so that a focused card wholly falls within its scope.

Perceptual component. This component is a layered neural network performing a bottom-up processing of the visual images analogously to what happens in the human perceptual system involving striate and extra-striate visual cortices. The component reflects the hierarchical nature of these cortices involving many levels of information processing, from the low-level retinotopic visual processing of features in striate cortex (V1), to the processing of higher-level image proprieties (shape, colour, etc.) in extra-striate cortices (V2 to V5) and different areas of infero-temporal and parietal cortex (DeYoe et al., 1996; Rizzolatti and Matelli, 2003; Konen and Kastner, 2008). The component also implements a perceptual working-memory, storing the features extracted from perceptual stimuli, that in the brain is supported by modal sensory cortices (Gazzaley and Nobre, 2012; Raffone et al., 2014).

Reward/motivation component. This component processes the input to compute the system’s internal reward signals and gives a motivational bias to the working memory processes. In brain, these processes rely on ventral basal ganglia (Humphries and Prescott, 2010; Mannella et al., 2013), the ventro-medial PFC, and the ventral ACC (Gläscher et al., 2008, 2012).

Executive working-memory. This component reproduces the functions of executive/abstract working memory, in particular it stores the possible sub-goals corresponding to the possible card matching rules. Executive working memory is supported by brain systems such as the dorsal-lateral portions of PFC that can store information on goals and behavioural strategies through recurrent circuits (Hartley and Speer, 2000; Braver and Bongiolatti, 2002; Barraclough et al., 2004), and can select them based on lateral inhibition mechanisms (Aron, 2007). As in brain working memory (Brunel and Wang, 2001; Gruber et al., 2006), the model working memory component implements these key processes (cf. Frank et al., 2001; O’Reilly and Frank, 2006): (a) the active maintenance of sub-goals in the absence of the perception of the corresponding stimuli; (b) the release (forgetting) of such information when it is no more relevant.

Perceptual manipulator. This component supports two processes. The first process involves the decision of the behavioural rules depending on the activation of the executive working-memory. This process mimics the role of the dorsal ACC in affective decision making (Bush et al., 2002; Heilbronner and Hayden, 2016). The second process involves the performance of the actual top-down manipulation of the perceptual contents of the perceptual system. The manipulation is based on a disinhibition mechanism that reproduces a main feature of the functioning of basal ganglia (Redgrave et al., 1999; Mannella and Baldassarre, 2015). This mechanism inhibits all internal representations activated by the bottom-up sensory information with the exception of the one that corresponds to the card matching rule to follow. In this way, only the colour or form or size features are used to compare the deck and target cards. The manipulator also employs a local selection process to enhance the activation of specific features seen in the stimuli and in agreement with the top-down bias (e.g., to select ‘red’ if the chosen behavioural rule is ‘colour’). This process mimics the top-down modulation of the high-level cortices exerted on the lower sensory cortices via the fronto-parietal cortical system (Gazzaley and Nobre, 2012; Vossel et al., 2014; Parks and Madden, 2013).

Visual comparator. This component compares the deck card and the foveated target card and returns their level of similarity (‘visual matching’). This component is inspired by findings related to same/not-same tasks (Perani et al., 1999) that have been shown to rely on the interplay between occipital/temporal cortices and dlPFC.

Motor components. A first motor component moves the visual sensor to scan the different target cards to search the one that matches the deck card based on the selected matching rule. This last mechanism guides the gaze in a top-down manner based on the visual comparator output: when there is not a visual match, this mechanism triggers a saccade that shifts the fovea to the following target card; when a match is found, the mechanism stops the gaze on the current target card and releases the arm action. When this happens, a second motor component controls a simulated manipulator that moves the deck card close to the selected target card as requested by the WCST. Note that here it is assumed that these attentional scanning and object-moving behaviours are acquired before the solution of the WCST and triggered by the top-down processes.

Bottom-up perceptual processes and top-down attentional processes. The model implements bottom-up and top-down information flows respectively corresponding to perception and attention processes (Intaité et al., 2013; Dijkstra et al., 2017). Perception involves the bottom-up transmission and progressive abstraction of visual information from the retina to higher cortical levels. Attention and imagination involve a top-down information flow through which brain frontal areas can activate or bias peripheral perceptual areas so that they tend to have a stronger activation in correspondence to relevant external stimuli (attention; Mechelli et al., 2004) or even to activate in the absence of them (imagination; Kosslyn, 1999). In the model, the selection of a specific matching rule within the working memory, and the consequent disinhibition of a certain attribute representation, starts a top-down activation flow that leads to generate images, at the lower levels of the perceptual component, that correspond to the selected attribute. The model uses this processes to ‘filter’ the input images of the deck card and of the target card under focus in order to compare them with respect to the current matching rule (i.e., either colour, shape, or size).

A relevant feature of the model is that it compares the deck and target cards at the low perceptual level. This comparison could have been performed on the basis of the high-level representations of cards, for example at the last layer of the perceptual component. As discussed in Section 2.2, the comparison taking place at the low-level mimics the brain functioning. Moreover, it might also have these computational advantages: (a) the possibility of exploiting the detailed information coming from the sensors, suitably selected by the top-down processes, to carry out operations that depend on it (e.g., operations that depend on the detailed shape of objects; Mechelli et al., 2004; Wolters and Raffone, 2008); (b) the possibility of using high-level abstract representations to generate lower-level detailed representations through information gathered ‘along the way’ from the intermediate representation levels; this more detailed information can then be useful to support processes needing it, for example fine-level comparisons (Gazzaley et al., 2008; Barcelo et al., 2000; Mangun, 1995; Woldorff et al., 1997).

Interaction loops. The functioning of the model involves three interaction loops with the environment (Figure 5) and these lead the model to perceive visual stimuli (images) having a substantial level of realism. A first ‘attentional loop’ involves the motion of the visual sensor, the processing of the image by the perceptual component, and the visual comparison of the deck card with the focused target card. A second ‘object-displacement loop’ involves the motor system displacing the objects and affecting the following visual perception. The third ‘feedback-manipulation loop’, the more complex and indirect of the three loops, processes the feedback to produce reward, uses it to update the relevance of the matching rule stored in the executive working-memory, and then selects a category representation. On this basis, the loop exerts a top-down bias on the operation of the other two loops.

These loops, involving circular interactions between the system components and the environment, give the model some elements of *embodiment* in that its actions affect its sensory input and internal representations, and this aspects enter the solutions found for solving the task (Nolfi and Floreano, 2000). Although representing a simplified form of embodiment, the loops capture the essence of the sensorimotor interactions involved in the solution of the WCST and are sufficient for the study of the top-down perceptual manipulation mechanism proposed here. At the same time, these elements are relevant to study the links between embodiment and flexible cognition, for example the model stops scanning of the target cards when it finds one that matches the deck card according to the selected behaviour rule: this triggers the action and the consequent feedback retroacting on the behaviour of the model.

2.4. Computational details of the model

This section explains the key computational features of the model, summarised in Figure 6. Further details and equations on the model functioning and learning are presented in the Supplementary Materials. The code of the model will be made available online in GitHub for public download in case of publication.

Algorithm 1 overviews the information flowing between the model components, the computations they perform, and the interactions of the model with the environment. The algorithm involves a first cycle (line

Algorithm 1 Model: Information flows, computations, and interaction loops with the environment.

```

1: for deckCard  $\in \{1, 2, \dots, 64\}$  do
2:   (deckCardImage, deckCardPosition)  $\leftarrow$  VisionComponentScan(deckCard)
3:   attributePreactivation  $\leftarrow$  DBNForwardSpreading(deckCardImage)
4:   category  $\leftarrow$  SoftMax(workingMemory)
5:   attribute  $\leftarrow$  DisinhibitionOfCategoryAttributes(attributePreactivation, category)
6:   reconstructedDeckCard  $\leftarrow$  DBNGeneration(attribute)
7:   match  $\leftarrow$  False
8:   for targetCard  $\in \{1, 2, 3, 4\}$  AND match = False do
9:     (targetCardImage, targetCardPosition)  $\leftarrow$  VisualComponentScan(targetCard)
10:    attributePreactivation  $\leftarrow$  DBNForwardSpreading(targetCardImage)
11:    attribute  $\leftarrow$  DisinhibitionOfCategoryAttributes(attributePreactivation, category)
12:    reconstructedTargCard  $\leftarrow$  DBNGeneration(attribute)
13:    match  $\leftarrow$  VisualComparison(reconstructedTargCard, reconstructedDeckCard)
14:  MotorComponentMoveDeckCard(targetCardPosition, deckCardPosition)
15:  feedback  $\leftarrow$  GetFeedback()
16:  UpdateWorking(feedback)

```

1) corresponding to the cards drawn from the deck. The system visually scans the drawn deck card (line 2) and then processes its features corresponding to the currently selected matching rule, stored in the working memory, and memorises them for later use (lines 3-6; a non-neural memory is used to this purpose). A second nested cycle allows the model to visually scan the target cards in sequence (line 8): for each target card the model reconstructs its features corresponding to the currently selected matching rule (lines 9-12) and then compares them with those of the deck card stored in memory (line 13). When a target card matches the deck card, the model stops scanning the target cards, moves the former below the last scanned

target card (line 14), and collects the corresponding feedback (line 15). Lastly, the model uses the feedback to update the working memory (lines 16).

Environment. The agent acts in a simulated environment formed by a squared space of 100×100 pixels. The environment contains ‘objects’ that the model can visually explore and move in space (see Figure 6). Objects are here cards representing polygons each characterised by a unique combination of three visual properties, each having one of four possible attributes: colour (red, green, blue, yellow), form (square, circle, triangle, bar), size (large, medium-large, medium-small, small). This set of attributes generates $4^3 = 64$ combinations (cards). With respect to the original task, we substituted the ‘number’ category with the ‘size’ category as different number of objects required a higher resolution to be perceived and this slowed too much the simulations. For the same reason, we also substituted the form attributes ‘stars’ and ‘crosses’ with the attributes ‘squares’ and ‘bars’. These changes did not alter the behaviour of the model and the comparisons with human behaviour.

