



Discussion Paper

On the functional anatomy of the urge-for-action

Stephen R. Jackson^{1,2}, Amy Parkinson², So Young Kim¹, Martin Schüermann²,
and Simon B. Eickhoff^{3,4}

¹Department of Brain and Cognitive Engineering, Korea University, Seoul, South Korea

²School of Psychology, University of Nottingham, Nottingham, UK

³Department of Psychiatry and Psychotherapy, RWTH Aachen University, Aachen, Germany

⁴Institute of Neuroscience and Medicine (INM – 2), Research Center Jülich, Jülich, Germany

Several common neuropsychiatric disorders (e.g., obsessive-compulsive disorder, Tourette syndrome (TS), autistic spectrum disorder) are associated with unpleasant bodily sensations that are perceived as an urge for action. Similarly, many of our everyday behaviors are also characterized by bodily sensations that we experience as urges for action. Where do these urges originate? In this paper, we consider the nature and the functional anatomy of “urges-for-action,” both in the context of everyday behaviors such as yawning, swallowing, and micturition, and in relation to clinical disorders in which the urge-for-action is considered pathological and substantially interferes with activities of daily living (e.g., TS). We review previous frameworks for thinking about behavioral urges and demonstrate that there is considerable overlap between the functional anatomy of urges associated with everyday behaviors such as swallowing, yawning, and micturition, and those urges associated with the generation of tics in TS. Specifically, we show that the limbic sensory and motor regions—insula and mid-cingulate cortex—are common to all of these behaviors, and we argue that this “motivation-for-action” network should be considered distinct from an “intentional action” network, associated with regions of premotor and parietal cortex, which may be responsible for the perception of “willed intention” during the execution of goal-directed actions.

Keywords: Urge; Urge-for-action; Habit; Insula; Tourette syndrome; Action.

Many of our everyday behaviors are characterized by bodily sensations that we experience either as an *urge* or a *desire* for action. For instance, we may experience a sensation that our bladder is full that is accompanied, to a greater or lesser extent, by an urge or desire to urinate (micturate). In extreme cases, this sense of fullness can be quite uncomfortable and the urge to urinate can be hard to suppress. Similarly, we may experience a tickle in our throat that is associated with an urge to cough or to swallow that can also be difficult to suppress voluntarily.

However, not all urges for action are necessarily preceded by bodily sensations of which we are aware. For example, we may suddenly experience a strong urge to yawn, or even find ourselves yawning, without being aware of a sensory “trigger” for the action. In this paper, we consider the nature and the functional anatomy of these “urges-for-action,” both in the context of everyday behaviors such as yawning, swallowing, and urinating, and in relation to clinical disorders in which the urge-for-action is considered pathological and substantially

Correspondence should be addressed to: Stephen R. Jackson, School of Psychology, University of Nottingham, Nottingham NG7 2RD, UK.
E-mail: stephen.jackson@nottingham.ac.uk

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interferes with activities of daily living (e.g., Tourette syndrome, obsessive-compulsive disorder, addiction).

A CONCEPTUAL MODEL OF THE URGE-FOR-ACTION

In common usage, the terms “urge” and “desire” are frequently encountered as both a verb (as in to “urge someone on”—i.e., to motivate, impel, or stimulate a person toward an action) and as a noun (as in “he felt an urge to shout”—i.e., a force, drive, or impulse that impels toward a goal). Furthermore, these terms are often used interchangeably with one another, and are frequently listed as synonyms.

Nevertheless, it has been suggested that there is an important distinction to be made between urges and desires (e.g., Cameron, 2002; Davenport, 2008). Thus, Cameron (2002), when discussing interoception, and the relationship between conscious awareness and visceral events, makes a distinction between “detection,” which is an organism’s reflexive response based solely upon afferent physiological information, and “perception,” which refers to an organism’s response based upon all information available to the organism (which might include learned information and expectations that might be generated as a result of learning). Similarly, Davenport, when discussing mechanisms associated with the urge-to-cough, defines an *urge* as a physical need to respond to a sensory stimulus, and a *desire* as the translation of an urge into what he refers to as “a central neural targeted goal” (Davenport, Sapienza, & Bolser, 2002). Davenport’s motivation-to-action model is presented in Figure 1.

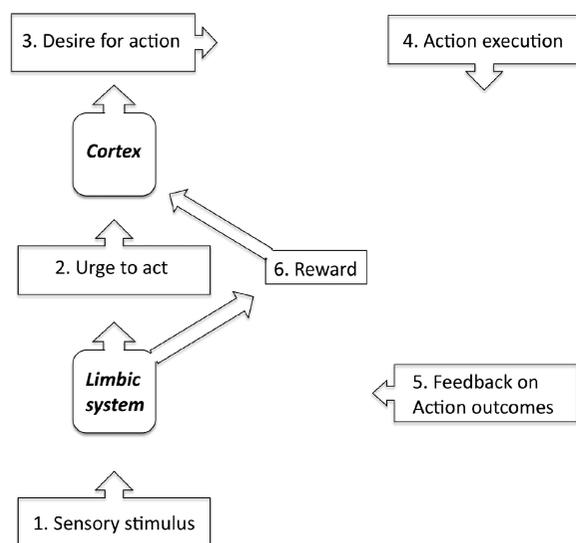


Figure 1. The motivation-for-action model proposed by Davenport to account for the urge to cough (adapted from Davenport, Sapienza, & Bolser, 2002).

Combining these two ideas we might conclude that an urge—as in a drive for action—need not enter conscious awareness, but that we are always aware of our desires. An example might help make this distinction clearer. Imagine that you are driving your car and you suddenly become aware of an uncomfortable sensation that your bladder is full, which you experience as the *urge to urinate*. Given that you can in all likelihood control this urge, you may then form a *desire to urinate* in which you construct a goal or plan which includes a representation of the behaviors required to complete the action (e.g., remembering that you passed a filling station a mile back and knowing that filling stations usually have public toilets) and a representation of the likely outcomes of the action. Can an urge exist if we are not aware of it? What factors determine whether an urge enters awareness? How is an urge to act different from an intention to act? These issues are discussed below.

ARE URGES SIMPLY REFLEXES?

As outlined above, urges are often defined as the drives or impulses that impel us to act. Nevertheless, it is argued that actions can, and frequently do, occur in the absence of any awareness of such drivers, as in the case where one finds oneself yawning without previously being aware of either the desire to yawn or of any bodily sensation that might reasonably be identified as giving rise to the yawn. Instead, one simply finds oneself yawning. In this case, it might be argued that this is a *reflexive* behavior and not an urge-for-action.

One possible distinguishing feature of urges, as distinct from reflexes, may be that urges are chiefly associated with actions that cannot be realized immediately and must be held in check until an appropriate time when they might be released. For instance, when we become aware of having a full bladder, we experience an “urge-to-void” because we do not simply void our bladder, but instead employ a coordinated set of central, autonomic, and peripheral neural mechanisms to withhold micturition until we are in an appropriate behavioral context. Similarly, in the case of yawning, we might define the urge-to-yawn as arising in circumstances where we are forced to try to stifle the yawn rather than in the situation where we find that we are yawning.

HOW ARE URGES RELATED TO AWARENESS?

One factor that may determine whether an urge enters awareness is the intensity of the physiological afferent.

It has been demonstrated in the context of the urge-to-cough that the perceived strength of the urge that is experienced is related to the intensity of stimulation. Specifically, when capsaicin is added to the breathing circuit, it results in a sensation that is perceived as an urge-to-cough. Furthermore, increasing capsaicin levels leads to a reliable increase in estimates of this urge (Davenport, Sapienza, & Bolser, 2002). Similarly, in our own unpublished studies of the effects of oropharyngeal stimulation on the urge-to-swallow, we have found that oropharyngeal stimulation using pulses of air produces both an urge-to-swallow and overt swallowing (for similar findings, see also Lowell et al., 2008). More importantly, we have found that increasing the intensity of oropharyngeal stimulation leads to an increase in the strength of the perceived urge-to-swallow. An important question therefore concerns the role of awareness, and by implication “desire,” in the initiation of urge-related actions.

