

time-spanning associations of sensory information that are stored in networks of perceptual and executive cortex.

Prefrontal integration works not only across time, but also across different sensory modalities such as audition and vision [19]. Contrary to a common misconception, nowhere in an ascending or descending cortical hierarchy does processing need to be exclusively serial. In part because of its dependence on feedback throughout, the processing in the perception–action cycle takes place not only in series but also in parallel. Koechlin *et al.* provide us with clear evidence that the cascading serial and parallel processing of action entails the orderly downward activation of the executive frontal hierarchy.

Future research

In cognitive neuroscience, the methodology of human studies is inextricably related to that of non-human primate studies. As the research of Koechlin *et al.* so beautifully exemplifies, modern neuroimaging in humans can test and substantiate hypotheses of cognitive function that derive from monkey studies. Conversely, imaging data on the cognitive activation of the human cortex lead to hypotheses of mechanism at the cellular level that can best be tested in the non-human primate. An urgent item in the neuroscientist's agenda, which will benefit both human and non-human methodologies, is to elucidate at the cellular level the neural–hemodynamic coupling underlying functional imaging methods such as fMRI.

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Conflict, consciousness, and control

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To what degree is executive conflict resolution dependent on conflict awareness? A recent study by Dehaene *et al.* compared neural responses to conflict elicited through either visible or subliminal primes. Despite behavioral conflict effects for both prime types, neural activity in a control network including the anterior cingulate cortex (ACC) was present only for visible primes. Along with other recent results, these findings have important implications for theories on the relationship between ACC, consciousness, and cognitive control.

What is consciousness for? An important step towards an empirical answer to this question would be the

establishment of precise boundaries between neurocognitive functions that can run outside of awareness, and functions that require consciousness as a necessary condition. The search for such boundaries should be particularly promising at the lines that delineate those operations that monitor and regulate ongoing processing in a goal-directed manner (often subsumed under the label 'executive control') from those domain-specific and often routine activities that execute the actual, task-specific computations. It has been often noted that we usually become aware of those aspects in the internal or external world that interfere or interrupt routine action – which are very same events that typically elicit executive control operations [1]. Interestingly, in recent biologically plausible network simulations, both consciousness and

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executive control have been equated with a state of representational coherence within a global computational work space [2,3]. By this theory, both the anterior cingulate cortex (ACC) and prefrontal cortex constitute crucial neural substrates of the global work space that enables consciousness and control.

Other models assume that important aspects of control can occur outside of awareness. Specifically, the so-called conflict-monitoring model proposes a thermostat-like feedback loop that assigns to ACC the role of a sensor of cognitive conflict [4,5]. If ACC registers high conflict values then a subsequent tightening of control is triggered (which in turn results in a reduction of conflict). Such a closed feedback loop can elegantly account for conflict adaptation effects [6] in which indications of behavioral conflict (e.g. in the flanker paradigm) are reduced on trials following trials with high conflict (but see [7]), or, for adaptive slowing following action errors, see [8]. Important in the current context is the fact that there is no point within this feedback cycle where awareness of conflict comes into play.

Probing the nature of the awareness–control relationship

How can we make progress regarding our understanding of the awareness–control relationship? Optimally, one would want to examine the neural and behavioral indicators of control, both as a function of awareness and, if possible, as a function of the integrity of the neural control network. If control is contingent on awareness then we should see neural and behavioral indications of control only when awareness is high, and when the control network is intact. Dehaene, Artiges, Naccache, Martelli *et al.* [9] attempted to achieve such a situation in a recently reported study, using number processing as task domain. Participants executed speeded judgments of numbers (printed in Arabic format or spelled out) in terms of their magnitude (smaller or larger than 5). Target numbers were preceded by primes that were either congruent or incongruent with the target number in terms of their magnitude.

Awareness of conflict was manipulated by using primes that were either invisible, because sandwiched between random letter strings, or clearly visible, because presented without a mask. We know from past research that invisible primes can elicit behavioral conflict (i.e. slower responses for incongruent than for congruent prime–target pairs) [10].

Integrity of the control network was varied through inclusion of schizophrenic patients as participants along with healthy controls. Schizophrenic patients are known to show structural and functional abnormalities in ACC and related prefrontal areas and thus allow examining how crucial these areas are for the emergence of an awareness–control relationship.

Both healthy controls and schizophrenic patients exhibited similar behavioral effects on indicators of number processing. For example, numerical distance (how far was the target number from 5), number format (Arabic or spelled out), and, most importantly, also the unconscious, masked congruency effect were virtually identical between the two groups. In other words, the

domain-specific processing of number information was not negatively affected in schizophrenic patients.