Visual sensor. The visual sensor returns a 28×28 pixel RGB image covering a limited portion of the environment. The resulting $28 \times 28 \times 3$ matrix is stored into a vector of 2,352 elements that represents the input to the perceptual component. The visual sensor is displaced by the top-down processes (saccades). In particular, the sensor is first directed towards the deck-card and then is directed towards the target cards whom it scans in sequence until it finds a target card that matches the deck-card.

Perceptual component. This component is implemented as a deep generative model, in particular a *Deep Belief Network* (DBN; Hinton et al., 2006; Le Roux and Bengio, 2008) composed of two stacked *Restricted Boltzmann Machines* (RBM; Hinton, 2012). The main features of the component are considered here while a detailed description of its functioning and learning processes are presented in detail in the Supplementary Materials. A RBM is formed by two layers of units, a ‘visible’ layer, and a ‘hidden’ layer, linked by fully connected connections. A distinctive feature of RBM networks, and hence of the DBN, is that information can flow in both a bottom-up and a top-down fashion within it. While the bottom-up flow of the network –from the visible layer to the hidden layer– causes a dimensionality reduction of the input pattern (Hinton and Salakhutdinov, 2006), the top-down flow –from the hidden layer to the visible layer– produces a visible input. The capacity of the network to use an activation of the last hidden layer to produce, through a top-down information flow, the possible input that corresponds to such activation is an important property called *generativity* (Bengio et al., 2017). This component was trained off-line through a novel algorithm (see Supplementary Materials) that allows the model to both extract the specific attributes of each card and to represent them in a distributed form. This allows the model to use generativity to simulate top-down attention processes. For example (Figure 6) if a ‘large, red, triangle’ deck-card and a ‘medium-large, red, square’ target card are perceived, and the category selected at the higher levels is ‘colour’, the model can produce the activation of a red blob at the lower levels, for each card in sequence, and decide that the two cards match. In Section 3.3 we show that the bidirectional activation of the component involving the bottom-up abstraction and the top-down reconstruction can be repeated many times to simulate the activity reverberations of the visual working-memory and study a possible loss of information in the presence of interfering distractors if stimulus-response delays are introduced. Considering that in the WCST the participants can freely look at both the deck card and the table cards as many time as desired, we assume there is no loss of information to perform the visual matching process and we so fixed the number of repetitions to one (i.e. a single bottom-up activation spreading followed by a single top-down reconstruction).

Executive working-memory. The perceptual component is formed by three units encoding the three matching rules (colour, form, and size). The activation of each unit encodes the likelihood that the corresponding behavioural rule is selected. The units have in particular a continuous value ranging from 0 (low chance) to 1 (high chance) and store a sustained representation of the possible matching rules to use on the basis of a recurrent self-connection. The activation is fuelled by the feedback signal taking a binary value in $\{0, 1\}$. The feedback signal affects only the activation of the unit encoding the last selected and used rule as follows:

$$m_{s,t} = (1 - \mu) \cdot m_{s,t-1} + \mu \cdot r \quad (1)$$

Figure 6: The architecture of the model highlighting the deep belief network for perception, the disinhibition mechanism for rule selection, and the rule values and softmax for the matching-rule selection. The figure shows a stimulus of the WCST at the bottom right: here the little square frames around the red triangle and the red square represent two 100×100 pixel images corresponding to a deck card and a target card collected by the system visual sensor in succeeding steps. The two analogous squared frames around the two red circles under the ‘visual comparator’ are the images resulting from the fact that the high-levels of the model are focusing on the category ‘colour’ and the attribute ‘red’ for comparing the two input cards.

where $m_{s,t}$ is the new activation of the rule unit, $s \in \{1, 2, 3\}$ is the index of the selected rule, $m_{s,t-1}$ is the previous activation of the unit, $(1 - \mu)$ is the strength of the unit recurrent connection, μ regulates the impact of the feedback on the memory, and r is the feedback signal that is equal to 1 in case of positive feedback (matching of the deck and target cards) and 0 otherwise. The parameter μ is set to a fixed value of 0.7 for positive feedback and to variable values for the negative feedback as the literature shows that this is a critical aspect for behavioural disengagement in the WCST (Monchi et al., 2004; Zanolie et al., 2008). Such negative value of the parameter μ is in particular the first of the three key model parameters investigated in the simulations reported here.

All the working-memory non-winning units decay exponentially towards a baseline value as follows:

$$m_{l,t} = (1 - \phi) \cdot m_{l,t-1} + \phi \cdot \alpha \quad (2)$$

where $m_{l,t}$ is the value related to the losing unit l ($l \in \{1, 2, 3\}; l \neq s$) at time t , $1 - \phi$ is the strength of the recurrent connection, and α (set to 0.5) is the baseline value to which the memory unit activation converges. A high value of ϕ causes a high rate of information forgetting. The parameter ϕ is the second of the three key model parameters investigated here.

Perceptual manipulator. This component implements three processes. The first process is a winner-take-all (WTA) competition that receives the values from the working memory as input, and chooses the matching rule on the basis of a *softmax* function:

$$Pr(k = s) = \frac{\exp(m_k / \tau)}{\sum_{q=1}^3 \exp(m_q / \tau)} \quad (3)$$

where $Pr(k = s)$ is the probability that the event that the matching rule k ($k \in \{1, 2, 3\}$) is the one selected ($k = s$), τ is the ‘temperature parameter’ of the *softmax* function regulating the randomness of the selection. A high value of τ causes a high randomness/exploration of the behavioural rules. The parameter τ is the

third of the three key model parameters investigated here. The probabilities $Pr(\cdot)$, summing up to 1, are used to stochastically select the matching rule to use. The second process leads the winner unit of the WTA competition to disinhibit, through a double inhibition mechanism, the units of the last DBN hidden layer corresponding to the chosen category. The third process is a localistic winner-take-all mechanism (LWTA; Srivastava et al., 2013), involving the units encoding the attributes of each category group, that is applied to the last DBN hidden layer before the disinhibition. Through this process, the unit having the maximum sigmoid activation (e.g. encoding ‘red’) is assigned an activation of 1, whereas the other units (e.g. encoding blue, green, and yellow) are assigned an activation of 0. This for example allows the activation of the attribute ‘red’ within the category ‘colour’.

Visual comparator. This component computes the Euclidean distance between the two reconstructed images of the deck card and of the focused target card. Using a fixed threshold β ($\beta = 0.1$), the component returns a Boolean value representing the result of the comparison (‘match’/‘not match’). This process is an abstraction of neural comparison processes (e.g., see Santucci et al., 2016).

Motor component. This component encompasses two mechanisms. The first mechanism receives the position of the deck and target cards and brings the visual sensor (saccades) on them in a sequential manner. This captures the essence of more sophisticated attentional mechanisms that the model could use in future work, for example a bottom-up attention mechanism based on image salient areas or an inhibition-of-return mechanism (Klein, 2000), used in a previous paper (Baldassarre et al., 2019).

The second mechanism of the motor component receives the position of the deck card and of the matched target card, and performs a movement bringing the deck card close to the matched target card. This action, here hard coded, is assumed to be learned by the system before the test (see Baldassarre et al., 2019).

2.5. Techniques used to analyse the model

We briefly mention here the techniques used to validate the model and analyse its behaviour and we expand their description in Supplementary Materials. The three key parameters of the model were searched through a brute-force search algorithms (Van Geit et al., 2008). The large number of models tested with this technique also allowed the performance of a *sensitivity analysis* of the found parameters (Hamby, 1994), in particular to investigate how the variation of the best-fitting parameters affected the model accuracy. We also performed focused extreme alterations of the model key parameters, with respect to their ideal values, to mimic some of the brain impairments reviewed in Section 2.1. Finally, we computationally investigated the model core mechanism supporting the internal manipulation of representations by performing tests where the RBM visual working memory component reverberates to store information during stimulus-response delays in the presence of distractors.

3. Results

We organise the presentation of the results in three parts. In the first part we validate the model by showing how it can reproduce the behaviour of healthy and pathological humans in the WCST, and how it can furnish a sound interpretation of the possible brain processes underlying human behaviours and errors exhibited in the test performance. In the second part, we further validate the model by exploring the relation existing between the model behaviour and its key parameters. In particular, we show the results of a correlation analysis further investigating the link between the model parameters and the behavioural indices exhibited by humans in the WCST solution, and present the results of a ‘lesion’ experiment in which the key model parameters are altered by setting them to extreme values. Third, we analyse the internal functioning of the three key elements of the model mechanism for the internal manipulation of representations, highlighting its key role for the production of flexible behaviour. The behaviour, the ‘reasoning processes’, and the ‘internal representations’ of the model can be seen in action in this video: <https://youtu.be/pnBWWqhULsE>

3.1. Validation of the model with human data

3.1.1. Model configurations that best fit the data from healthy and pathological humans

Table 1 shows the values of the model key parameters found with the automatic search method (μ : sensitivity to negative feedback errors; ϕ : working-memory forgetting speed; τ : exploration/distractibility) that best fit the target data. The ‘pathological model’ having parameters that best fit the data related to frontal patients from (Heaton et al., 2000) shows a lower μ , a higher ϕ , and a similar τ compared to the ‘healthy model’ that best fit the control participants from (Heaton et al., 2000). This suggests that frontal patients: (a) are less flexible to adapt their behaviour after a negative feedback (μ); and (b) have a lower capacity to remember and reason about the behaviour to undertake based on experience (ϕ). These results agree with the literature proposing that frontal patients exhibit a mix of deficits involving the tendency to not consider contrary environmental feedback, and hence to persevere in non adaptive behaviours, and also to have a poor executive functioning involving working memory, behaviour monitoring, and reasoning (e.g., see Barceló, 1999).