According to the motivation-to-action model represented in Figure 1, actions are initiated only after a desire to perform an action has been formed. However, we do not see this step as necessary and would amend this model, so as to allow for actions to be initiated directly, without the need to first construct an explicit “desire for action.” Two factors motivate this amendment. First, it strikes us that in many instances actions (e.g., yawning) can be triggered without our necessarily being aware of any explicit desire. Second, in many clinical conditions (e.g., Tourette syndrome), as we shall see below, *unwanted* actions or behaviors, which individuals struggle actively to suppress, are nevertheless preceded by strong premonitory urges. In our view, it is difficult to reconcile the concept of a “desire,” which is often defined as “a longing or craving for something that brings satisfaction or enjoyment,” with unwanted actions, the execution of which is experienced as unpleasant and distressing.

If we accept the premise outlined above that urges-for-action are often accompanied by bodily sensations, then it strikes us that an important distinction can be drawn between being aware of a bodily sensation and being aware of an urge-for-action. This distinction can be best illustrated by considering the following examples. In the case of an itch, we may be aware of experiencing both an itch (bodily sensation) and an urge to scratch the itch (urge-for-action). By contrast, while we may become aware of an urge-to-yawn, it is not entirely clear that we are ever aware of the bodily sensation that gives rise to the urge to yawn. Furthermore, this becomes more important if we accept the argument outlined above that urges occur primarily in circumstances in which actions may need to be suppressed or their execution deferred. In such circumstances, we might distinguish between suppression of the

action associated with the urge-for-action, or suppression of the *bodily sensation* giving rise to the urge. This distinction has important clinical implications (see below), and an interesting issue for future research will be to determine whether the suppression of bodily sensations and the suppression of urges-for-action differ in terms of their functional anatomy.

HOW IS AN URGE TO ACT DIFFERENT FROM AN INTENTION TO ACT?

The kinds of actions that we have considered as representative of urges-for-action are highly automatic, habitual responses that occur primarily in response to sensory stimulation. These might include brushing an insect off your arm, scratching an itch, yawning when tired, coughing in response to a tickle in your throat, etc. While such actions can, in some circumstances, be executed with little or no awareness of the sensory stimulation that triggered the action, as when one finds oneself yawning or coughing, we have argued that a key characteristic of urges-for-action is that they involve the suppression or deferment of an action. Such actions might therefore be contrasted to intentional, goal-directed, forms of action.

The circumstances in which the “willed intention” to execute an action can be shown to follow the brain processes involved in the preparation for action were famously studied by Benjamin Libet (Libet, Gleason, Wright, & Pearl, 1983), and more recently by Patrick Haggard and colleagues (e.g., Haggard, 2005; Haggard & Eimer, 1999; Sirigu et al., 2004). In Libet’s task, participants fixated on a time-varying, rotating visual spot and were instructed to make a voluntary hand movement whenever they felt the “urge” to do so. Participants were asked to indicate the location occupied by the moving spot when they had first felt the urge to move their hand. Libet showed that this “W judgment” occurred some 200 ms prior to movement onset, but, more importantly, he also showed that the preparatory brain activity that precedes voluntary action, the so-called “readiness potential,” itself preceded the “W judgment” by several hundred milliseconds. Such readiness potentials arise in the premotor regions of cortex, including both the supplementary motor area (SMA) and the presupplementary motor area (pre-SMA), regions that have been linked to the planning and preparation of intentional, goal-directed, actions and sequences of actions (Deecke & Kornhuber, 1978).

Haggard has argued that conscious awareness of our intention to act arises during the preparatory processes that precede an action, and is linked to the joint activity of premotor and parietal brain areas (Haggard, 2005).

In support of this view, he has shown that patients with damage to the parietal cortex show a specific impairment in reporting when they became aware of their intention to move (i.e., Libet's "W judgment"). The proposal that the parietal cortex may maintain a dynamically updated state estimate of the current postural configuration of the body (the body schema) is well supported by neuropsychological (e.g., Wolpert, Goodbody, & Husain, 1998) and recent fMRI studies (e.g., Parkinson, Condon, & Jackson, 2010; Pellijeff, Bonilha, Morgan, McKenzie, & Jackson, 2006).

While it is clearly the case that in such experiments individuals can report when they first perceived themselves to have formed an "intention" to move, it is another thing entirely to argue that such conscious "intentions" typically precede everyday actions. Thus, when I am sitting at my desk typing and I break off to reach for my coffee cup I am not aware of forming an intention prior to each keystroke that I make or of forming an intention to reach for my coffee. Instead, I am aware of the actions I am making. Similarly, while it is clearly demonstrated that our actions are preceded by neural activity, as discussed by Libet and by Haggard and colleagues, it is currently unclear how these activations relate to the phenomenology of intention.

Haggard and others (e.g., Blakemore, Wolpert, & Frith, 2002; Haggard, 2005) have argued that the sense-of-agency that typically accompanies the execution of voluntary movements arises as a result of internal forward sensory models that generate a prediction of the sensory consequences of an action that is then matched against afferent sensory signals. It has been proposed that in cases where the link between these sensory predictions and confirmatory sensory input is broken, neurological syndromes such as anosagnosia (lack of awareness of injury) or somatoparaphrenia (denial of limb ownership) may occur (Tsakiris, 2010). Interestingly, both of these disorders have been linked to damage of the anterior insular cortex of the right hemisphere (Baier & Karnath, 2008; Karnath, Baier, & Nagele, 2005). However, it is important to note that this sense of agency may in fact have a significant postdictive or reconstructive component (Moore, Lagnado, Deal, & Haggard, 2009; Wegner, 2002) and thus is not necessarily an unambiguous index of intentionality.

URGES-FOR-ACTION, TICS, AND TOURETTE SYNDROME

Tics are involuntary, repetitive, stereotyped behaviors that occur with a limited duration. Motor tics can be simple or complex in appearance, ranging from repetitive movements to coordinated action sequences

(Leckman, 2002). Verbal tics can consist of repeating words or utterances (palilalia), producing inappropriate or obscene utterances (coprolalia), or the repetition of another's words (echolalia).

Tics occur in bouts, typically many times in a single day, and are the most common form of movement disorder in children, with a prevalence of 1–29% depending upon the precise characteristics of the study population, the diagnostic criteria used, and the study design and methods employed (Leckman, 2002). Tics include a continuum of disorders: transient tic disorder (TTD), chronic tic disorder (CTD), nonspecific tic disorder (NSTD), and Tourette syndrome (TS). The etiology of tics is poorly understood and probably involves a complex interaction between genetic and environmental factors that exert an influence over brain development.

TS is a developmental neuropsychiatric disorder that lies at the extreme of the tic disorder spectrum and is characterized by the presence of chronic vocal and motor tics (Leckman, 2002). The neurological basis of TS is unclear; however, it is agreed that the basal ganglia, including circuits that link the striatum to the frontal lobes, are dysfunctional (Albin & Mink, 2006). A specific model of basal ganglia dysregulation in TS has been proposed as follows. Subsets of striatal neurons (matrisomes) are thought to become abnormally active in inappropriate contexts, leading to the disinhibition of thalamocortical circuits that in turn lead to tics. Activity-dependent dopamine inappropriately reinforces such activity, leading to stereotyped repetition of behavior (Albin & Mink, 2006). Brain-imaging and postmortem studies provide general support for the view that cortical–striatal–thalamocortical pathways are dysfunctional in TS (Gerard & Peterson, 2003). Furthermore, deep-brain stimulation of the globus pallidus or the thalamus has been shown to be effective in suppressing tics in individuals with TS (e.g., Ackermans et al., 2011).

