

Adaptation by binding: a learning account of cognitive control

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Cognitive control refers to the ability to repress our instantaneous urges in favor of more appropriate responses. Current debate concerns whether cognitive control effects that are studied in the laboratory (e.g. Stroop tasks) actually reflect the operation of a cognitive control system (adaptation theory) or instead merely reflect side effects of feature binding processes (binding theory). The two perspectives can be integrated by conceptualizing cognitive control as resulting from interactions between binding processes (as instantiated in Hebbian learning) and arousal. Conflict situations such as Stroop incongruent-stimuli lead to arousal and nor-adrenalin release throughout the brain, which facilitates binding between task-relevant cortical areas. Our proposal emphasizes an intimate link between cognitive and emotional processing.

Introduction

When a road sign indicates that our familiar road from work to home is blocked, we immediately can make a detour, rather than getting blocked at a construction work site. This is an instance of cognitive control (see [Glossary](#)), or the ability to repress our instantaneous urges in favor of less obvious but more appropriate responses. To study this in the laboratory, congruency tasks (e.g. Stroop, Simon and Eriksen flanker) are often used, in which modulations of congruency effects are regarded as indices of cognitive control. For example, in a Stroop task the goal is to name the ink color of a word which can be either congruent (e.g. **RED**) or incongruent (e.g. **BLUE**) with the word itself. The extent to which irrelevant (in the example, word) information can be ignored is taken as an index of cognitive control. One key finding is that if the previous trial is incongruent, the congruency effect is smaller on the current trial (Gratton effect, [1]), which is interpreted as increased control after an incongruent trial [2]. Besides previous-trial modulation of the congruency effect, other modulations have been discussed as well, relevant neural systems have been identified and different theories have been proposed to account for the many findings in this literature [3–7].

An important issue for theories of cognitive control is dealing with the fact that the cognitive system has to know when and where to intervene to influence processing to optimize performance. Botvinick and colleagues [2] partly addressed this in their conflict monitoring theory by proposing that the amount of energy at the response level

determines when a cognitive control intervention is required. How the cognitive system has to know where to intervene (e.g. prioritizing color processing areas in the Stroop task) was not addressed, however.

An empirical but related issue is that many recent findings have emphasized the associative nature of cognitive control. For example, if in a Stroop task some color words are presented mostly congruently, and other color words mostly incongruently, the congruency effect is larger for the former type of stimuli ([Box 1](#)). This indicates that the cognitive control system not only selectively enhances particular tasks but also particular stimulus features. Inspired by this and other associative effects, an alternative interpretation of cognitive control effects has been put forward. This alternative holds that Gratton and similar effects are not related to cognitive control at all, but instead are the result of binding processes operating across stimulus–stimulus and stimulus–response representations [8–10]. For example, Hommel and colleagues [8] argue that such cognitive-control-like effects emerge from binding features into event files. This binding process is necessary for successful object processing [11] and action planning [12]. In this framework, the Gratton effect, for example, can be explained in terms of fast responding on trials in which all stimulus and response features are repeated or all features change (congruent followed by congruent and incongruent followed by incongruent). In contrast to theories that interpret these behavioral effects as instances of cognitive control (which we term adaptation theories), we collectively refer to such theories as binding theories [8,9].

Glossary

Cognitive control: the ability to suppress dominant responses in favor of less obvious but more appropriate ones. An example is ignoring verbal information and responding to color in incongruent stimuli such as **GREEN** in a Stroop task.

Congruency effect: performance (e.g. response time) difference between incongruent (**GREEN**) and congruent trials (**GREEN**) in congruency task (e.g. Stroop).

Gain: the ‘slope’ of a sigmoid function. In particular, for neurons with a sigmoid transformation function receiving input *net*, the output function is defined as $1 / (1 + \exp(-\text{gain} \times \text{net}))$.