Considering the data on Parkinson participants and the related control group Paolo et al. (1995), a first remarkable element emerging from Table 1, showing the parameters of the model that best fit the data, is that control participants have memory forgetting speed (ϕ) similar to the one of the frontal patient group of Heaton et al. (2000). This has an interesting explanation captured by the model: the frontal patient group had an average age of 42 ± 14.32 years whereas the Parkinson control group had an average age of 69.74 ± 6.96 years, so this latter group was probably affected by an aged-related weakening of the working memory (Daselaar et al., 2013). The parameters of the model that best fit the Parkinson data show a lower sensitivity to negative feedback (μ) with respect to the paired control group. This might be related to their altered capacity to process reward and feedback, a hallmark feature of the disease (deficits of the dopamine system also involve the capacity to process negative outcomes, aside positive ones, possibly due to the difficulty of processing reward prediction errors; Volpato et al., 2016). The comparison also shows a higher distractibility (τ). This might be related to the Parkinson participants’ lower capacity to ‘lock-in’ on correct behaviours once found, a relevant function of the dopamine system (Fiore et al., 2014). Unexpectedly, the comparison also shows a low working-memory forgetting (ϕ), even if still higher than the one of younger healthy participants from the study of Heaton et al. (2000). This could be due to the effect of Parkinson treatments on the executive role of working memory that contributes to decision making, possibly affecting the reasoning-by-exclusion process involved in the WCST performance (Fallon et al., 2017).

	Error sensitivity (μ)	Forgetting speed (ϕ)	Distract- ibility (τ)
Healthy participants	0.26	0.26	0.14
Frontal patients	0.05	0.47	0.14
Parkinson healthy participants	0.16	0.47	0.14
Parkinson patients	0.05	0.37	0.17

Table 1: Values of the parameters of the models that best fit the target WCST data related to the behavioural indices of healthy participants and frontal patients (data from Heaton et al., 2000), and of Parkinson controls and patients (data from Paolo et al., 1995).

The parameter search technique also allowed us to perform an analysis probing how the model fitting accuracy responds to the systematic variation of the three key model parameters. The results of such analysis for the frontal patients and the related healthy controls from Heaton et al. (2000), presented in detail in Supplementary Materials, indicate that: (a) healthy participants can be characterised by multiple alternative values of distractibility and sensitivity to choice errors where the two compensate (e.g., a high distractibility goes with a high error sensitivity) and a variable forgetting rate; (b) instead, frontal patients tend to feature a stable low reactivity to errors and a medium distractibility, while again being robust to variable distractibility. These results further validate the model capacity of furnishing an integrated interpretation of the target data.

3.1.2. WCST indices of the healthy and pathological models and corresponding human groups

In this section we further validate the model by showing the accuracy with which the model versions having the parameter configurations discussed in the previous section accurately reproduces the multiple behavioural indexes exhibited by the corresponding groups of human participants. For each model parameter set (human group), we compared 59 simulated participants (which differed for having different seeds of the random number generator) with the 59 frontal participants, and other 59 simulated participants with the 362 healthy participants, considered in Heaton et al. (2000). Figure 7 shows the average values of the indices of the healthy humans and of the model, while Figure 8 shows an analogous comparison for frontal patients. The comparisons show that the model reproduces with high accuracy the values of the WCST indexes of all the human groups considered. Table 2 presents the p-values of a statistical comparison between the behavioural indices of the models and those of the human groups. The indices are non statistically different ($p > 0.05$) with the exception of: CC, which is higher in the two models with respect to the human participants (healthy human versus healthy model: 5.18 ± 1.52 vs 5.9 ± 0.4 , $p < .01$; pathological human versus pathological model: 3.46 ± 2.25 vs 4.6 ± 1.0 , $p < .01$), and FMS, which is higher in the healthy model with respect to the humans (1.4 ± 1.3 versus 0.67 ± 1.09 , $p < .01$). These differences are due to the very low variability of the model behaviour (see standard deviation in the figures) that causes a statistical disproportionate weight of small mean differences. Such lower variability of the model data is caused by the lower noise of its processes with respect to those of the human brain that can accomplish several functions and thus exhibits a higher variability in the WCST solution.

Regarding the experiments related to the Parkinson patients and the paired healthy control group reported in Paolo et al. (1995), most WCST indices of the model are non statistically different from those of the human groups. Again a statistical difference is present only for CC and FMS, higher for both models, for the same reasons considered above for the case of frontal patients. Overall, these results further show the capacity of the model to reproduce the multiple behaviours of the target human groups in great detail.

Figure 7: Healthy condition: comparison between the healthy model group and the healthy human group (** indicates a statistical significance of $p < 0.01$).

Participants	Indices				
	CC	TE	PE	NPE	FMS
Healthy (Heaton et al., 2000)	<i>.001</i>	.800	.748	.920	<i>.001</i>
Frontal (Heaton et al., 2000)	<i>.001</i>	.784	.794	.953	.565
Healthy (Paolo et al., 1995)	<i>.004</i>	.873	.763	.969	<i>.003</i>
Parkinson (Paolo et al., 1995)	<i>.004</i>	.678	.635	.964	<i>.000</i>

Table 2: Statistical comparison (p-values, two-tail t-tests) of human data vs. model data involving the healthy and pathological conditions (data from Heaton et al., 2000) and healthy and Parkinson conditions (data from Paolo et al., 1995). Italics highlights the p values that are statistically significant ($p < 0.05$).

Figure 8: Pathological condition: comparison between the artificial impaired group and the human frontal patients (** indicates a statistical significance of $p < 0.01$).

3.2. Study of the model internal functioning

3.2.1. Relation between the model key parameters and the WCST behavioural indices

In this section we analyse the relations between the three key model parameters and the WCST indices by considering their correlations as measured by the Pearson’s r (Table 3) and a suitable visualisation able to indicate possible non-linear relations between them (Figure S3 in Supplementray Materials). The analysis shows that the number of completed categories (index CC), indicating the model global performance, tends to be high with high error sensitivity (μ ; $r = +0.25$), low forgetting (ϕ ; $r = -0.14$), and low distractibility (τ ; $r = -0.67$). The analysis also indicates that the total number of errors (TE) has a negative link with the error sensitivity (μ ; $r = -0.60$), and a positive one with distractibility (τ ; $r = +0.34$). This is coherent with the fact that a higher reactivity to feedback and a lower distractibility are expected to cause less errors in the task. The analysis further shows that perseverative errors (PE) have a robust negative link with negative feedback processing (μ ; $r = -0.58$), in agreement with the classic literature on the WCST that associates perseverative rigid behaviours with a difficulty to adapt the behaviour following a negative feedback (Dehaene and Changeux, 1991). The analysis additionally indicates that non-perseverative errors (NPE) have remarkable positive correlation with distractibility and erratic behaviours (τ ; $r = +0.75$) and a moderate correlation with forgetting (ϕ ; $r = +0.24$), thus confirming the often-claimed relation between such type of errors and the lack of focus plus the failure to ‘reason by exclusion’ (based on the selection of the behavioural rule that have not yet been tried out, see Dehaene and Changeux, 1991; Barceló and Knight, 2002). Interestingly, NPE negatively correlates with the sensitivity to negative feedback (μ ; $r = -0.26$), suggesting that reasoning by exclusion strongly relies on the capacity to value feedback. Finally, the FMS shows a strong correlation with distractibility (τ ; $r = +0.73$), thus confirming that the difficulty to maintain a correct behaviour once found is strongly dependent on the capacity to keep the internal focus and commitment on the selected decision-making rule. Overall, these results agree with the literature (Section 2.1) and with the results obtained by different previous models (Section 4.2).

3.2.2. Effects of focused alterations of the model on the WCST behavioural indices

The simulated lesion technique allowed us to further investigate the role of each single key model parameter, and the related cognitive function and brain area, in the production of flexible behaviour measured by the WCST indices. In this respect, Section S4.3 and Figure S5 in Supplementary Materials show the possible correspondences between the three altered parameters, set to extreme values, and brain lesions. Table 4 in particular shows the three sets of parameters used to obtain the three versions of the model that we investigated. The first model, called the ‘extreme perseverative model’ (EPM) for ease of reference, is characterised by a very low value of μ . This alteration lowers the sensitivity to negative feedback following incorrect actions and might correspond to a malfunctioning of the ventral ACC involved in the motivational processing of errors (Lie et al., 2006). Such structure, in concert with medial and ventral cortical and sub-cortical areas, regulates negative emotions (Etkin et al., 2011) and the processing of the affective valence of

Indices	Parameters		
	μ	ϕ	τ
CC	0.25	- 0.14	- 0.67
TE	- 0.60	0.17	0.34
PE	- 0.58	0.07	- 0.05
NPE	- 0.26	0.24	0.75
FMS	0.04	0.00	0.73

Table 3: Pearson’s r indicating the correlation between the key parameters of the model (μ , ϕ , τ) and the different WCST indices. All correlations, with the exception of the one related to ϕ -FMS, are statistical significant ($p < 0.001$). Correlations stronger than $|0.3|$ are highlighted in *Italics*.

stimuli (Roy et al., 2012). The second model, called ‘distracted model’ (DM), is characterised by a very high value of τ . This alteration might correspond to an impairment of the dorsal ACC that, by interacting with dorso-frontal cortices, is involved in decision-making and response selection (Bush et al., 2002; Heilbronner and Hayden, 2016). The third model, called ‘irrational model’ (IM), is characterised by a high value of ϕ . This alteration causes the working-memory component to have a high forgetting rate for previously chosen rules and might correspond to an impairment of the brain system supporting executive working memory, in particular the dlPFC and its loops with basal ganglia (Mannella et al., 2013).

	μ	ϕ	τ
Extreme perseverative model	0.001	0.26	0.14
Distracted model	0.26	0.26	0.4
Irrational model	0.26	1	0.14

Table 4: Parameter values of the models impaired to produce focused alterations. Values in *Italics* represent the parameters that were altered with respect to the values found by fitting the healthy participants of Heaton et al. (2000).

A global view of the error proportions of the three altered models (Figure 9) confirms that the EPM (having low sensitivity to negative feedback) and the DM (having a highly variable decision making) have an opposite PE/NPE imbalance: the EPM has a high PE and low NPE; the DM has a low PE and high NPE. Moreover, the EPM has few FMS errors while the DM has many. The IM (having a high working-memory forgetting rate) shows slightly more errors than the healthy model, with an imbalance toward NPE mainly due to the impairment of the reasoning-by-exclusion process.