The occurrence of repetitive, stereotypical behaviors in TS has been linked to operation of the brain "reward" and "habit" systems, and tics have been likened to an inappropriate overextension of habit learning (Graybiel, 2008). Key characteristics of habitual behaviors are that they are largely learnt, occur repeatedly, are performed almost automatically, and often involve stereotypical, ordered, action sequences (Graybiel, 2008). In this context, it is important to note that many individuals with TS report that their tics are often preceded by "premonitory sensory phenomena" (PSPs), which are described as the presence of uncomfortable cognitive or bodily sensations (e.g., tension, pressure, tickle), that precede the execution of a tic, and are experienced as a strong *urge for motor discharge* (Banaschewki, Woerner, & Rothenberger,

2003). Furthermore, whereas individuals with TS perceive a relatively constant demand to suppress their tics in social situations, and while the voluntary suppression of tics is possible in many cases, individuals with TS nevertheless report that it can be uncomfortable and stressful to suppress tics, and that the urge to tic becomes uncontrollable after a period of suppression. It is therefore likely that some tics at least are learnt motor or vocal behaviors that function to alleviate or reduce uncomfortable bodily sensations.

Functional anatomy of tics in TS

Several attempts have been made to investigate the brain regions associated with the occurrence of tics in TS using human neuroimaging techniques. These studies have indicated that the neural mechanisms responsible for triggering of tics may in fact differ from those involved in voluntary movements (Bohlhalter et al. 2006). One notable study was that reported by Hallett and colleagues, which used functional magnetic resonance imaging (fMRI) to examine brain areas activated immediately preceding the spontaneous occurrence of motor and/or vocal tics, and thus likely to be associated with the urge to tic (Bohlhalter et al., 2006). This study identified a network of brain areas that were activated immediately prior to tic onset, and, most importantly, identified the insular cortex, the anterior cingulate cortex, and the parietal operculum, which includes the secondary somatosensory cortex (SII) (Eickhoff, Amunts, Mohlberg, & Zilles, 2006), as the most likely anatomic regions responsible for the uncomfortable feelings associated with premonitory urges to tic (Bohlhalter et al., 2006). Consistent with this proposal, electrical stimulation of the insular cortex or the parietal operculum can elicit unpleasant somatosensory or visceral sensations (Augustine, 1996; Ostrowsky et al., 2002; Penfield & Faulk, 1955). By contrast, electrical stimulation of the medial frontal lobes produces motor outputs in the face and upper limbs comparable to tics (Bancaud et al., 1976; Lim et al., 1994; Talairach et al., 1973).

The proposal that the insular and cingulate cortices are associated with the uncomfortable feelings associated with the urge to tic in TS is consistent with the putative role of these areas in the neural representation of bodily states more generally (interoception), and the initiation of behaviors associated with these bodily representations (for reviews, see Craig, 2002, 2009; Naqvi & Bechara, 2008). Thus, Craig suggests that these two regions are linked functionally and can be thought of as the limbic sensory and motor areas. He has proposed that these two areas form part of a functional

brain system that is associated with the *awareness* of bodily states (particularly the right insular cortex) and the maintenance of homeostasis (Craig, 2009; cf. Damasio, 1999).

It is important to note that Craig's particular view of interoception includes a representation of all body states relevant to homeostasis, including pain, temperature, taste, visceral sensation, inflammation, itch, and many aspects of touch and proprioception that are often viewed as part of an "exteroceptive" somatosensory system (Craig, 2003). Consistent with this view, recent functional brain-imaging studies have demonstrated that punctate somatosensory stimulation of the upper limbs produces significant increases in brain activity—blood oxygen level-dependent (BOLD) response—bilaterally within the insular cortex (e.g., Jackson, Parkinson, Pears, & Nam, 2011; Parkinson et al., 2011). However, neurophysiological studies suggest that the insular cortex may play a particularly important role in representing the emotional significance of somatosensory signals. Thus, it has been shown that a neural pathway, consisting of unmyelinated fibers, projects to the insula (Olausson et al., 2002; Vallbo, Olausson, & Wessberg, 1999), and that these fibers are associated with affective or sensual touch (e.g., pleasant touch sensation).

Brain-imaging and neurological studies also indicate that the posterior and mid-insular cortex may play an important role in body ownership and our sense of agency (control) over our body. Thus, a positron emission tomography (PET) imaging study reported by Tsakiris, Hesse, Boy, Haggard, and Fink (2007) reported that body ownership, as indexed by the strength of the rubber hand illusion, was associated with activation increases within the right posterior insula and right frontal operculum. Similarly, Karnath and colleagues have shown that lesions involving the right insula impair body awareness, and the sense of limb ownership (e.g., Baier & Karnath, 2008; Karnath, Baier, & Nagele, 2005).

Arguably, the most direct neuropsychological evidence that the insular cortex is key to the experience of urges for action comes from a study that investigated the effect of insula lesions on the urge to smoke in those addicted to smoking (Naqvi, Rudrauf, Damasio, & Bechara, 2007). This study compared smokers who had sustained damage involving the insula with a group of smokers whose damage involved other brain areas, but spared the insula. The study investigated changes in smoking behavior post-stroke and demonstrated that smokers whose brain damage involved the insula were significantly more likely than smokers with lesions sparing the insula to exhibit a "disruption of smoking addiction." Importantly, individuals described this disruption of addiction as like their body "forgetting the urge to smoke" (Naqvi et al., 2007).

LIMITATIONS OF INDIVIDUAL BRAIN-IMAGING STUDIES

Functional brain-imaging studies using fMRI have become central to cognitive neuroscience; however, it should be recognized that such studies have limitations. Many of these are well known and relate to the constraints imposed by hemodynamic signals (Logothetis, 2008). A discussion of these limitations is generally beyond the scope of this paper; however, below, we briefly outline some issues that specifically relate to difficulties in interpreting fMRI activations associated with the urge to tic in individuals with TS.

First, one obvious difficulty associated with interpreting the meaning of the patterns of BOLD activity reported in fMRI studies that have sought to identify brain regions associated with the occurrence of tics in TS, is that individuals with TS are instructed to remain still in the MRI scanner and to suppress their tics. Thus, the regions activated can reflect brain areas associated with the generation of tics or brain areas linked to their active suppression. Second, recent evidence suggests that individuals with neurodevelopmental disorders may follow unique developmental trajectories whereby they undergo compensatory, neuroplastic changes in brain structure and function that help them gain control over their symptoms (Jackson, Parkinson, Jung, et al., 2011). As a consequence, individuals with TS may exhibit differences in functional anatomy, compared to typically developing individuals, even when they are performing an identical behavioral task with comparable levels of task performance. Third, the functional anatomy of the urge to tic in TS may differ from the functional anatomy of other forms of the urge for action. In fact, a related limitation of fMRI studies is that it is very often difficult to carry out the range of control studies that might be conducted when using non-imaging experimental techniques. Finally, an important limitation of individual fMRI studies is that it is very often difficult to compare across studies. Thus, a comparison of individual fMRI studies of, for example, the urge to urinate and the urge to swallow, might reveal differences in functional anatomy because these behaviors have different underlying neural circuitry, or because of differences in the following factors: the behavioral paradigms used, the scanner hardware and imaging protocols adopted, analysis protocols and statistical thresholds, etc.

This last limitation can be overcome, however, through the use of quantitative meta-analytic studies. Such studies permit an estimation of the fMRI BOLD response associated with different behaviors by drawing upon the entire body of published studies within a particular behavioral domain. One method that has proven popular recently has been the activation likelihood

estimation (ALE) method developed by Turkeltaub, Eden, Jones, and Zeffiro (2002) and modified by Eickhoff and colleagues (Eickhoff et al., 2009).

A QUANTITATIVE META-ANALYTIC COMPARISON OF THE URGE TO MICTURATE AND THE URGE TO SWALLOW

Here we report the use of the ALE method to directly compare brain activity associated with the urge to urinate (micturition) and the urge to swallow.