The pattern of results was very different for visible primes: no matter whether congruent or incongruent, response times were substantial longer than for masked primes, suggesting additional control demands when *potentially* interfering information is presented. Importantly, this control cost was increased for schizophrenic patients by a factor of three. A plausible interpretation of this pattern is that with ‘normal’ interference resolution missing, patients were forced into a strategy of withholding responses until prime effects had dissipated. More difficult to interpret is the fact that the actual prime–target congruency effect showed a small, paradoxical reversal in patients, but not in controls (Dehaene *et al.* provide possible interpretations [9]).

Brain imaging responses from fMRI analyses were consistent with a dissociation between unconscious, within-module processing on the one hand, and conscious conflict regulation on the other. Compared with the resting state, number-processing areas in posterior cortex exhibited similar levels of activation in both controls and patients. However, ACC and related frontal sites were generally active only in controls, but not in patients. Perhaps most important, prime-induced conflict had a clear effect on ACC activity (higher for incongruent than for congruent primes), but only if the primes were visible. Unconscious conflict did not seem to register in ACC. By contrast, and consistent with the behavioral congruency effects, schizophrenic patients exhibited conflict-related ACC activity neither for masked nor for unmasked primes.

At least when taken at face value, these findings suggest that consciousness of conflict is a necessary boundary condition for the ACC-related control network to come into play. Furthermore, intact control in response to conscious conflict requires an intact ACC-prefrontal network. Clearly, the finding that conflict-related activity is contingent on awareness would be inconsistent with the position that ACC is merely a ‘dumb’ sensor of conflict [4,5].

There is, however, one important caveat associated with this general interpretation. Specifically, for controls, behavioral conflict effects were about twice as large when primes were visible than when they were masked. As Dehaene *et al.* [9] readily admit, this leaves the possibility that rather than consciousness being a necessary condition for conflict-related ACC activity, conflict-related ACC activity might be the necessary condition for awareness of conflict. It may be that with larger unconscious conflict effects, ACC-related activity would have been obtained.

Other studies using awareness–control designs

The results of the Dehaene *et al.* study may not be fully conclusive. However, they do highlight an important approach to the question how exactly consciousness and neurocognitive aspects of control are related. In fact, there are now results from a handful of studies using the same basic strategy of contrasting behavioral and/or neural responses to unconscious and conscious control demands

Table 1. Studies using an awareness–control design

Study	Tasks	Awareness of conflict/errors	
		Yes	No
Dehaene <i>et al.</i> [9]	Size discrimination of numbers preceded by masked or visible number primes	fMRI activity in ACC/prefrontal areas Behavioral difference between schizophrenics and controls regarding conflict effect	No fMRI activity in ACC/frontal network Same behavioral conflict effect for schizophrenics and controls
Kunde [11]	Discrimination of arrows preceded by masked or visible arrow primes	Presence of conflict adaptation effect attributed to ACC (Botvnick <i>et al.</i>)	No conflict adaptation effect
Nieuwenhuis <i>et al.</i> [12]	Antisaccades to a target stimulus; trialwise assessment of saccade-error awareness	Presence of ERN Presence of error positivity Presence of corrective post-error slowing	Presence of ERN Absence of error positivity Absence of post-error slowing
Scheffers and Coles [14]	2-choice flanker task under data-limited conditions; trialwise assessment of error awareness	Large ERN after perceived errors	Small ERN after uncertain errors
Stephan <i>et al.</i> [15]	Synchronized tapping to either subliminally or supraliminally perturbed, external beats	fMRI activity in ACC/DLPFC Presence of behavioral motor adjustments	fMRI activity in ventral/ medial prefrontal areas Presence of behavioral motor adjustments

(see Table 1). Does a clear picture emerge when these studies are examined in conjunction?

Interestingly, there is one study that looked at behavioral adaptations to conflict (which according to the conflict-monitoring model are triggered through the ACC) and which achieved roughly comparable conflict effects for masked and visible [11]. In line with the notion that consciousness is a precondition for ACC-triggered conflict regulation, the conflict-adaptation effect occurred only when subjects were aware of the primes. Unfortunately, neural measures were not assessed here, thus, we have no direct information how ACC behaved in this situation.

A related result was reported by Nieuwenhuis *et al.*, who looked at eye-movement errors in an anti-saccade paradigm. Via trial-by-trial self-report, the authors were able to distinguish between eye-movement errors subjects were aware of and errors that went unnoticed [12]. Post-error slowing, which is often regarded to be an ACC-triggered adaptive response to errors [8], was only found after conscious errors. The authors also looked at the error-related negativity (ERN), which is typically associated with the ACC [13]. Surprisingly, at least in the face of the results by Dehaene *et al.*, the ERN did not differ between conscious and non-conscious errors. Interestingly, this latter result seems at least somewhat at odds with a study using a choice response-time task [14] in which the ERN was found to increase as a function of subjective error certainty, independently of whether or not an error had actually occurred.