3.3. Analysis of the functioning of the model mechanism of internal representation manipulation

While the previous sections showed the high capacity of the model to match and account for the data on the behaviour of the WCST human participants, this section presents some results directed to show how the model behaviour depends on the processes implemented by the three core components instantiating the hypothesis proposed here, namely the executive working-memory, the top-down representation manipulator, and the visual working memory. To this purpose, we first study the relations between the activation of the executive working-memory units and the resulting model actions and errors in healthy and pathological conditions. Then we study the internal functioning of the model perceptual component, in particular showing how the top-down manipulator dynamically affects its internal representations of the input stimuli. Finally, we study the capacity of the top-down manipulator and the visual working memory to store relevant information in the presence of external time delays and distractors.

Executive working memory dynamics. To illustrate the functioning of the working memory component, we considered (a) the ‘healthy model’ (HM) and pathological model (PM) having the parameters found by fitting the data from Heaton et al. (2000) (Figure 10), and (b) the three altered versions of the model

Errors profiles of models with lesions compared to healthy model

Figure 9: Proportion of errors in the altered models compared to the healthy model. HM: healthy model; EPM: extreme perseverative model; DM: distracted model; IM; irrational model; PE: perseverative errors; NPE: non-perseverative errors; FMS: failure-to-maintain set errors.

considered in the previous section, namely the extreme perseverative model (EPM), distracted model (DM), and irrational model (IM) (Figure 11).

Healthy model (HM)

Pathological model (PM)

Figure 10: Internal functioning of the executive working memory of the healthy model (HM) and the pathological model (PM). Each line represents the activation of a memory unit encoding a specific matching rule: thick red line: colour-based matching rule; dotted thin blue line: shape-based matching rule; continuous yellow line: size-based matching rule. The dots at the top of graphs indicate single instances of correct responses (CR) or errors (PE, NPE, FMS).

In the graphs, the parts of the curves rising from 0.5 to 1.0 during ten correct responses (CR) indicate a successfully completed card category. Curves decreasing from 1 to 0.5 indicate that the desirability of a matching rule decreases, possibly causing the selection of a different rule. Low values of two curves followed by the increase of the third curve indicate an inferential reasoning by exclusion. Sequences of several small peaks above the baseline (0.5) after a category change suggest a failure of such reasoning process. A stable horizontal curve coupled with many errors corresponds to a strong perseveration tendency (e.g., see the EPM graph). Conversely, a graph with several increments and decrements of different curves indicates an erratic behaviour (e.g., see the DM graph).

Extreme perseverative model (EPM)

Distracted model (DM)

Irrational model (IM)

Figure 11: Internal functioning of the executive working memory of the models with focused damages (EPM, DM, IM). Each line represents the activation of a memory unit encoding a specific matching rule: thick red line: colour-based matching rule; dotted thin blue line: shape-based matching rule; continuous yellow line: size-based matching rule. The dots at the top of graphs indicate the instances of correct responses (CR) or errors (PE, NPE, FMS).

The HM has an overall good performance (it completes the WCST six categories, Figure 10) and performs a correct reasoning after category changes, possibly after one or two errors and ‘inference by exclusion’. Notice how even if this model corresponds to a ‘healthy condition’, it still exhibits exploratory behaviours that might sometimes look as pathological behaviours, e.g. in the choice interval 85–95. The PM (Figure 10) exhibits both perseveration (e.g., see the many PE in the choice interval 15-25) and inefficient reasoning failures (e.g., many NPE in the choice interval 45-55). The PE are also exacerbated by a limitation of the Heaton’s version of the WCST for which sometimes the deck and target cards have more than one attribute in common and this can produce a positive feedback notwithstanding the participant makes the selection based on a wrong matching rule (Dehaene and Changeux, 1991; e.g., this happens often in the choice interval 90-115).

The EPM (Figure 11) shows a behaviour similar to the PM but characterised by a more severe insensitivity to feedback. This impairment causes a higher number of PE compared to the PM (e.g., see choice interval 65-115). The model is also more strongly affected by the WCST Heaton’s version limitation indicated above than the PM. The DM (Figure 11) shows an erratic behaviour caused by a severe impairment of the decision-making processes. The lowest values of its working-memory units are lower than those of the other models because this model often chooses a strategy that has already a low desirability. The IM (Figure 11) exhibits a healthy behaviour but with a strong impairment of the capacity for reasoning by exclusion. In particular, the graph highlights that this deficit strongly affects the performance when the model should change the match rule but fails to do so, thus incurring in a PE or a NPE. Note that, as it happens in the experiments with human participants, the simulated experimenter (represented by a software routine that detects the errors) has no access to the model decision making processes. For this reason it might incorrectly score a distraction error as PE notwithstanding this is not due to a repeated intentional wrong rule selection but rather to an erratic decision process.

The rule-based activations of the model executive working memory appear qualitatively similar to those found in the neurons of the dlPFC during the solution of variants of WCST with non-human primates (Mansouri et al., 2006b; Buschman et al., 2012). These results and the model features support the idea that the storing capacities of the model working memory and its update could represent key processes for the internal manipulation of representations.

Perceptual component: internal representations. After training (see Supplementary Materials), the *Deep Belief Network* implementing the component is able to both extract the specific attributes of each card, at its higher level, and to generate images corresponding to such attributes, at the input-level. The latter capacity, used by the model to compare the WCST cards with respect to the selected category of attributes, is based on the *generativity* of the component. To investigate the quality of these representations, we analysed the images reconstructed by the component when single units from the first and second hidden layers of the network are manually activated in isolation. Figure 12 shows the images generated by activating the units of the first hidden layer (left graphs) or the units of the second hidden layer (right graphs). The figure shows that the images generated by the activation of single units of the first hidden layer involve different attributes of categories (e.g. mixed colours, forms, sizes). Instead, the images obtained by activating the single units of the second hidden layer involve disentangled representations of a specific category attribute independently of the other attributes. For example, a unit produces the ‘prototype’ of the blue colour independently of the object size and shape, and another unit produces the prototype of the ‘triangle’ shape independently of the object colour and size.

The presence of different internal representations at different levels of abstraction within the first and second hidden layer reflect what also happens in brain. For example, the neurons of the primary visual cortex extract several low-level visual features from the retina images (Rentzeperis et al., 2014) whereas the neurons of the higher-order visual cortices tend to respond to macro-aspects of objects (Bracci et al., 2017; Folstein et al., 2015). Although not further investigated here with the model, these different representations could be used by brain to flexibly carry out different tasks requiring representations of precepts at a different levels of abstraction.

Figure 12: *Left*: Images generated by activating a sample of single neurons of the first hidden layer, showing how each encodes a mixture of colour, shape, and size attributes. *Right*: Images generated by activating single neurons of the second hidden layer, showing how each encodes a specific disentangled category attribute. This can be seen by considering that the three rows of graphs refer to the three categories (from top to bottom: colour, form, size) and the four columns refer to different category attributes (colour: yellow, red, blue, green; form: bar, triangle, circle, square; size: small, medium-small, medium-large, large).

Dynamics of the manipulator and visual working memory. Here we illustrate the results of the tests of the top-down manipulator and the perceptual component working as visual working memory. In particular, we analyse the time-dependent loss of information of the visual working memory about an initial image while the system is disturbed by distractors. This is particular measured on the basis of a ‘correctness index’ measuring the probability of retaining and representing an initially perceived image in the presence of distractors (see Supplementary Materials for details). Figure 13 shows the results of the tests corresponding to a different number of resonance cycles ($d \in \{10, 100, 1000, 10000\}$) and different levels of focused retention (ζ ; a value $\zeta = 1$ implies that the DBN is fully focused on the input memory, $\zeta = 0$ means that it is fully driven by the distractor, and $\zeta = 0.5$ means the it assigns the same weight to the memory and to the distractor).

The figure shows that the simulation with $\zeta = 0$, performing a reconstruction that exclusively depends on the distractor, exhibits a probability of 75% to generate an incorrect reconstruction (due to the fact that 1 time out of 4 the attribute of the distractor reconstructed by the component matches the attribute of the initial image to be remembered by chance). Instead, when the network fully focuses on the image to be remembered ($\zeta = 1$) the reconstruction error is null. This contrasts the behaviour of classical DBM networks that exhibit a progressive loss of the original information after multiple reverberation cycles (Hinton, 2012), similarly to what happens in the case of distraction and ‘mind-wandering’ (Smallwood and Schooler, 2015; Mason et al., 2007). The reason is that the top-down manipulator biases the activation of the DBN during the reverberations so that these remain locked into a stable attractor corresponding to the information to be remembered, akin to focused attention. This shows that the representation internal manipulation mechanism is capable of selecting a desired representation with high level of stability. With intermediate values of focus ($0 < \zeta < 1$), the system exhibits a loss of information that gets more severe with the increase of time delay/number of perceived distractors. Overall, the results show the importance of the category-based top-down manipulation of representations to preserve task relevant representations in the presence of additional external patterns.

3.4. Proposal of a modified WCST to study the manipulation of visual working memory contents

The test on time delays and distractors suggests the formulation of a possible computer-based variant of the WCST that would allow a more direct test of the hypothesis proposed here for which the manipulation of internal representations is at the basis of cognitive flexibility. The proposed new test integrates into the WCST experimental protocol some elements of the protocols used to investigate the effects of delays and interfering stimuli on perceptual working memory (Oberauer and Lewandowsky, 2008; Souza and Oberauer, 2015).

Figure 14 shows the key phases of the new experimental protocol: (a) the participant presses one of three buttons to manifest the sorting rule that s/he intends to use; other manipulations are possible, for

Figure 13: Loss of information (y-axis: correctness index) in time (x-axis: measured as number of resonance cycles) and intensities of distracting noise (curves corresponding to different ζ levels). Each curve point represents an average of 30 repeated simulations.

example the rule might be externally indicated to the participant, etc.; (b) the deck-card is displayed for a certain time: the display time might be shortened to augment the interference of the following distractors; (c) one or more distractors are displayed during the stimulus-response delay: distractors might be formed by randomly selected cards, blank inputs, or other items, and the delay might be set to different lengths to challenge the memory in different ways; (d) the participant is shown the target cards and has to choose one of them by pressing one of four buttons. These features of the protocol have the following rationale: (a) the initial declaration of the rule to use allows the study of how it affects the top-down control of the visual memory; (b) the deck-card is the stimulus from which the participant extracts the visual attribute to remember: the correct one is known by the computer-program because of point 'a'; (c) the manipulation of the delay duration and typology of distractors allows the manipulation of the interference with the working memory; (d) the participant's response can be analysed quantitatively: for example the test allow one not only to score the classic WCST errors, but also memory 'retention errors' and response times. Possible additional factors could be studied, for example by introducing a verbal shadowing mechanism to evaluate the support of the executive working memory by inner verbal rehearsal mechanisms (Baldo et al., 2005).