Study selection criteria

Functional neuroimaging studies were retrieved via searches in the PubMed, ISI Web of Knowledge, and Scopus databases, as well as identified by reference tracing and through reviews. Experiments reported in these papers that corresponded to the core behavioral contrasts under consideration, such as contrast of urine withholding against a resting baseline, urine voiding against baseline, and volitional swallowing against baseline, were included in the meta-analyses if they fulfilled the following criteria: analyses must be computed across the whole brain and not restricted by partial coverage or regions of interest analyses; coordinates must be reported in an XYZ format, either in MNI or Talairach space; only experiments that investigated differences between stimulation conditions in healthy control population were included; and experiments focusing on between-group differences were excluded. No selection was made on the basis of the applied statistical threshold, as all studies were obtained from peer-reviewed journals. Additional methodological information is provided in detail in the online supplementary material, available via the 'Supplementary' tab on the article's online page (<http://dx.doi.org/10.1080/17588928.2011.604717>).

Experiments investigating the functional anatomy of *swallowing* were selected if they contrasted saliva swallowing, water swallowing, overt swallowing, or covert swallowing with a rest condition or other suitable control condition. Experiments investigating the functional anatomy of *micturition* were selected if they contrasted micturition, urine withholding, bladder filling, or the urge to void with a rest condition or other suitable control condition. See Supplementary Material for further details.

The quantitative comparison of ALEs across studies of swallowing revealed widespread clusters of activation that exceeded the conservative statistical threshold (Figure 2A). The areas of cortex that exceeded threshold included primary motor cortex (BA 4), premotor cortex

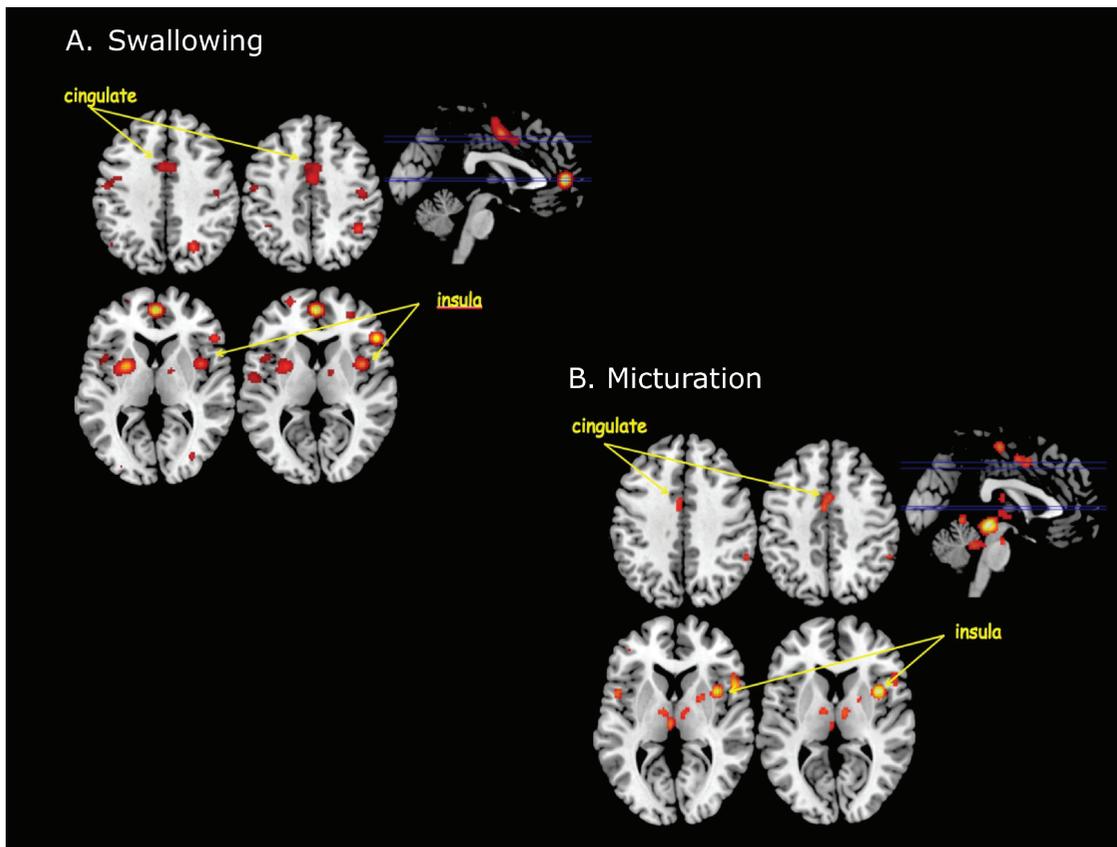


Figure 2. (A) Main results of an ALE meta-analysis of neuroimaging studies of swallowing. This analysis revealed a number of activation foci that survived conservative statistical correction ($p < .05$ corrected for false discovery rate). Among these were activations within the insular cortex and the dorsal mid-cingulate cortex. (B) Main results of an ALE meta-analysis of neuroimaging studies of micturition. Again this analysis revealed statistically significant foci of activation within the insular cortex and the dorsal mid-cingulate cortex.

(BA 6), frontal cortex (BA 9, 10, 44, 45), parietal cortex (BA 7, 39, 40), cingulate cortex (BA 24, 31), and insular cortex (BA 13). Subcortical activations included the putamen, thalamus (ventral anterior nucleus), and claustrum. Quantitative comparison of ALEs across studies of micturition also revealed widespread clusters of activation in both cortex and subcortical brain areas (Figure 2B). Areas of cortex that exceeded threshold included premotor cortex (BA 6), frontal cortex (BA 44), parietal cortex (BA 40), cingulate cortex (BA 24, 32), and insular cortex (BA 13). Subcortical activations included the cerebellum, putamen, thalamus (medial dorsal and ventral lateral nuclei), and claustrum.

To determine whether areas of overlap exist between brain regions activated during swallowing, or when individuals have an urge to swallow, and regions activated when individuals urinate, or have an urge to urinate, we carried out a conjunction analysis between the swallowing and micturition ALE maps. This analysis confirmed that, of the widespread regions activated in both studies, only two areas survived statistical comparison ($p < .05$): the insular cortex of the

right hemisphere and the mid-cingulate cortex bilaterally (Figure 3). This finding is consistent with the view, outlined above, that the insular cortex, particularly the right insula, may play an important role in the awareness of bodily sensations, including behavioral urges. It is noteworthy that the two behaviors chosen for study here, swallowing and micturition, involve body areas (i.e., the mouth and oropharyngeal area, and the bladder and genitals) that are located far from one another, and have representations in primary sensorimotor cortex that are also quite distinct and spatially separate.

An fMRI study of the urge to yawn

To further investigate this issue, we sought to investigate the functional anatomy of the urge to yawn. As there are insufficient neuroimaging studies currently published to permit an ALE meta-analysis, we carried out an fMRI study of the urge to yawn. Full methodological information is provided in detail in the online supplementary material.