Gratton effect: smaller congruency effect after incongruent trials than after congruent trials. This has been observed in all congruency tasks (Stroop, Simon and Eriksen flanker)

Response conflict: a measure of conflict reflecting the amount of competition between competing responses. When there are only two responses with activations *a* and *b*, response conflict reduces to $a \times b$. Hence, if either *a* or *b* equals zero (i.e. only one response activated), there is no response conflict.

Signal-to-noise ratio (SNR): the extent to which neurons respond more strongly to task-relevant stimuli (signal) than to neutral (e.g. fixation point) or distractor stimuli (noise). In neurons with a sigmoid transformation function, SNR depends on the gain of this function.

Box 1. Associative modulations of behavioral control effects

One inspiration point for our model was the modulation of the congruency effect in cognitive control tasks. Despite important caveats that were raised about their interpretation [9], such modulations at least partly reflect cognitive control [44,45]. One effect is that the congruency cost is modulated by the blockwise proportion of congruent stimuli [46]. In line with Refs [2,47], our model assumes that this blockwise effect has the same origin as the Gratton effect (but see Ref. [48]). Modulation can also be associated with specific stimulus features. For example, if color yellow is presented with a higher congruency proportion than color red, the congruency effect is larger for yellow. This is the item-specific congruency effect (ISPC) [3] (Figure 1b and 3b in main text). Similarly, if stimuli on the left-side location are presented with a higher proportion of congruency than on the right, the congruency effect is larger on the left. This is the context-specific congruency effect [49,50]. Further, the adaptation of the congruency effect (i.e. Gratton effect) is specific to the currently processed input dimension [51]. There is no Gratton effect (actually, a reversed one) if the relevant input dimension changes (i.e. a task switch). Based on these data, an associative basis for congruency modulations was proposed [13,47].

Modulations of the task switch cost have also been studied. One prominent theory states that the task switch cost results from task set reconfiguration [37]. A different line of theorizing starts from the finding that the switch cost is absent when there is no stimulus overlap between the two tasks [52]. Allport and colleagues [53] interpreted this as indicating that the switch cost is due to task-set inertia, meaning that the task set from the previous trial is carried over to the next trial (in which the task set from the previous trial is irrelevant). Later, authors observed that the switch cost was, for a large part, item-specific [54], leading to the idea of associative task-set inertia. Stimuli are bound to the task to be performed, causing interference when a different task has to be performed on a later trial. Consistent with this, activity in regions specific for the task that is not being executed (e.g. face areas during word processing when the participant is switching between face and word processing) predicts the behavioral switch cost [55]. In line with our model, such associative effects have been conceptualized in terms of Hebbian learning [56]. Finally, recent work also emphasizes the associative nature of inhibitory processes [57].

Adaptation by binding

To deal with the conceptual and empirical issues mentioned earlier, we recently proposed that cognitive control might be the result of interactions between arousal and online learning processes [13] (Box 2). To understand this proposal, consider again a participant in a Stroop experiment. There is a word input dimension and a color input dimension with a separate node for each value within a dimension, and each node projects to its corresponding response ('yellow', 'green', 'blue' or 'red') [14] (Figure 1a). If a trial is incongruent (e.g. GREEN in red), there is conflict at the response level which is detected by a conflict monitoring system (thought to be located in medial frontal cortex [MFC]). This conceptualization is the same as in the conflict monitoring theory. Contrary to that model, however, in our model the conflict monitoring system does not pass this information to a working memory system that

holds the task demand information, but triggers an arousal response in a neuromodulatory system (e.g. locus coeruleus [LC]) (Figure 2a). This system interacts with ongoing Hebbian (associative) learning [15] and influences binding of active representations online. In particular, on conflict trials Hebbian learning is increased. Hebbian learning acts on active representations, and because active representations are usually task-relevant, the result is a better adaptation to the task – cognitive control (Figure 3). Hence, because of the Hebbian nature of learning, the issues noted earlier are dealt with. First, the system does not need to be told where to influence processing: it simply influences all active representations, and active representations tend to be task-relevant. Second, for the very same reason, the resulting cognitive control will be of an associative nature. In this way, our adaptation by binding theory encompasses both adaptation theories and binding theories in the sense that cognitive control is conceptualized as a binding process. In the following two sections, we discuss the neural substrate of the proposed system and point out predictions at the behavioral level.