The protocol could allow the test of our hypothesis, in particular to ascertain the presence of a top-down bias manipulating the representations within the visual working memory versus the alternative hypothesis for which all processes to solve the WCST take place at the high level as proposed by previous models and theories. For example, one might manipulate distractors in ways that tend to change the representations at the low level but not at the high level, and measure as a consequence different retention errors and/or reaction times. For example, the participant might choose the 'shape' rule, implying the selection of a specific attribute of the deck card, say the 'circle' of a 'small red circle' card, and then the computer might present either 'reinforcing distractors', say cards as the deck card, or 'interfering distractors', say cards with 'medium-small/medium-large/large blu/green/yellow circles'. The latter distractors should interfere with the visual working memory (that encodes also non-relevant features) but not with the central executive working memory (that encodes the attribute 'circle' in a disentangled way) and thus produce different

retention errors and/or reaction times. This is just a preliminary idea to be refined and other manipulations could be thought in order to produce measurable differential effects on the visual working memory and the executive working memory. Brain imaging techniques could also be used to investigate the different involvement of low-level visual working memories to perform tasks requiring a different engagement of the executive working memory and the visual working memory.

Figure 14: One trial of the new WCST protocol proposed here usable to study the effects of the top-down bias on the sustained retention of information of the visual working memory in the presence of distracting stimuli. Phases of the trial: selection of the card sorting rule; display of the deck-card; display of a sequence of distractors; participant’s response.

4. Discussion

4.1. Discussion of the main contributions

The novel hypothesis we proposed here states that flexible cognition relies on the top-down manipulation of internal low-level perceptual representations. These representations can then support a suitable sensory-motor interaction with the environment leading to the solution of the task. The hypothesis agrees with the empirical evidence on the brain showing how imagination processes involve low-level cortical areas (Kosslyn, 1999). Moreover, it is also corroborated by the fact that prefrontal cortex is strongly connected with parietal cortex, in turn forming highly integrated sub-systems with motor areas (Rizzolatti and Craighero, 2004; Passingham and Wise, 2012); functionally, these systems play an important role in representing ‘affordances’, encoding the conditions in which actions can be successfully executed (Fagg and Arbib, 1998; Baldassarre et al., 2019), and play a key role in the online control of action movements (Jeannerod et al., 1995; Thill et al., 2013). The hypothesis, operationalised in a computational model, diverges from previous proposals incorporated in models of cognitive flexibility and the WCST, considered in detailed in the following section, that directly link the selection of behavioural rules to the selection of actions rather than to the manipulation of lower-level representations.

The computational model represents a new tool for the quantitative study of the proposed hypothesis. This possibility has been shown here by validating the model with data from multiple WCST experiments, run both with healthy participants and frontal/Parkinson patients, often reproduced in isolation in previous models (Table 2 and Figure 8). For example, the model confirmed the key role of error sensitivity for the production of perseverative errors and the key role of distractibility for the production of non-perseverative errors. The capacity of the model to reproduce and explain these errors and other behavioural indices was also shown with a correlation analysis (Table 3) and by lesioning key parameters of the model (Table 4 and Figure 9). In addition, a qualitative analysis of the activation of the executive working memory of the model (Figure 11) highlighted the different possible causes of non-perseverative errors. In particular, the analysis corroborated the theoretical proposals of some studies (Dehaene and Changeux, 1991; Barceló and Knight,

2002) suggesting that non-perseverative errors could be caused by an impairment of working memory, an impairment of reasoning processes, or attentional failures (distractions).

The core mechanism of the model allows the behavioural rule selected within the high-level executive working memory to exert a top-down bias on the lower perceptual levels of the model to generate representations of the input reflecting the selected rule. A qualitative analysis of the internal representations of the model executive working memory and perceptual areas showed the key role that such internal manipulation process can play for flexible behaviour, in particular by allowing the system to ‘see reality’ (e.g., the cards) in a ‘rule-biased way’ suitable to carry out the task (Figures 10 and 11). The activation of the model units at high and low levels are compatible with those found in the prefrontal cortex during the solution of the WCST (Mansouri et al., 2006b; Buschman et al., 2012) and in the visual extrastriate cortices in categorisation tasks (Bracci et al., 2017; Folstein et al., 2015).

Additional tests of the model not yet corresponding to specific empirical experiments also showed, in line with what happens in the brain (Raffone et al., 2014; Oberauer and Lewandowsky, 2008; Souza and Oberauer, 2015), that the model perceptual areas can work as perceptual working memory. This allowed us to test more in depth the core, mechanism of the model based on the executive-working-memory top-down bias by measuring how it is able to protect the contents of the perceptual areas from spontaneous drifts in time, and from distractors (Figure 13). The results showed how the top-down bias might have different strengths, now regulated externally, to tune the mixing of the top-down generated images and new incoming information. In the tests run here such additional information represents ‘distractors’ but in other tasks it might be relevant to integrate such information with previous stimuli.

The latter tests also supported the proposal of a variant of the WCST (Figure 14) that might allow a more direct empirical evaluation of the proposed hypothesis. The new test in particular aims to create the conditions for which a mere selection of behavioural rules at the abstract high-level executive working memory is not enough to support the solution of a task and requires also the activation of lower-level perceptual areas to recover relevant details of the stimuli. This would ensure that in such conditions the core mechanism hypothesised here is actually operating, thus paving the way to a focused study of its features.

4.2. Comparison with other models of the WCST

In this section we compare the model presented here with other models proposed to study the cognitive processes and neural mechanisms underlying the solution of the WCST. A main outcome of this analysis is that no previous model has linked the selection of categories and attributes underlying the solution of the WCST to the manipulation of perceptual representations within low-level perceptual areas. A secondary outcome of this analysis, relevant to validate the model and hence the hypothesis proposed here, is that no previous model presented an account of different human groups’ performance and behavioural indices as comprehensive as the one presented here (but some models tackled aspects not considered here, e.g. the WCST performance of schizophrenic patients, Berdia and Metz, 1998, or patients with substance addition, Bishara et al., 2010).

Dehaene and Changeux (1991) proposed a seminal model of the WCST that incorporates a mechanism at the molecular level that supports reward processing and synaptic plasticity. The model is based on an architecture encompassing the selection of rules and their integration with percepts in order to select actions. The model was tested for its capacity to reproduce perseverative errors.

Berdia and Metz (1998) proposed a model that simulates neural noise and synaptic instability based on two parameters, ‘noise’ and ‘gain’, and linked these to the poor WCST performance of schizophrenic patients. The model considers attention processes related to the competition between categories but it does not investigate their relation with perceptual working memory. The model reproduces perseverative and non-perseverative errors in normal and schizophrenic participants but it does not reproduce and account for failure-to-maintain errors.

Kaplan et al. (2006) reproduced the WCST with a model using a *Hamming network* (a feed-forward neural network solving pattern recognition problems; Lippmann, 1987) to generate new strategies, and a *Hopfield model* (an associative neural network; Hopfield, 1982) to store them. These networks are used to

reproduce both perseverative and failure-to-maintain errors, proposing that the first are caused by rigidity and the second by attention failures. The model does not consider non-perseverative errors and reproduces the WCST as a ‘rule selection task’ without considering visual working memory and matching mechanisms. Various versions of the model were tested by changing two parameters, the Hopfield threshold and the Hamming distance, but they were not compared with different healthy and pathological human groups.

Bishara et al. (2010) proposed a model that solves the WCST and investigates the cognitive profile of patients with a substance addiction. The model encompasses an abstract component computing positive feedback, negative feedback, and a ‘choice consistence’ (attention focus), and also two different parameters regulating the sensitivity to negative and positive feedback based on the neuroscientific literature showing a dissociation between the two (Monchi et al., 2004). Despite this evidence, Steinke et al. (2018) apply the model to the study of Parkinson patients and find, in agreement with what seen here, that the response to negative feedback is sufficient to fit their performance.

Rigotti et al. (2010) proposed a recurrent neural network that shows a rule selectivity in a WCST involving only ‘form’ and ‘colour’ categories. The model reproduces internal neuronal dynamics that involve mixed selectivity neurons, suggesting that randomly connected neurons spontaneously exhibit mixed selectivity. The model does not propose an architecture to solve the WCST but rather it focuses on the internal processes needed to solve context-dependent tasks with the purpose of investigating how integrated neural networks can support the selection and storage of behavioural strategies.

Caso and Cooper (2017) proposed a computational model that operationalises the ‘schema theory’ proposed by Schmidt (1976) on the basis of a model architecture based on the neuroanatomy of basal-ganglia. The work focuses only on perseverative and failure-to-maintain errors and accounts only for the behaviour of a healthy human group. The work underlines the important function played by basal ganglia, a fundamental ‘selection machine’ in the brain (Redgrave et al., 1999), a function also incorporated in the model presented here.

The models considered this far highlight the cognitive processes supporting the solution of the WCST in healthy and pathological participants. Another set of models focus on mimicking the PFC learning mechanisms supporting various working memory functions. One of these models, presented by Rougier et al. (2005), is used to reproduce the results of the WCST and has features shared with the other models of this type. The model, implemented withing the framework called ‘Leabra’ (O’Reilly and Munakata, 2000), is in particular formed by various neural maps corresponding to input layers, parietal cortices, prefrontal cortices, and motor output layers. The model is tested with the WCST and simulates the production of perseverative errors when the PFC layer is lesioned, but it does not consider other types of errors. Another model of the set (the ‘PBWM model’), proposed by O’Reilly and Frank (2006), simulates various functions of working memory by using an actor-critic model architecture (Sutton et al., 1998) to reproduce the functions and macro-anatomy of the basal-ganglia. The model is in particular used to show the role of ‘gating units’ possibly used by basal ganglia to perform the upload, storing, and download of information in working memory. Hazy et al. (2007) propose an evolution of the previous model implementing other functions of basal ganglia to make the gating process suitable to solve different tasks. Finally, Kriete et al. (2013) propose a comparison of the different variants of the PBWM model and also propose the implementation of ‘indirection processes’ that the brain might possibly use to execute symbolic processing.