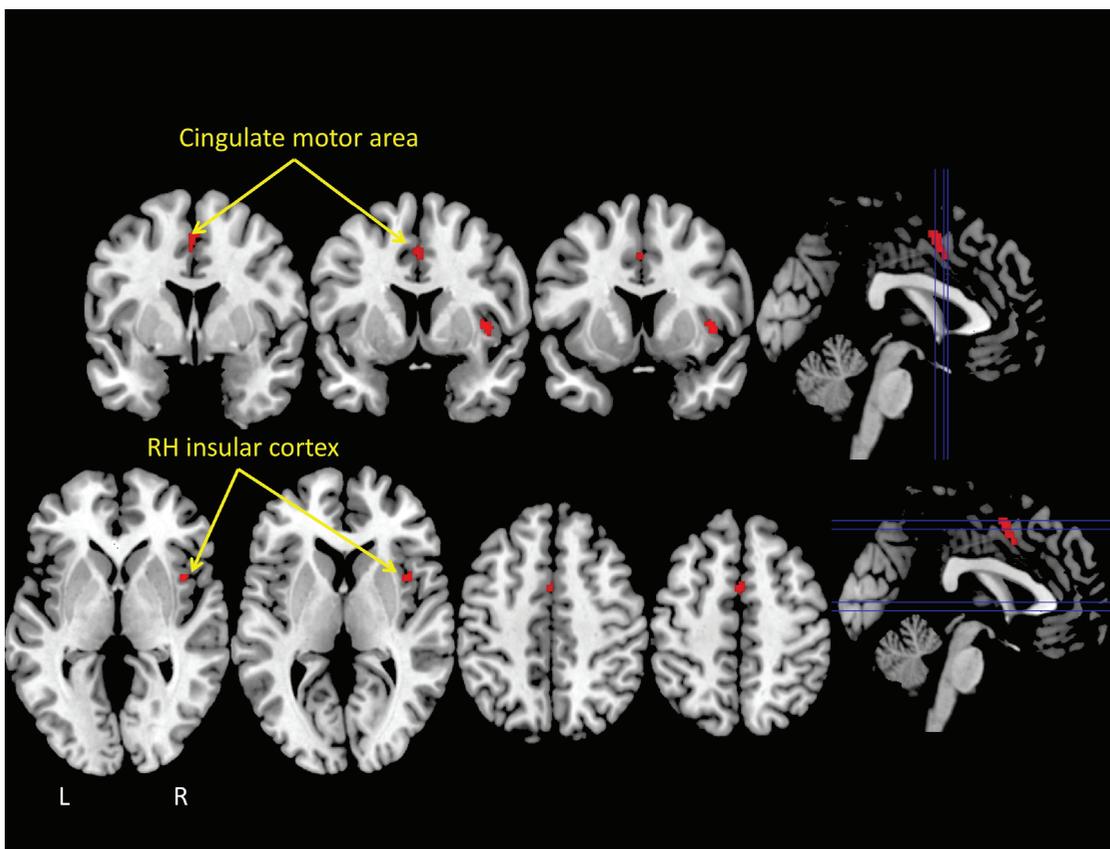


Figure 3. The results of a statistical “conjunction” analysis between the ALE meta-analyses of swallowing and micturition illustrated in Figure 2. The conjunction analysis revealed only two brain areas that reached statistical threshold: the insular cortex of the right hemisphere (RH) and the mid-cingulate cortex (cingulate motor area) bilaterally.

While being scanned, participants observed a sequence of video clips, each approximately 12 s in length, which illustrated an actor yawning. These stimuli had been previously shown to induce high levels of spontaneous yawning in a previous fMRI study (Schüermann et al., 2005). In the current study, participants were instructed to suppress their yawns (which they were able to do successfully) but were required to report periods during which they experienced a strong urge to yawn.

fMRI and anatomic data analysis

Anatomic images were transformed into the Talairach coordinate system and co-registered with each fMRI data set. Regional activation maps were obtained with a single-subject GLM (general linear model) for each individual. We defined a single predictor that modeled the periods that participants reported experiencing the urge to yawn. All 10 individuals included in the analyses reported successfully suppressing their yawns, and inspection of the motion data confirmed this. Second-level analyses involved calculating three-dimensional

statistical parametric maps with separate-subject predictors for the group, using a random effects GLM (RFX). The resulting fMRI activity maps were thresholded at a Z value of 3.29 corresponding to $p < .001_{\text{uncorrected}}$ with a minimum cluster threshold of at least 20 voxels. The results of this analysis revealed a number of statistically significant clusters of activation. Details are provided in Table 1.

Details of statistically significant fMRI BOLD activations associated with the urge to yawn are presented in Table 1 and Figure 4. Importantly, the analyses of the fMRI BOLD response associated with participants' subjective reports of their urge to yawn revealed that both the cingulate motor area (CMA) and the insular cortex bilaterally were activated when individuals reported an urge to yawn.

To examine further whether the coordinates of the yawning activations overlapped with the activation foci observed for the ALE analyses of swallowing and micturition reported above, we obtained ALEs for the peak activations of the yawning CMA and insula activations so that they might be compared directly with the results of the

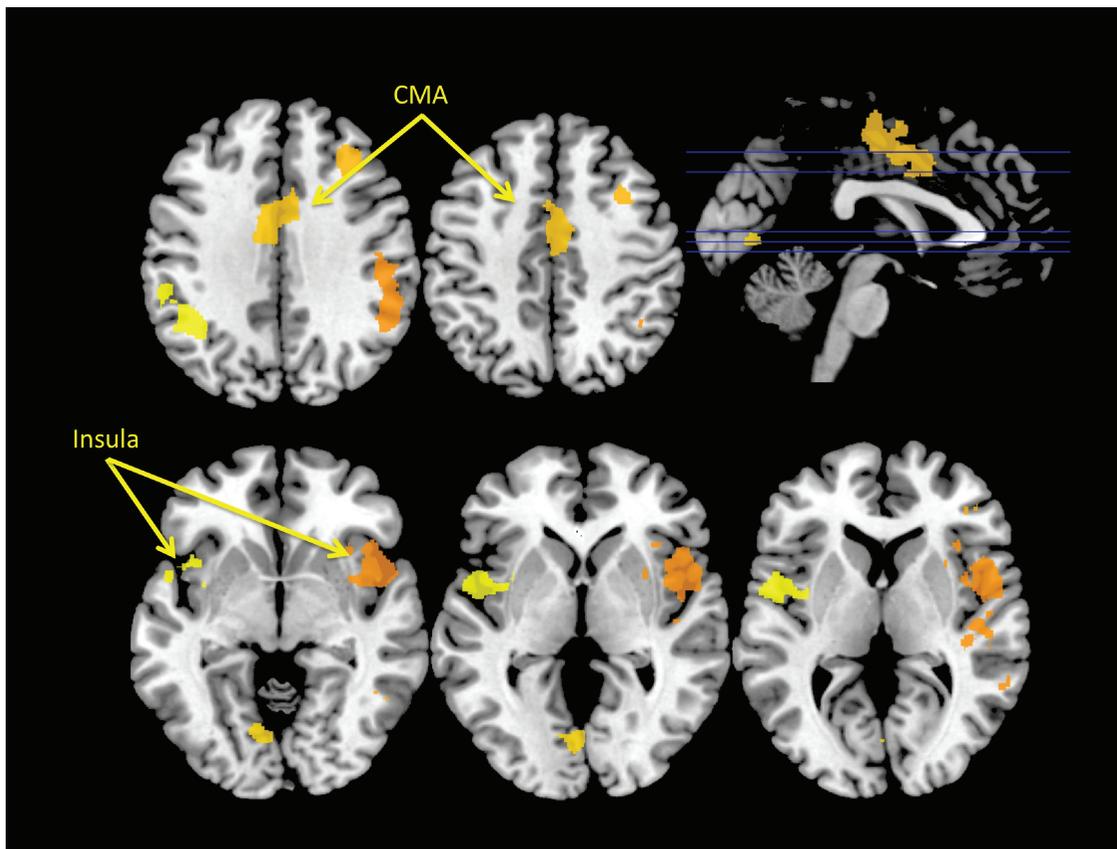


Figure 4. Regions exhibiting a statistically significant increase in blood oxygen level-dependent (BOLD) signal corresponding to the self-reported urge to yawn in an fMRI study of yawning. Again this analysis revealed statistically significant foci of activation within the insular cortex and the dorsal mid-cingulate cortex. CMA: cingulate motor area.