Box 2. Response incongruency leads to adaptation (Gratton effect)

Here, we describe what happens on an incongruent trial such as GREEN, and how this leads to a Gratton effect (Figure 3a in main text). Other effects can be derived in a similar way.

- Color RED is activated in the color input layer, and word GREEN in the word input layer (as in Figure 1b in main text).
- Both input activations activate a different response. This is recognized as response conflict by MFC.
- MFC passes this signal on to LC, which sends a noradrenergic modulatory signal throughout the brain which influences Hebbian learning.
- After every trial, network weights are adapted through Hebbian learning. There is more learning in high-conflict situations (incongruent trials) than in low-conflict situations (congruent trials). For simplicity, in the implementation reported in [13], only task-demand-to-input weights are adapted. In general, we envision that all weights attached to active neurons can be adapted.
- Because task-relevant representations are active, their connections will be strengthened. Because of the increased connectivity of the color task demand unit after an incongruent trial, this unit can influence input units more strongly on the next trial, leading to increased control. Because not only the current color (in the example, RED) but also other colors are slightly active, the Gratton effect extends across stimuli even though it is basically driven by associative learning.

Neural implementation*Prefrontal cortex*

We assumed that the conflict monitoring system is located in MFC. MFC does not only calculate response conflict but also performs a monitoring function. It evaluates how well the system is doing, expressed in terms of response conflict [2], error [16], error likelihood [5], pain or social exclusion [17], or other measures; more widely MFC is thought to assign values to actions [17,18]. All of these signals can, in addition to response conflict, be used for the purpose of performance optimization. Within MFC, different areas probably compute different signals depending on where exactly they receive input from. For example, the ventral part of anterior cingulate cortex (ACC), an area within MFC, receives prominent input from orbitofrontal cortex, whereas dorsal ACC (also in MFC) receives input from (pre)motor cortex (reviewed in Ref. [19]). In line with this, response conflict, as measured in typical congruency tasks, consistently activates dorsal ACC but not ventral ACC [4].