At last, ‘COVIS’, proposed by Ashby et al. (1998), represents both a theoretical framework and a computational implementation of neural structures supporting category-learning processes. The model is based on a hybridisation of symbolic and sub-symbolic mechanisms and is grounded on the idea that brain performs category learning through a procedural implicit system, mostly involving sub-cortical structures such as basal ganglia, and a logical explicit system, mostly involving cortical areas. The model reproduces the WCST data collected from healthy participants and Parkinson patients (Hélie et al., 2012), highlighting the role of dopamine shortage in the executive deficits exhibited by Parkinson patients.

This analysis shows that these models are based on the direct sequence of processes, highlighted in Figure 4, involving ‘rule-decision, selection of sub-goal, and action performance’. Instead, our hypothesis and model posit that the high-level decision making processes do not directly select action but rather manipulate ‘backward’ the internal low-level representations of stimuli that then trigger the execution of the correct actions. These processes are also supported by interactive sensorimotor loops with the environment

allowing the system to compare the low-level perceptual representations of stimuli, suitably manipulated by the high-level decision making processes on the basis of the pursued goal and sub-goals.

5. Conclusions and future work

In this work we proposed a new hypothesis to explain flexible cognition as manifested by human participants engaged in the solution of the Wisconsin Card Sorting Test (WCST). The hypothesis posits that flexible cognition relies on goal-directed processes that manipulate low-level perceptual representations that in turn support the production of suitable actions. This hypothesis is novel with respect to previous proposals and models of the WCST as these are all based on decision making mechanisms directly supporting action selection.

The hypothesis has been operationalised through the proposal of a computational model. The model relies on three main processes that we propose to be supported by specific brain systems. The first process involves the executive working memory, relying on the brain prefrontal cortex and ventro-medial basal ganglia, that stores goals and behavioural rules. The second process involves perceptual working memories, relying on the hierarchies of perceptual cortical systems, able to extract and retain information at different levels of abstraction. The third process involves the internal manipulation of perceptual representations, relying on the brain system formed by fronto-parietal cortices and the underlying dorso-medial basal ganglia, that selects the representations in the perceptual working memory on the basis of the activation of the executive working memory. We validated the model by showing how it can reproduce and account for a large set of behavioural indices and data related to healthy and pathological participants of the WCST to an extent that goes beyond what done individually by each previous model.

We also used the proposed model as a basis to propose a modified version of the WCST that would allow a more direct test of the proposed hypothesis. In particular, the new test could allow the manipulation of stimuli in ways that would affect the low-level visual working memory contents but not the high-level executive working memory, thus showing that the manipulation of such low-level contents indeed supports flexible cognition.

5.1. Limitations and future directions

Notwithstanding the contributions highlighted in the previous section, the model currently has some limitations that might be faced in future work. A relevant aspect of the architecture to improve regards the information flow between the model components. A general strategy to use to this purpose could be to use deep neural networks (Bengio et al., 2017) as done for the visual component (see Naselaris et al., 2018, for this strategy). Another possibly complementary strategy could be to ground the information flows of the model on an architecture mimicking the macro-structure of the relevant brain components (e.g., as done in Baldassarre et al., 2013; Mannella and Baldassarre, 2015).

Regarding the model components, a first limitation involves the simplicity of the executive working memory component, now formed by few neural units encoding the possible matching rules. This component might be improved by using mechanisms employed in other models of working memory, thus improving the biological plausibility of the model (e.g., O'Reilly and Frank, 2006; Rigotti et al., 2010), or in deep neural networks (e.g., Hochreiter and Schmidhuber, 1997).

Another component of the model that might be enhanced is the overt attentional system, now relying only on a bottom-up attention process leading the model to explore all stimuli in a stereotyped sequential way. Although sufficient to study the WCST, this component might be improved with the addition of a top-down attention process for the goal-directed exploration of the elements in the environment, thus improving the embodiment of the model and allowing it to solve other tasks (e.g., see Ognibene and Baldassarre, 2015; Sperati and Baldassarre, 2018).

Another important aspect of the model to enhance is the process it employs to acquire category and attribute representations. Now the model uses a supervised learning algorithm, where the supervision comes from a non-specified external mechanism, for example other agents. Social learning might be important for the acquisition of categories, but we think that in humans most category learning derives from direct experiences in the environment. In the future, we thus aim to employ other algorithms, in particular reinforcement

learning algorithms (Sutton et al., 1998; Caligiore et al., 2019), to support the model autonomous learning of categories based on the feedback from the environment following the performance of actions. To this purpose, the embodied nature of the model supporting a direct interaction with the environment would be crucial, for example the model might acquire categories and attributes through the solution of multiple tasks. This might allow the use of the model to face other neuro-psychological tasks.

A final improvement involves the key mechanism of the model related to the internal manipulation of representations. Now this mechanism operates only on the highest level of the Deep Belief Network used to implement the visual hierarchy. In this respect, an important enhancement of the model would be a manipulator operating at multiple levels of abstraction of the hierarchy rather than only at one. This would allow the model to *directly* manipulate representations having different levels of detail as needed by downstream processes. For example, the manipulator could focus not only on object attributes (e.g., ‘circular shape’) but also on their lower-level features (e.g., different edges and corners of shapes) or on the relations between objects forming a scene (the latter would require the addition of more abstract layers to the model); similarly it could focus on sub-goals forming overall goals; on the single actions forming the action sequences needed to pursue goals; or on the predictions related to the consequences of actions.

We think that, if suitably developed in these ways, the model could show how the mechanism for the manipulation of internal representations proposed here might indeed be behind the multifaceted manifestations of the cognitive flexibility exhibited by humans.

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7. Competing information

The authors have no financial, general, or institutional competing interests.

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Neuropsychological analysis of the task: supplementary tables

The architecture of the model presented in the main test was supported by an extensive literature review directed to isolate the parts of brain, and the related functions, supporting the performance of the Wisconsin Card Sorting Test (WCST). Table S1 summarises the works considered, the brain areas they identified, and the brain-imaging techniques used to this purpose.

Highly active cortical areas during the WCST performance

References	Structures	Methods
Lie, Specht, Marshall, and Fink (2006)	dlPFC, vmPFC, sup PC, ACC, TPC, Cb	fMRI 1.5-T
Nagahama et al. (2005)	mPFC, PC, inf FG, ACC, smG	SPECT
Periañez et al. (2004)	inf FG, ACC, smG	MEG
Konishi et al. (2003)	sup FG, inf FG	fMRI 1.5-T
Konishi et al. (2002)	mPFC, ant Ins, Prec, TPj, IFC, sup P	fMRI 1.5-T
Wang, Kakigi, and Hoshiyama (2001)	dPFC, mFC, inf FG, smG, inf FG	MEG
Monchi et al. (2001)	dPFC, mFC, inf FG, smG, inf FG	fMRI 1.5-T
Rogers et al. (2000)	dlPFC, Caud, OT Path	PET O15
Lombardi et al. (1999)	dPFC, Caud	PET, MRI 1.5-T
Mentzel et al. (1998)	mPFC, dPFC, Th, BG	fMRI 1.5-T

Errors depending on lesion sites in the WCST performance

References	Lesioned structures: errors occurred
Gläscher et al. (2012)	ACC: + PE
Barcelò and Knight (2002)	dlPFC: + PE, + NPE
Stuss et al. (2000)	dlPF: - CAT, + PE, mPFC: + FMS
Corcoran and Upton (1993)	Hip: - CAT, + PE
Milner (1963)	dlPFC: - CAT, + TE, + PE
Others	- CAT, + TE, +PE

Table S1: **Top:** Works reporting evidence on the brain areas that are highly activated during the WCST performance, and the brain-imaging techniques they used. **Bottom:** performance errors occurred in correspondence to different lesion sites. Acronyms: PFC: prefrontal cortex; PC: parietal cortex; TPC: temporo-parietal cortex; ACC: anterior cingulate cortex; Cb: cerebellum; TPJ: temporo-parietal junction; BG: basal ganglia; Put: putamen; Caud: caudate nucleus; Th: thalamus; dlPFC: dorso-lateral PFC; dPFC: dorsal PFC; vmPFC: ventro-medial PFC; mPFC: medial PFC; Sup. PC: superior PC; PPC: post-parietal cortex; inf FG: inferior frontal gyrus; sup FG: superior frontal gyrus; SMG: superior marginal gyrus; IFC: inferior frontal cortex; Prec: precuneus; ant Ins: anterior insula; sup PL: superior parietal lobule; mid Th: medial thalamus; PMC: pre-motor cortex; OT Path.: occipital-temporal pathway. CC: completed categories; TE: total errors; PE: perseverative errors; NPE: non-perseverative errors; FMS: failure-to-maintain sets.

Methods: computational details of the perceptual component

Architecture and activation of the perceptual component

As illustrated in the main text, the perceptual component is based on a Deep Belief Network (DBN) having 3 layers (Hinton et al., 2006; Hinton and Salakhutdinov, 2006; Hinton, 2012). The first ‘visible layer’ is directly activated by the input from the visual sensor and hence is formed by 2352 ‘visible’ units. The second layer (‘first hidden layer’) is formed by 150 ‘hidden’ units. The third inner layer (‘second hidden layer’) is formed by 12 hidden units chunked in 3 groups (categories) each encompassing 4 units (attributes). The first and second layer form a first Restricted Boltzmann Machines (RBM); the second and third layer form a second RBM stacked on the first one.