TABLE 1

Coordinates for center-of-gravity and peak activations for statistically significant clusters of activation associated with the urge to yawn

| <i>Location</i> | <i>Mean X</i> | <i>Mean Y</i> | <i>Mean Z</i> | <i>Peak X</i> | <i>Peak Y</i> | <i>Peak Z</i> | <i>Voxels</i> | <i>Z value</i> | <i>p value</i> |
|-----------------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|----------------|----------------|
| Right parietal cortex | 51.2 | -40.8 | 30.0 | 50 | -32 | 33 | 2386 | 5.85 | .00000 |
| Right insular cortex | 48.2 | 4.4 | 4.9 | 47 | 4 | -3 | 3663 | 6.23 | .00000 |
| Cingulate cortex | 0.25 | -5.0 | 44.4 | -11 | -8 | 30 | 3361 | 6.86 | .00000 |
| Left parietal cortex | -47.4 | -43.5 | 29.6 | -43 | -44 | 27 | 1713 | 5.95 | .00000 |
| Left insular cortex | -52.3 | -7.4 | 14.5 | -43 | -20 | 24 | 3133 | 5.89 | .00000 |

ALE results for swallowing and micturition. Furthermore, we also obtained ALEs for the peak activations associated with the urge to tic in individuals with TS reported by Bohlhalter et al. (2006). These data are presented in Figure 5, which illustrates that all four behavioral domains overlap in the region of the mid-cingulate cortex and the insular cortex of the right hemisphere.

Picard and Strick (2001) review the location and functional anatomy of the motor areas located on the medial surface of the human brain. In addition to identifying the supplementary motor area (SMA) and pre-SMA, these authors identify three separable areas within the human cingulate cortex: a caudal cingulate

zone (CCZ) situated ventral to the SMA, and a rostral cingulate zone (RCZ) that is further subdivided into anterior and posterior subregions. It is noteworthy that the cingulate fMRI BOLD activations associated with the urge for action in three everyday behaviors (i.e., swallowing, micturition, and yawning), and with the urge to tic in TS, are each located in a region of cingulate cortex that corresponds closely to the CCZ. While the RCZ is associated with conflict detection, attention and arousal processes, and the selection of action, the CCZ is, by contrast, associated with the execution of simple movements and is also activated in response to bodily stimulation such as the delivery of painful cutaneous

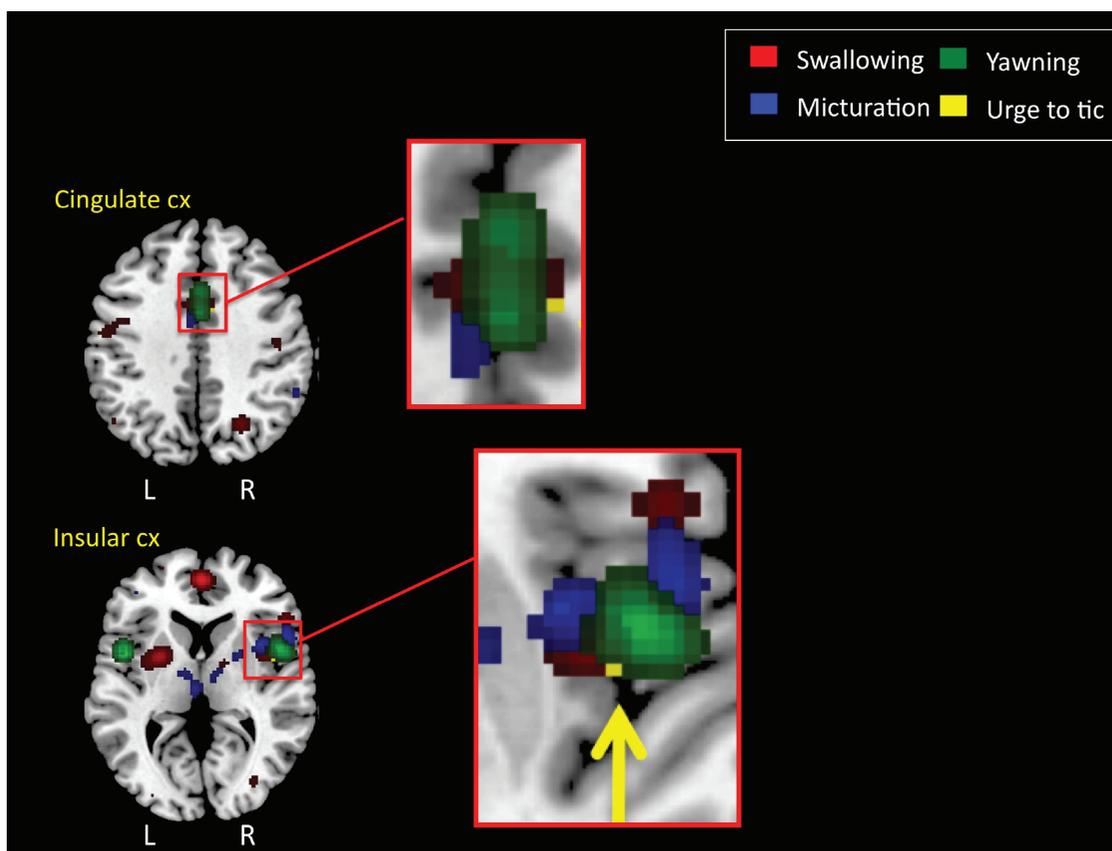


Figure 5. Regions of overlap between ALE meta-analytic studies of swallowing and micturition and fMRI studies of the urge to tic in individuals with TS (Bohlhalter et al., 2006) and the urge to yawn in neurologically normal adults. Again these analyses reveal regions of overlap within the insular cortex (CX) of the right hemisphere and the mid-cingulate cortex bilaterally.

heat and cold stimuli (Picard & Strick, 2001). It should be noted that whereas the SMA has itself been linked to the conscious intention to move (see Desmurget & Sirigu, 2009), and while the CCZ and SMA may be co-activated during movement execution, the SMA and CCA should be considered functionally distinct from one another (Picard & Strick, 2001).

EFFECTIVE CONNECTIVITY BETWEEN INSULAR AND CINGULATE CORTICES

The insula and anterior cingulate cortex have been considered to be the input and output regions of a functional system that is engaged in cognitive, affective, and behavioral contexts (Craig, 2009; Medford & Critchley, 2010). Consistent with this proposal there is now considerable evidence that these regions are jointly active across a wide range of experimental conditions (for a recent review, see Medford & Critchley, 2010). In addition, functional connectivity analyses of resting state fMRI BOLD, using seed regions located

within the insula, have shown that (1) the anterior insula is connected functionally with the anterior and mid-cingulate cortex; and (2) the mid- and posterior regions of the insula are connected only with the posterior region of the mid-cingulate cortex (Taylor, Seminowicz, & Davis, 2009).

To investigate the effective, or directional, connectivity of the anterior cingulate and insular cortices, we used the Granger causality mapping (GCM) technique. GCM implements a statistical concept of causality that is based on temporal prediction. Unlike some other methods used to examine effective connectivity, GCM makes no *a priori* assumptions concerning the connectivity of the seed region, but examines the association between the BOLD time course of the seed region and the time course of each voxel outside the seed region. In the current study, two reference or “seed” regions were defined from the BOLD activations associated with the urge-to-yawn versus rest RFX contrast referred to above. The first “seed” region was located within the mid-cingulate cortex, and the second within the insula cortex of the right hemisphere (see the online supplementary material for additional detail).