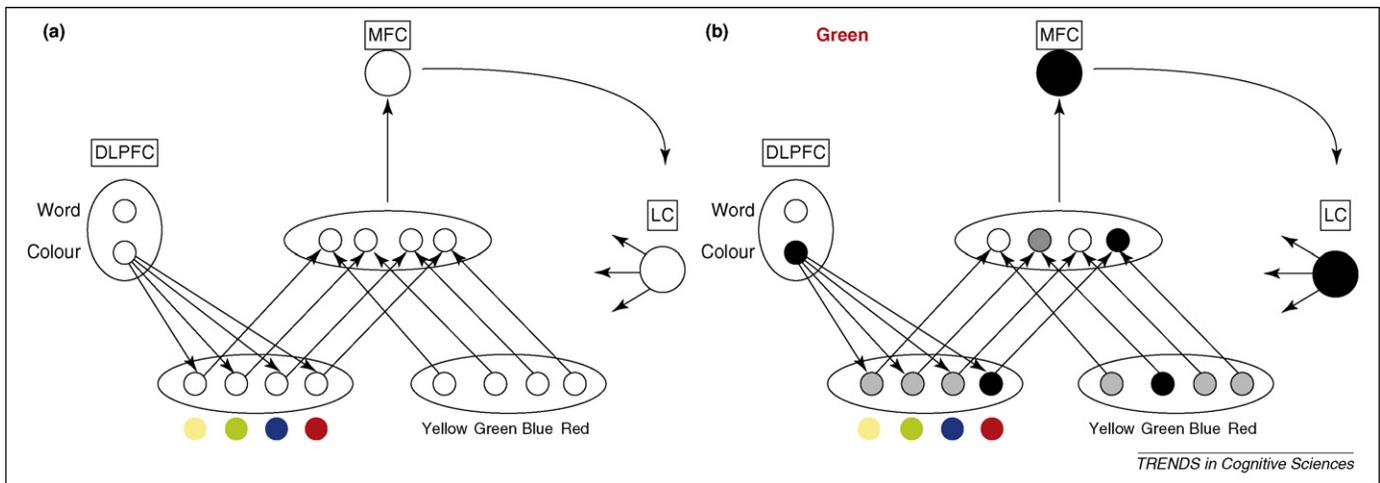


Figure 1. Schematic model for the Stroop task. **(a)** Basic model. There are two input layers, one for color information and one for word information. Both project independently to a response layer. Both also receive top-down input from a task-demand layer. If, for example, color is the relevant stimulus dimension, this dimension is selectively enhanced because of the top-down input from the color task demand neuron. The amount of conflict at the response layer is detected by a performance monitor in medial frontal cortex (MFC). Conflict signals from MFC are sent to subcortical area locus coeruleus (LC), which triggers a signal throughout cortex that learning should be increased. **(b)** Schematic illustration of the item-specific congruency effect (ISPC) (see also Box 1) in the Stroop task. If one particular ink color (e.g. red) is often presented incongruently during a block of trials, its congruency effect becomes smaller. In the model, this is because the color is associated with a large amount of conflict and as a result the connection from the color task demand unit to this color's input unit becomes very strong.

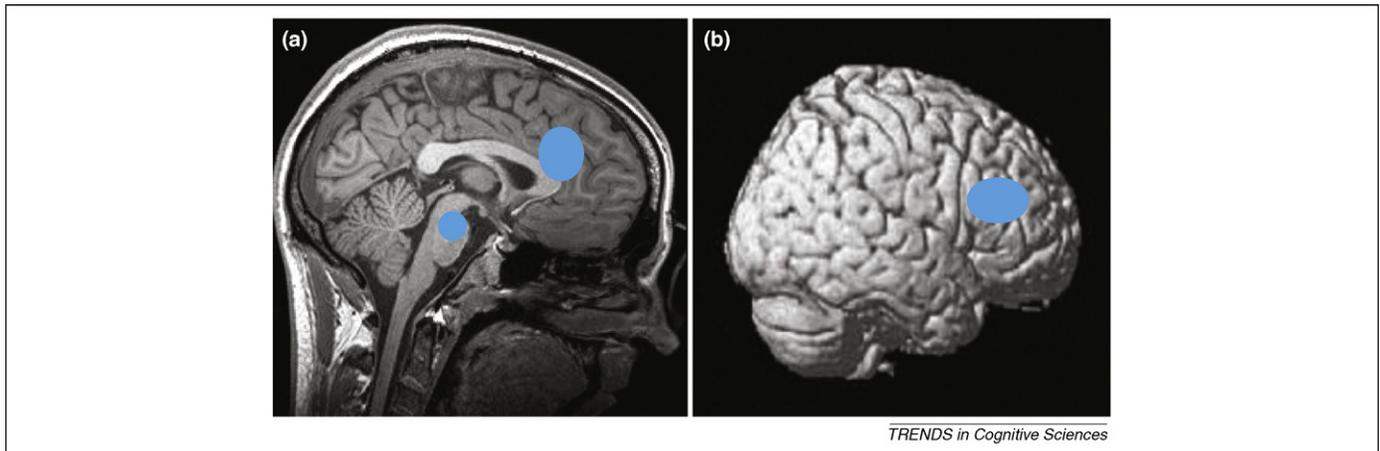


Figure 2. Anatomical localization of three of the main components of the model. **(a)** Approximate locations of medial frontal cortex (MFC) and locus coeruleus (LC). **(b)** Approximate location of dorsolateral prefrontal cortex (DLPFC).