The bottom-up and top-down activation of the DBN works as follows. The activation potential p_j of the unit j of a receiving layer of the network is computed as:

$$p_j = \sum_i w_{ji} \cdot x_i \quad (4)$$

where x_i is the activation of a unit i of the sending layer and w_{ji} is a connection weight linking the two units used for both the bottom-up and the top-down information flow. As we shall see below, in some moments of the network functioning the activation of a unit, x_j , is computed on the basis of a continuous sigmoid transfer function $f[\cdot]$:

$$x_j = f[p_j] \in (0, 1) \quad (5)$$

where:

$$f[p_j] = \frac{1}{1 + e^{-p_j}} \quad (6)$$

In other moments, discussed below, the activation potential of a unit is used to determine its binary activation on the basis of a stochastic process:

$$x_j = \begin{cases} 0 & \text{if } n \geq f[p_j] \\ 1 & \text{if } n < f[p_j] \end{cases} \quad (7)$$

where n is a random number sampled in $(0, 1)$ with a uniform distribution.

During the solution of WCST, the bottom-up information flow (perception) starts with the activation of the visible layer, proceeds with the first hidden layer *sigmoid* activation, and terminates with the second hidden layer *sigmoid* activation. The top-down DBN information flow, based on the generative nature of the two piled RBMs forming the DBN, starts with the activation of the second hidden layer. The units within this layer, receiving the bias from the top-down manipulator, assume a binary value in $\{0, 1\}$ to encode one attribute for the selected category. The top-down information flow continues with the activation of the first hidden layer and terminates with the activation of the visible layer.

Training of the perceptual component

This section illustrates the learning processes of the DBN that, as in human participants, take place before performing the WCST. These processes are as follows: (a) the first RBM of the DBN acquires an internal representation of the low-level features of the input pattern from the cards through *contrastive divergence* (Hinton, 2012), the standard unsupervised learning algorithm of RBMs; (b) the second RBM learns the category attributes of cards through a supervised learning algorithm: this algorithm uses contrastive divergence but substitutes the spontaneous firing of the ‘hidden’ units of such rule with a suitable desired activation pattern. To the best of our knowledge, the latter algorithm is novel (cf. Reed et al., 2014). We now consider these learning processes more in detail.

For a given card image d ($d \in D = \{1, 2, \dots, 64\}$, where D are the indexes of the different cards) the connection weights w_{ji} of the first RBM, linking a unit i of the visible unit layer (2352 units) and unit j of the first hidden layer (150 units), are updated as follows:

$$\Delta_d w_{ji} = \eta \cdot (v \cdot h - v' \cdot h') \quad (8)$$

where $\Delta_d w_{ji}$ is the update of the connection weight, η is a learning rate ($\eta = 0.01$), v is the activation of the visible unit due to the *input pattern*, h is the *stochastic activation* of the hidden unit computed on the basis of the activation of the visible units, v' is the ‘reconstructed input’, i.e. the *sigmoidal activation* of the visible unit caused by the stochastic activation of the hidden units, h' is a *sigmoidal activation* of the hidden units caused by the reconstructed input. Intuitively, the algorithm updates the connection weights to minimize the difference (‘contrast’) between the activation of the hidden units following the initial input activation, and their ‘spontaneous’ activation caused by the reconstructed input (‘spontaneous’ as the reconstructed input is caused by a sample of the first stochastic activation of the hidden units). The update of each

connection weight is done in a *batch* way by summing up the effects of the updates related to all D cards:

$$\Delta_b w_{ji} = \sum_d^D \Delta_d w_{ji} + \delta \cdot \Delta_{b-1} w_{ji} \quad (9)$$

where b indicates the batch index (multiple successive batches are performed during learning) and δ is a coefficient of the *momentum* mechanism used to speed up learning ($\delta = 0.9$).

The second RBM is formed by the the first DBN hidden layer (150 units, now playing the role of ‘visible units’) and the second DBN hidden layer (12 units, playing the role of ‘hidden units’; η was set to a higher value, 0.1, with respect to the first RBM given its lower number of units). The new supervised learning algorithm was implemented by substituting the stochastic activation of the hidden layer of the RBM with desired values from $\{0, 1\}$ representing the actual attributes of the input image, for example ‘red’, ‘circle’, ‘small’. This is the only change with respect to the unsupervised-learning contrastive divergence algorithm, so the formulas presented above were also used here. The effect of this update is that the input pattern tends to cause the desired output pattern (correct attributes) at the level of the second RBM hidden layer (this is the more abstract representation of the DBM). Biologically, these learning processes abstract the acquisition of the representations of different classes thorough the performance of multiple tasks under the guidance of rewards/punishments following actions.

Figure S1 shows the reconstruction error during the training of the two RBMs. The error was computed as:

$$E = \sum_d^{|D|} \frac{\|\mathbf{v}_d - \mathbf{v}'_d\|_1}{|D|} \quad (10)$$

where $\mathbf{v}$ is the original input vector, $\mathbf{v}'$ is the reconstructed input vector, $\|\cdot\|_1$ is the L1 norm, and $|D|$ ($|D| = 64$) is the number of the input images (cards) and also of the size of the learning ‘batch’ used to train the component. For the second RBM, the graph in the figure also shows the number of cards (out of 64) whose attributes were correctly identified by the DBN. The graphs show that the first RBM achieved a reconstruction error of 0.005 after 37.000 batches while the second RBM achieved a reconstruction error of 0.1 after 130 batches showing a high efficiency of the supervised learning process used here.

Figure S1: Learning process of the two RBMs forming the perceptual component. Left: first RBM, moving average over 300 learning batches of the reconstruction error. Right: second RBM, reconstruction error and number of cards whose attributes were correctly classified by the RBM (and DBN).

To directly evaluate the quality of the training outcome, Figure S2 shows the capacity of the two RBMs to reconstruct the image at the level of the DBN input layer thanks to their generative nature. To test the capability of the first RBM, we performed an input→hidden1→input sigmoid-based activation spreading: the first input activation produced a distributed internal representation at the level of the first hidden layer (‘hidden causes’ of the input), and then the resulting hidden activation pattern was used to reconstruct the input with a backward activation spreading. To test the whole DBN, the input reconstruction was done

through an input→hidden1→hidden2→hidden1→input activation spreading (activation of hidden layer 1 was based on the *sigmoid* function; the activation of hidden layer 2 was based on the *hardmax* function extracting the attributes of the image, e.g. ‘green, big, circle’). The figures show that the input reconstructions performed by the first RBM are more accurate than those generated by the whole DBN due to the stronger abstraction performed by the DBN hidden layer 2 compared to the DBN hidden layer 1. The quality of the images based on the DBN hidden layer 2 is however still sufficient to support an effective comparisons of cards.

Figure S2: Input images and related reconstructions performed by the first RBM or by the whole DBN.

Methods: further details on the model parameter search and model validation

Estimation of the model key parameters

Some of the model parameters are very important to determine the overall behaviour of the model exhibited in the solution of the WCST, so it was important to systematically search and test them. These parameters were: μ : sensitivity to negative feedback errors; ϕ : working-memory forgetting speed; τ : exploration/distractibility. The parameter search technique used allowed us to fit the data of different groups of participants of the WCST (healthy humans, frontal patients, and Parkinson patients) and on this basis to characterise some of the cognitive processes underlying their behaviour, in particular the different types of errors exhibited while solving the task.

The parameters were estimated in particular by using a *brute force search algorithm* (Van Geit et al., 2008) directed to minimise the difference between the WCST indices obtained by the model and those of humans. The estimated parameters had the following ranges: $\phi \in (0.0, 1.0)$; $\mu \in (0.0, 1.0)$; $\tau \in (0.0, 0.3)$. To apply the algorithm we divided each parameter range in 10 equally separated values, thus in total we had $10^3 = 1,000$ combinations of parameters. For each parameter combination we ran 30 repeated simulations over which we computed the average values of the WCST indices. These average values were compared with the average of a given target human group to select the parameter set that gave the best fit. The comparison was based on the Mean Squared Error (MSE) computed as follows:

$$MSE = \frac{\|\mathbf{y} - \mathbf{y}'\|_2^2}{n} \quad (11)$$

where $\mathbf{y}$ is the vector of mean indices of the human group, $\mathbf{y}'$ is the vector of mean indices of the model, $\|\cdot\|_2$ is the L2 norm, and n is the length of the vectors.

We applied this procedure to human data related to healthy participants and frontal patients presented in Heaton et al. (2000); these data are paired for age, education level, and IQ for the two groups. The healthy group was formed by 356 participants and the pathological group by 59 patients having a local or diffused frontal lesion. To further validate the model, we also applied the procedure to data related to Parkinson patients and control participants presented in Paolo et al. (1995); these data are paired for age, education, and cognitive decline (Dementia Rating Scale).

The large set of parameters tested also allowed us to run a sensitivity analysis (Hamby, 1994). This was in particular directed to investigate how the MSE of different groups of human participants, and their behavioural indices, responded to a systematic variation of the model key parameters.

Focused damages of the model key processes

To study the role of the model parameters in depth, we executed alterations of one of the three key model parameters while leaving the other two parameters set to the values found by fitting the healthy participants of Heaton et al. (2000). These tests allow a clear identification of the causal relation between the cognitive aspects affected by each parameter and the WCST indices. Figure S3 shows the functional architecture of the system highlighting the locus of the impairment, the possible corresponding sites in brain, and the overall effects produced. The methodology used is akin to the classical ‘lesion approach’ often used in bio-constrained models. This classic approach was not applicable to our model because the lesion of its key areas (the working memory, manipulator, and motivational components) impaired the model behaviour too strongly. Instead, the alteration of the model key parameters allow a partial damage of the model functioning.

Figure S3: This schema shows the model architecture and three ‘focused lesions’, obtained through specific parameter alterations, that we applied to obtain three prototypical pathological conditions. Dots with a different grey intensity represent the three alterations (‘lesions’) while the coloured bolts summarise the decrease of performance/increase of errors that they cause in the WCST performance. For example lesion I, mimicking effects analogous to those produced by a brain lesion of ventral ACC and vmPFC and impairing the motivation system, cause a decrease of CC and an increase of TE and PE.

Test of the manipulator and visual-working memory

We now illustrate in detail the procedure used to study the retention capacity of the model visual working memory component in the presence of time delays and interfering distractors. The analysis of this aspect of the model allows us to show the functioning of the model key mechanism for the manipulation of internal representations. This test is needed as the WCST protocol allows the participants to freely look at the deck card and the target cards multiple times and so it does not allow to probe the presence of top-down generative representations as these mix with the continuous input. The new test also suggested a new variant of the WCST paradigm, illustrated in the Section ‘Discussion’ of the main article, that might be used to more directly investigate the mechanism.