TABLE 2
Results of GCM analysis of effective connectivity for mid-cingulate cortex and right hemisphere insula “seed” regions

| <i>Seed area</i> | <i>Mean Talairach coordinates</i> | | | <i>Center-of-gravity in Talairach coordinates</i> | | |
|---|-----------------------------------|----------|----------|---|-----|----|
| | <i>X</i> | <i>Y</i> | <i>Z</i> | | | |
| Mid-cingulate cortex | 0.25 | -5.0 | 44.4 | | | |
| <i>Regions exerting an influence over the “seed” area</i> | | | | | | |
| | | | | -30 | 20 | 7 |
| | | | | 30 | 20 | -2 |
| | | | | -9 | -16 | -2 |
| | | | | 12 | -17 | 1 |
| <i>Regions influenced by the “seed” area</i> | | | | | | |
| | | | | -55 | 8 | 2 |
| | | | | 52 | 11 | -2 |
| | | | | -2 | -4 | 7 |
| | | | | 3 | -4 | 6 |
| <i>Seed area</i> | <i>X</i> | <i>Y</i> | <i>Z</i> | | | |
| Right insular cortex | 48.2 | 4.4 | 4.9 | | | |
| <i>Regions exerting an influence over the “seed” area</i> | | | | | | |
| | | | | -42 | 8 | 5 |
| | | | | -1 | 3 | 44 |
| | | | | -11 | -19 | 5 |
| | | | | 11 | -17 | 5 |
| <i>Regions influenced by the “seed” area</i> | | | | | | |
| | | | | -14 | -14 | 16 |
| | | | | 15 | -11 | 17 |
| | | | | -1 | -17 | 9 |
| | | | | 3 | -17 | 8 |

The GCM analyses revealed a number of brain areas with effective connectivity values that exceeded statistical threshold ($p < .001$). The Talairach coordinates of these areas are presented in Table 2. For the anterior cingulate cortex seed region, the GCM analysis identified four brain areas that likely *exerted an influence over the “seed” region*. These were the anterior portion of the insular cortex in the left and right hemisphere, and the anterior portion of the thalamus bilaterally. These regions are shown in blue in Figure 6. The GCM analysis also identified four brain areas that were themselves *influenced by the “seed” region*. These were the mid/posterior region of the insular cortex in the left and right hemisphere, and the centromedial region of the thalamus bilaterally. These regions are shown in pink in Figure 6.

In addition to revealing patterns of effective connectivity between the thalamus and the cingulate motor areas, the GCM confirmed that the cingulate motor region is influenced by the anterior portion of the insular cortex (i.e., the BOLD response in the anterior insular cortex predicts the BOLD response in the cingulate motor region). This finding is entirely consistent with the view of Craig (2002, 2009) that the insular and cingulate cortices form the input and output regions of a functional

system, and can be characterized as the limbic sensory and motor areas. Importantly, the GCM analysis confirms that the cingulate motor region also exerts an influence over the activation of a different region of the insular cortex; specifically the mid-insular cortex. This can be clearly seen in Figure 6A, which illustrates insular regions exerting an influence over the cingulate motor region (blue) and being influenced by the cingulate motor region (pink). Later in this paper, we speculate on the likely functional significance of this anterior insula → cingulate → mid-insular loop.

For the right hemisphere insular cortex seed region, the GCM analysis identified four brain areas that likely *exerted an influence over the “seed” region* (Table 2). These were the anterior portion of the insular cortex in the left hemisphere, the mid-portion of the cingulate cortex (cingulate motor area), and the centromedial portion of the thalamus bilaterally. These regions are shown in blue in Figure 7. The GCM analysis also identified four regions of the thalamus that were themselves *influenced by the “seed” region*. These were the ventral lateral region of the thalamus bilaterally, and the medial dorsal region of the thalamus bilaterally. These regions are shown in pink in Figure 7.

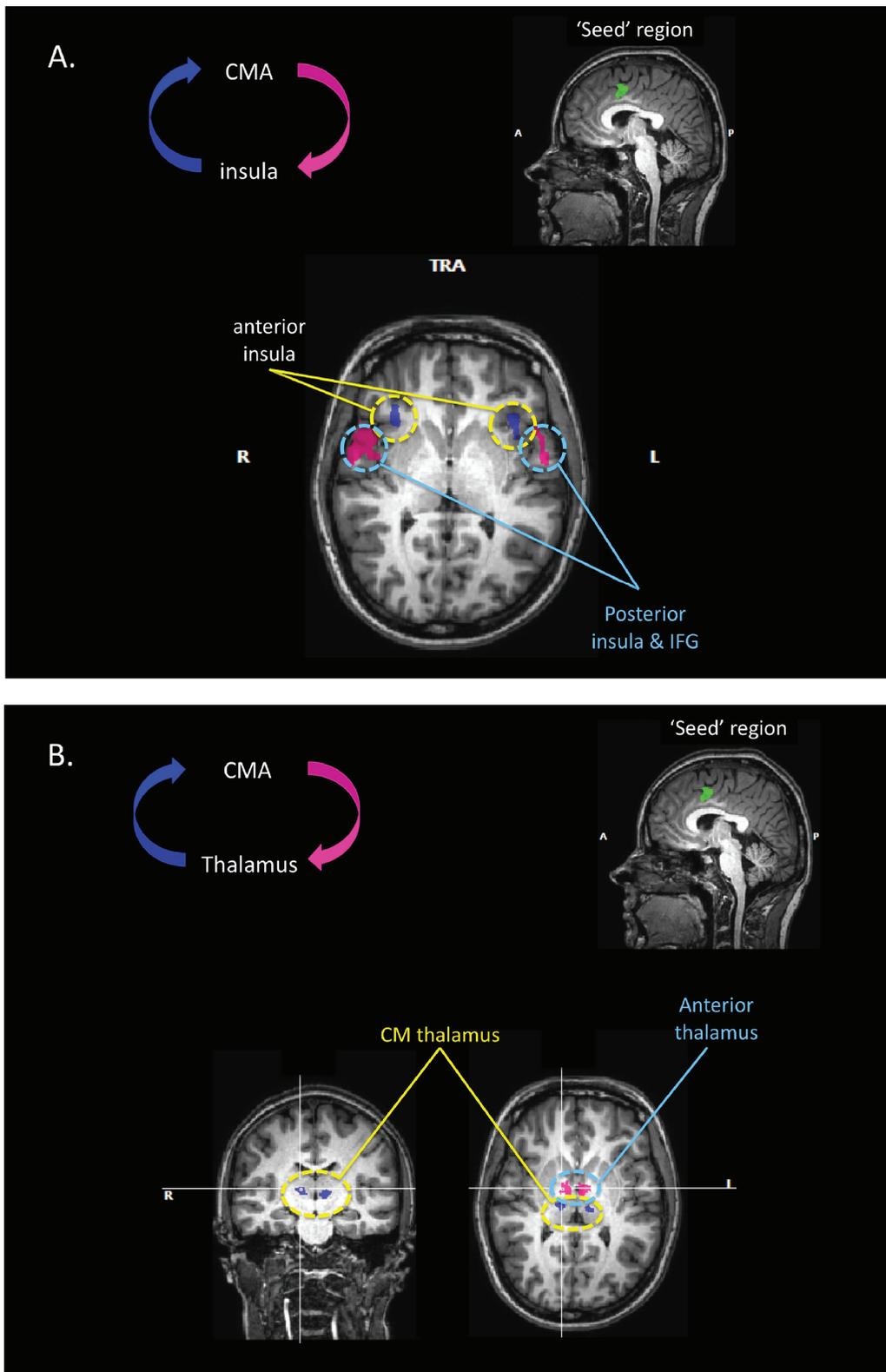


Figure 6. (A) Results of the effective connectivity analyses, based upon Granger causality mapping (GCM), of the yawning fMRI study. In this case, the “seed” region for the GCM has been defined as the region of the mid-cingulate cortex significantly activated during the urge to yawn. The GCM analysis revealed that regions of the anterior insula bilaterally exert a significant influence over the seed region (blue), whereas regions of the mid-insula and inferior frontal lobe bilaterally are influenced by the seed area (pink). TRA: transverse; IFG: inferior frontal gyrus. (B) Further results of the GCM analysis based upon the mid-cingulate “seed” region. The analysis also revealed that regions of the centromedial thalamus bilaterally exert a significant influence over the seed region (blue), and bilateral regions of the anterior thalamus are influenced by the seed area (pink). CMA: cingulate motor area.