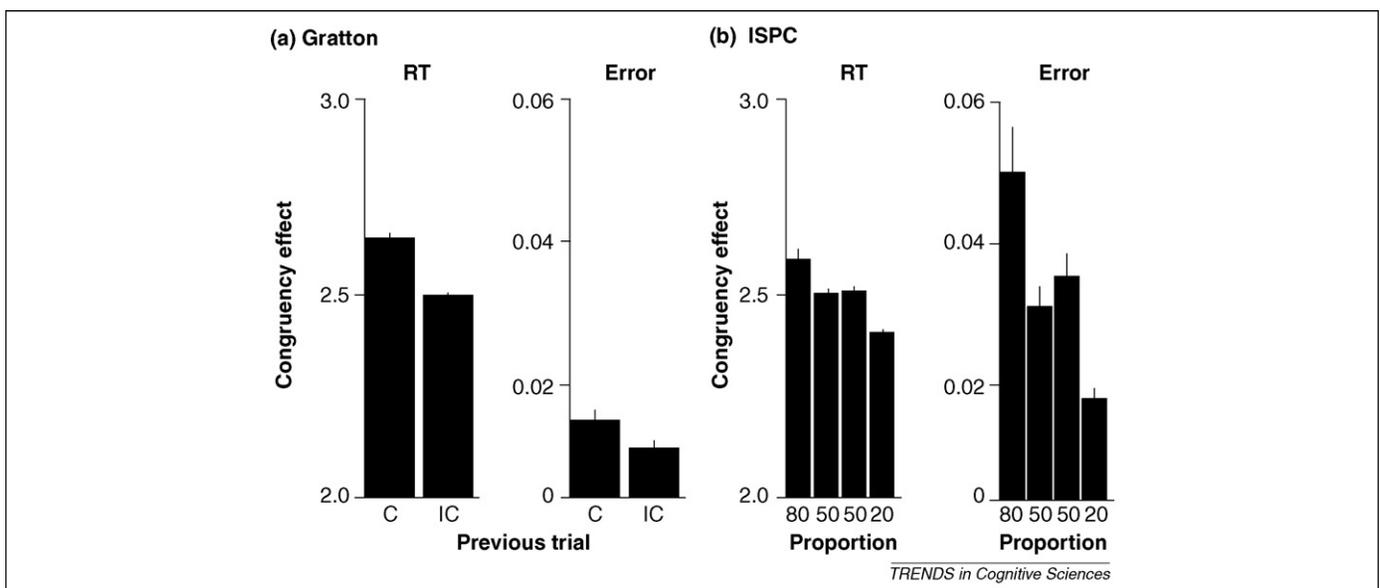


Figure 3. Simulated congruency effects in reaction times (RT) and error rates. **(a)** Gratton effect. C, previous trial congruent; IC, previous trial incongruent. **(b)** Item-specific congruency effect (ISPC). Numbers on the X-axis refer to the proportion of congruency for different colors.

Important for our proposal is that both ventral and dorsal ACC project to brainstem nuclei that potentiate the autonomic nervous system. As a consequence, stimulation of either dorsal or ventral ACC leads to autonomic responses (i.e. arousal; Refs. [19,20]).

In the model, we postulated a working memory structure that biases posterior cortical processing areas [21]. As in conflict monitoring theory, we propose that this structure resides in dorsolateral prefrontal cortex (DLPFC) (Figure 2b), as this area is known to be involved in working memory and top-down biasing of sensory processing areas. One difference with conflict monitoring theory is that in our model, DLPFC does not directly receive input from MFC; MFC exerts its effect on DLPFC indirectly through LC-related processing. Hence, it provides an alternative interpretation for the correlation between MFC activation on the current trial of a congruency task and DLPFC activation on the following trial [4].