Cognitive neuroscience literature defines working memory as a storing system that can maintain information for a limited time window and allows the manipulation of such information for the preparation of behaviour (Fuster and Bressler, 2015; Constantinidis and Klingberg, 2016). The computational literature offers many examples of working-memory models (Minami and Inui, 2001; O’Reilly and Frank, 2006; Pascanu and Jaeger, 2011; Lemaire and Portrat, 2018). These models are able to store input information, usually encoded in an abstract form, either in a ‘localistic way’ (a single neural unit encodes a single input pattern) or in a ‘sparse way’ (many units encode a single input pattern). In all cases, these models maintain an abstract representation of the input or internal patterns feeding them but are not able to reproduce those patterns as it can be done by the model presented here thanks to the generative capabilities of the DBN. The test we propose draws from the literature on perceptual working memory showing that the retention capacity of visual features depends on both the time delays and interfering stimuli (Oberauer and Lewandowsky, 2008; Souza and Oberauer, 2015). However, the test has also a novel feature that allows the study of the effects of the top-down bias on the memory dynamics.

As we have seen above, the DBN used here to implement the model perceptual component can support a bidirectional flow of information from the input layers to the hidden layers and vice versa for multiple cycles. This reverberation process, called ‘Gibbs sampling’ (Bengio et al., 2017), is at the core of the learning algorithm used by the network. The reverberation allows the simulation of a dynamic working memory that stores information for a certain time window. The reverberation process can also be influenced by the bias of the model manipulator that can force a specific activation (e.g., a certain category and attribute) within the visual working memory. This process is particularly interesting as the spontaneous reverberation of the DBN leads it to explore different patterns in time (Hinton et al., 2006), similarly to ‘mind wandering’. Moreover, if the input units of the network are activated by additional distracting patterns after the presentation of a relevant input pattern to be remembered, the network reverberation will also tend to encode a mixed representation of the two, thus allowing the simulation of interference. In this case, the manipulator bias might lead the memory to not only focus on the features of interest of the relevant input, but also to have a more stable dynamics in the presence of the internal drift tendency and the external distractors, an effect that can be studied with the test we now illustrate more in detail.

The DBN component was presented an input card to be remembered for a certain amount of time, corresponding to a certain number of reverberation cycles. We define a ‘reverberation cycle’ as the bottom-up information spreading followed by the top-down manipulator-biased information spreading leading to form a reconstructed input pattern; this pattern feeds the next reverberation cycle. Distractors are presented as follows. During each reverberation cycle we present the visual working memory a distracting input pattern (a card randomly chosen from the deck) by adding it to the reconstructed input; the resulting mixed pattern is used by the DBN for the next reverberation cycle. The mixing pattern was in particular obtained by activating each DBN input unit as follows:

$$x_t = \zeta \cdot x_{t-1} + (1 - \zeta) \cdot d_t \quad (12)$$

where x_t is the input unit at reverberation cycle t ($t = 0, 1, \dots, n$ with n representing the total number of reverberation cycles), x_{t-1} is the reconstructed input produced by the previous reverberation cycle (at $t = 0$ the component receives only the relevant card input without the distractor), ζ is an important *retention parameter* regulating the model capacity to maintain a memory of the target card, and d_t is the distractor pixel activating the input unit.

The test was repeated, using an already trained DBN, with different time delays (i.e., different number of reverberation cycles: $n \in \{10, 100, 1000, 10000\}$) and different values of the retention parameter ($\zeta \in \{0, 0.2, 0.5, 0.8, 1\}$). For each combination of the two parameters, we ran 12 different ‘trials’ of the test in each of which the top-down manipulator was set to select one specific attribute (out of 4) of one specific category (out of 3) while the system was presented a card having that category and attribute. Each of this trials was repeated for 30 times with different seeds of the random number generator. For each combination of parameters, we measured the proportion (‘correctness index’) of repetitions where the DBN was able to give, at the end of the time delay, a reconstructed input equal to the one of the first reverberation cycle of the trial: the reconstructed input of the first reverberation cycle is not affected by the memory shift and the distractors, so it represents the correct reconstruction that the component should produce if it manages to retain the desired input feature.

Results: further details

Sensitivity analysis results

In this section we present the results of the sensitivity analysis directed to evaluate how the key model parameters affect the MSE related to the data of the healthy and frontal pathological participants of Heaton et al. (2000). Recall that the key parameters involved in these studies have this meaning: μ : sensitivity to negative feedback errors; ϕ : working-memory forgetting speed; τ : exploration/distractibility.

Figure S4 shows the MSE of the tested combinations of parameter values. The simulated healthy participants have a low MSE (indicating a high accuracy of the model data fitting) for various combinations of the parameter values. These involve either low values for both the error sensitivity (μ) and distractibility (τ), or medium-high values for both, while the forgetting parameter (ϕ) can assume different values. This might indicate that a higher distractibility can be compensated for by a higher sensitivity to choice errors. The fitting of data related to frontal patients shows a lower number of parameter sets that produce a low MSE, in particular requiring a low reactivity to negative feedback (μ) and medium distractibility (τ); instead, the model is more robust to the variability of the forgetting parameter (ϕ) as for the case of healthy participants.

Figure S4: Mean Squared Error (MSE) of the combinations of the three searched parameters (x, y, and z axes), in the case of healthy humans (left graph) and pathological humans (right graph). Red spheres represent low values of MSE, hence a behaviour of the model close to the one of the target group, while yellow spheres represent high values.

The sensitivity analysis also allowed the evaluation of how the behavioural of the healthy group varied in correspondence to a systematic variation of the three key model parameters. Figure S5 shows in particular 3D plots indicating the relation between the model three key parameters and each of the WCST behavioural indexes. The ellipses overlaid to the graphs indicate the areas of the parameter space that produce high values of the considered index. Overall the graphs confirm the correlation analysis presented in the main text.

Figure S5: Relation between the model three key parameters and the WCST behavioural indexes. Blue dots indicate low values of the indices whereas red dots indicate high values.

Behavioural indices of the model with focused damages: statistical comparisons

The main text presented a comparison of the behavioural indices of three models each obtained by setting one of the three key model parameters to an extreme value while setting the remaining two to the values obtained by fitting the data of the healthy participants from Heaton et al. (2000). The three models were in particular as follows: (1) ‘Extreme perseverative model’ (EPM): very low value of μ lowering the sensitivity to negative feedback following incorrect actions; (2) ‘Distracted model’ (DM): very high value of τ involving an erratic decision making process; (3) ‘Irrational model’ (IM): high value of ϕ implying a high forgetting rate for previously chosen rules. The main text presents an overview of how the indices of the three models are in comparison to those of the healthy model (HM). Here we integrate such analysis by giving further details on such comparison (Figure S6).

With respect to the HM, the EPM, characterised by a low sensitivity to negative errors (low μ), has a lower CC index (1.9 ± 0.9 vs. 5.9 ± 0.4 , $p < .001$), and a higher TE index (74.5 ± 10.1 vs. 23.4 ± 5.5 , $p < .001$) caused by a high number of PE (63.0 ± 11.8 vs. 12.4 ± 3.8 , $p < .001$) while the number of NPE is not statistically different (11.5 ± 5.8 vs. 11.0 ± 4.2 , $p > .05$). The EPM incurs in fewer FMS errors compared to the healthy model (0.5 ± 0.7 vs. 1.4 ± 1.3 , $p < .001$). This is due to the extreme perseverative behaviour which causes a high level of PE (85% of total errors) but also prevents it to mistakenly switch to other

different actions after a correct response.

Figure S6: Comparison of the WCST indices of the healthy model, the extreme perseverative model, the distracted model, and the irrational model. Asterisks indicate a statistical difference between an impaired model and the healthy model (* indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$).

The DM, characterised by a high variability of decisions (high τ), shows a lower CC than the HM (0.7 ± 0.9 vs. 5.9 ± 0.4 , $p < 0.001$) and an error profile symmetrical with respect to the EPM. In particular, compared to the HM, it has a higher number of TE (44.3 ± 5.2 vs. 23.4 ± 5.5 , $p < .001$), caused by 62% of NPE (27.6 ± 4.4 vs. 11.0 ± 4.2 , $p < .001$) and 38% of PE (16.7 ± 3.7 vs. 12.4 ± 3.8 , $p < .001$). The DM also has a higher number of FMS errors (2.9 ± 1.4 vs. 1.4 ± 1.3 , $p < 0.001$). Despite the DM has a higher value of PE with respect to the healthy model (16.7 ± 3.7 vs. 12.4 ± 3.8 , $p < .001$) the model is not affected by a perseverative tendency, as indicated by a higher percentage of NPE with respect to PE (62% vs 38%). This result is caused by the fact that the classic version of the WCST used here has a distortion for which a random choice of the behavioural rule (colour, form, or size) has a probability of 0.33 of resulting in a PE, so a distracted behaviour might appear as perseverative.

The IM, characterised by a high level of working-memory forgetting (high ϕ), has a slightly lower CC compared to the healthy model (5.6 ± 0.8 vs. 5.9 ± 0.4 , $p < .05$) and the lowest value of TE with respect to the other altered models. In particular, it has a higher number of TE compared to the HM (29.7 ± 9.0 vs. 23.4 ± 5.5 , $p < .001$), caused by a 52% of NPE (15.4 ± 5.7 vs. 11.0 ± 4.2 , $p < .001$) and a 48% of PE (14.4 ± 4.5 vs. 12.4 ± 3.8 , $p < .05$). The IM does not have a statistically different FMS value compared to the HM (1.1 ± 1.1 vs. 1.4 ± 1.3 , $p > .05$). The fundamental deficit of this model is hence marked by a high percent of NPE with respect to PE caused by a malfunctioning of the *reasoning by exclusion* process. In particular, the model is not able to perform a correct reasoning because in each turn it tends to forget the previously performed actions. The increased PE can be related to the previously described distortion of the WCST for which an error caused by an erratic behaviour is scored as a perseverative error (PE).

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