Finally, a finding that is in line with the general neuroanatomical results obtained by Dehaene *et al.* was reported in a study that looked at rhythmic synchronization to a steady beat, perturbed by temporal distortions that were either above or below awareness threshold [15]. Only adjustments to conscious perturbations elicited

widespread neural responses that included ACC and dorsolateral prefrontal cortex.

There is some convergence across studies in that awareness seems crucial for at least some types of regulation [9,11,12], and also for indications of ACC-related activity [9,14,15]. This pattern seems more in line with the assertion that awareness is at least an important factor for control-related ACC activity. At the same time, enough inconsistencies [12] remain to preclude any firm conclusion in this regard.

Outlook for future

A fruitful next step in this general approach would be a more precise conceptualization and assessment of consciousness. Recent work, involving the first author of the targeted paper could lead the way [16]. The authors applied network simulations of their workspace framework, which equates a globally coherent, representational state with consciousness, to the attentional blink phenomenon (i.e. subjects' frequent failures to consciously identify a target that follows an initial target within a rapid, serial stream of non-targets [17]). An important prediction derived from the model simulations was that coherent representational states (and thus awareness of an event) should behave in an all-or-none fashion: either you experience something consciously or you don't. A subsequent, behavioral assessment of subjective target-awareness ratings (ranging from 'not seen' to 'maximal visibility') in the attentional-blink task confirmed this prediction: participants' ratings clustered at either zero or at full awareness with virtually no scores between the two extremes.

If awareness of an event actually possesses such a bimodal quality, then this could serve as an important signature for distinguishing two types of brain areas: those that rely on awareness and those that are potentially involved in triggering states of awareness. For example, if

conflict-triggered ACC activity is a result of awareness, then it should exhibit similar all-on-none activation patterns. Alternatively, if ACC is involved in triggering awareness of conflict then ACC activity should vary in a continuous manner with awareness arising only beyond a particular threshold.

Questions about the neural basis of consciousness and its adaptive functions are among the hardest in cognitive neuroscience. Even with the results discussed here, ultimate answers might still remain in the dark. Clearly, though, some light has been cast on the next steps ahead.

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Binocular battles on multiple fronts

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The visual percept fluctuates over time when dissimilar patterns are shown to the two eyes (binocular rivalry). Where in the brain are the corresponding fluctuations of neuronal activity? Conflicting results from studies using various techniques have rendered this question unresolved at present. A recent paper by Wilson, however, promises to reconcile previous disagreements, as it demonstrates that rivalry can be located at different stages of the neuronal hierarchy, depending on the nature of stimulation.

When the brain receives conflicting information about the outer world, it adopts a strategy of changing its interpretation over time, rather than sticking to a single interpretation or holding multiple interpretations simultaneously. As an extreme case, consider your left eye viewing a vertical grating while the right eye views a horizontal grating, as illustrated in Figure 1a. Instead of seeing both patterns superimposed or, alternatively, one exclusively, you will see the vertical grating for several seconds and

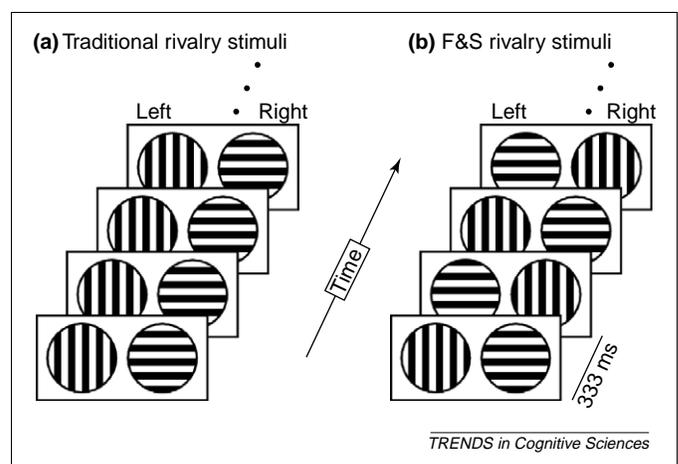


Figure 1. Schematic diagram of stimulus displays presented to Wilson's neuronal model of rivalry [3]. (a) Time course of traditional rivalry patterns. Vertical and horizontal gratings were continuously presented to the left eye and the right eye, respectively. (b) Time course of 'F&S' rivalry patterns. Vertical and horizontal gratings were swapped between the eyes every 333 ms, and were flickering on-off at 18 Hz (not shown).

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