LC and Hebbian learning

In Ref. [13], we proposed that LC is a good candidate for fulfilling the role of neuromodulatory center in our model. LC receives prominent projections from ACC (also dorsal; Ref. [22]), and it projects throughout cortex. In response to a signal from ACC (or MFC more widely), we assume that LC triggers noradrenalin (NA) throughout the brain, which influences online learning processes. To understand this arousal-learning interaction in more detail, consider the Hebbian learning rule, which states that weight changes between two connected cells are proportional to the product of presynaptic and postsynaptic activity:

$$\Delta w_{ij} = \lambda \times x_i \times x_j \quad (\text{Equation 1})$$

where x_i and x_j are the activation of the sending cell i and receiving cell j , respectively. There is strong physiological evidence for this rule; in particular the experimental protocol of long-term potentiation (LTP) shows striking similarities to Equation 1 and is thought to be crucial for learning [23].

Virtually all learning rules in computational neuroscience (e.g. competitive learning, backpropagation) can be considered as variants of the Hebbian learning rule [24]. An important means of introducing variations to the Hebbian learning rule is by modulating the learning rate parameter λ by a reinforcement term, which functionally leads to a variable learning rate [25]. Recently, it was argued that also volatility, or instability of the environment, might increase the learning rate [26]. In highly volatile environments, new regularities need to be extracted from the environment and therefore it is adaptive to speed up learning. We propose that arousal can speed up learning; volatility would then be one factor to increase arousal, possibly through the frequent detection of unpredicted events in volatile (unpredictable) contexts. It was found [26] that higher volatility was associated with higher ACC activation, consistent with the idea that volatility increases arousal. This proposal is consistent with the ubiquitous finding in the psychology of learning that surprising stimuli lead to faster learning [27], and with the fact that emotion enhances memories [28]. Finally, advocates of binding theory [29] have also

argued that binding processes can be modulated by arousal.

LC activation might facilitate learning directly by increasing the learning rate. This principle was implemented in our model by making the learning rate dependent on the amount of conflict. This follows up on a long tradition of theories postulating that NA triggers a 'now print' signal [30,31] to the brain, suggesting currently active representations should be bound together. At the neurophysiological level, NA has indeed been shown to facilitate LTP [32].

An alternative and influential theory of LC functioning is the adaptive gain theory of Aston-Jones and Cohen [22]. According to these authors, NA increases the gain of task-relevant neurons [33,34]. In tonic response mode, in which LC activity is extremely high (stress), the gain is increased so strongly that also distractor stimuli influence response selection and behavior is not task-related. This situation results in a search for a new adapted response repertoire (exploration). In phasic mode, when performance is better and stress is reduced relative to tonic mode, the gain of task-relevant neurons is more appropriately and selectively increased on presentation of task-relevant stimuli. This increases the signal-to-noise ratio (SNR) of (task-relevant) neurons, leading the organism to exploit its (appropriate) response repertoire and to optimize task-related behavior. Although this theory of LC functioning might seem contradictory to our own, it is actually complementary, in that it provides an alternative way of implementing NA-modulated learning. Note first that our proposal is clearly limited to the phasic (exploitation) mode of LC responding. Adaptation by binding theory is concerned with situations in which task performance is usually high (but not perfect), and it operates at a fast time scale (i.e. locked to stimulus presentation). In phasic mode, LC release increases SNR, which means increasing pre- and post-synaptic activity (x_i , x_j in Equation 1) of active neurons. This leads to larger weight updates Δw_{ij} and hence to faster learning. Hence, besides increasing SNR, increasing gain might also facilitate learning.

If our account is true, one could wonder why LC activation is not typically reported in cognitive control imaging studies. One possible reason is that LC is very small, and would not survive standard voxel extent correction procedures. More widely, to study its role in cognitive control, it might be necessary to scan this area specifically, as was done for other subcortical areas [35].

Behavioral implications of adaptation by binding

One prediction emerging from adaptation by binding theory is that incongruency, as measured in congruency tasks (e.g. Stroop), leads to autonomic responses. This has indeed been observed [36]. Second, arousal-inducing but task-irrelevant stimuli should induce a stronger focus on task-relevant stimuli (i.e. Gratton-like effect). This remains to be tested.

Besides the congruency effect, a second often-studied effect in the cognitive control literature is the switch cost, which is the (response time [RT]) difference between task switch and task repetition trials [37]. In contrast to the congruency effect, the switch cost is larger after an

Box 3. Outstanding questions

- Why does impaired connectivity between frontal cortex regions lead to a diminished error-related negativity (ERN) wave [58]?
- How is error detection related to conflict, control, arousal and adaptation?
- It has been suggested that cognitive control can be executed online (i.e. within a task trial) [59], although the evidence as yet is not conclusive. If it exists, how is it related to between-trial cognitive control?
- Which neuromodulators are involved in arousal-modulated learning? Can psychiatric disorders associated with these neuromodulators (e.g. schizophrenia) be understood from this point of view?
- How do arousal- modulated and reinforcement-modulated learning interact?
- Can the framework described in this article be applied to the early stages of task application, that is, translating verbal instructions to stimulus–response mappings?
- Can arousal-modulated learning be understood from an optimality (Bayesian) perspective?

incongruent trial than after a congruent one [38,39]. Although our model was not designed to capture switch costs, it predicts this because incongruency leads to stronger task-stimulus bindings which helps performance on task repetition trials but impairs performance on switch trials. In general, the model predicts that switch costs can be bound to specific stimulus or context features, even task-irrelevant ones. Although there is preliminary evidence for this [40], it remains to be investigated more thoroughly.

Because adaptation by binding theory interprets cognitive control phenomena as instances of more general interactions between learning and arousal, predictions to other domains are possible as well. Adaptation by binding predicts that all connections between representations active at the time an arousal signal arrives, are strengthened, also if they are irrelevant to the task. Consistent with this, implicit learning (of task-irrelevant information) seems to depend on conflict, or arousal more widely. One instance is implicit sequence learning, which is investigated in serial RT tasks in which subjects press different buttons depending on stimulus color (e.g. button 1 for red stimulus, button 2 for blue stimulus, and so on [41]). Unknown to the participants, the stimulus sequence obeys an underlying regularity. Implicit learning of this sequence is evident from decreasing RTs, with RT increase when a new, or random, sequence is introduced. Unintended learning of such sequences depends on task demands. In Ref. [42], for instance, it was demonstrated that a sequence of words was better learned if the task was less automatic and more effortful. For example, more implicit learning was observed when participants had to categorize words than when they had to read them. This can easily be incorporated in our model because less automatic mapping rules lead to more conflict (just like color naming trials lead to more conflict than word naming trials in a Stroop task) and hence more LC activation. The release of NA results in stronger associations between representations involved in encoding sequences in this task.

Another instance of implicit learning is implicit perceptual learning. In Ref. [43], dots were presented that were

moving in a given direction (e.g. upward) with 5% coherence (below the detection threshold), coupled with task-relevant stimuli. Dots moving in another direction (e.g. downwards) were coupled with task-irrelevant stimuli. Although irrelevant to the task, they observed that perceptual learning of movement direction occurred after the main task, but only for the motion direction associated with task-relevant stimuli. They attributed this to diffuse reinforcement signals on task-relevant trials boosting both task-relevant processes and task-irrelevant ones (here, in brain areas for movement detection). From our perspective, it could be assumed that arousal (rather than reinforcement) is sufficient for this effect (Box 3).

To sum up, we propose that many aspects of cognitive control can be understood as modulations of Hebbian learning. This integrates different accounts of cognitive control phenomena, and also links the traditionally separate domains of learning, emotion and cognitive control.

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