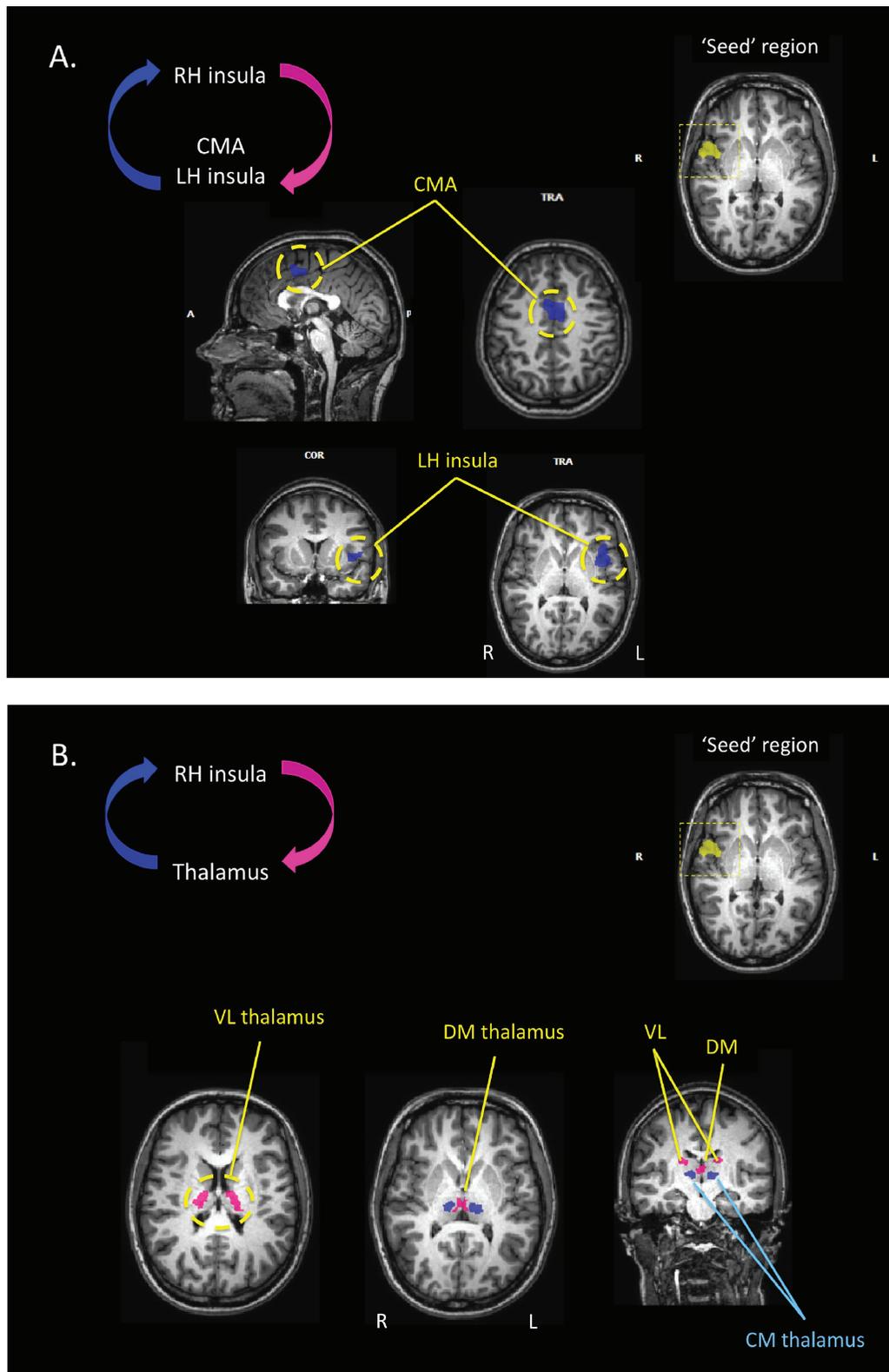


Figure 7. (A) Results of the effective connectivity analyses, based upon Granger causality mapping (GCM), of the yawning fMRI study. In this case, the “seed” region for the GCM has been defined as the region of the insular cortex of the right hemisphere that was significantly activated during the urge to yawn. The GCM analysis revealed that corresponding regions of the insular cortex within the left hemisphere, and the mid-cingulate cortex bilaterally, each exert a significant influence over the seed region (blue). CMA: cingulate motor area; TRA: transverse. (B) Further results of the GCM analysis based upon the right insula “seed” region. The analysis also revealed that regions of the centromedial thalamus bilaterally exert a significant influence over the seed region (blue), and that bilateral regions of the ventral-lateral and dorsomedial thalamus are influenced by the seed area (pink).

It is important to keep in mind that the patterns of effective connectivity revealed by the GCM analyses do not necessarily reflect anatomic connections. Nevertheless, the patterns of connectivity revealed by the GCM are consistent with known anatomy and function of specific thalamocortical connections. For instance, the anterior thalamic nuclei receive their primary input from the hypothalamus, project to the cingulate cortex, and are associated with visceral and emotional processing. In the current study, the GCM analysis confirms that the activity of the anterior thalamus exerts an influence over the cingulate cortex and thus provides a route by which emotional and visceral signals might influence the selection of motor responses.

The centromedian nuclei of the thalamus are a primary source of thalamostriatal projections and play a key role in motor function. In the current study, the GCM analyses confirm that the centromedian region of the thalamus is *influenced* by the activation of the cingulate cortex but in turn exerts an *influence over* the activity of the right insular cortex. This pattern of connectivity suggests that motor processes in the cingulate motor regions of cortex may gain influence over motor selection mechanisms within the striatum via their influence over the centromedian thalamus. Furthermore, the centromedian thalamus may also signal outcomes of the motor selection process to the insula. We speculate that the insular cortex may accumulate evidence on the outcomes of the action, determine whether the conditions giving rise to the urge for action have been resolved, and, if appropriate, generate a sense that the urge for action has been satisfied (see below). In the current context, it is of interest to note that deep-brain stimulation (DBS) of the centromedian region of the thalamus has been demonstrated to be an effective treatment for intractable TS and produces a substantial reduction in the occurrence of tics (Ackermans et al., 2011).

The GCM analysis also revealed that the right hemisphere insular cortex “seed” area is influenced by the BOLD activation within the ventral lateral and dorsal medial regions of the thalamus. The ventral lateral nuclei of the thalamus receive their input from the basal ganglia and cerebellum and send outputs to motor regions of cortex. As illustrated in Figure 1, a key aspect of the motivation-for-action model outlined above is that information about the outcomes of motor events is relayed to the limbic system, where it might be used to determine whether the conditions giving rise to the urge for action have been resolved. The medial dorsal thalamic nuclei are known to receive their inputs primarily from prefrontal and limbic regions of cortex, and project to association areas of the frontal lobe.

These nuclei have been associated with complex aspects of cognition, including attentional control and multitasking, goal-directed action planning, and learning and working memory.

A ROLE FOR INSULAR CORTEX IN SENSORIMOTOR PREDICTION?

Our everyday movements often involve interactions between our body and physical objects located within our environment, and engage multiple sensorimotor systems acting in concert. Action selection mechanisms must therefore take account of information about the current state of the motor apparatus (our body) and also of the behavior of objects within our immediate environment. Recent computational neuroscience approaches to the selection and control of movement (e.g., Wolpert, 1997; Wolpert & Ghahramani, 2000) and to reinforcement learning (e.g., Dayan & Niv, 2008) have emphasized the importance of prediction mechanisms to these processes.

It has been argued that efficient motor behavior relies to a large extent upon *predictive* mechanisms that provide accurate estimates, or “internal models,” of the changing state of our body and the objects with which we interact. Internal “forward” models are thought to compute dynamic estimates of the body state and to predict the sensory consequences of actions (Wolpert & Ghahramani, 2000). In this view, prediction is necessary to compensate for delays associated with the processing of sensory information, but afferent sensory information is critically important for maintaining the accuracy of internal models and is used to monitor and correct for prediction errors, thereby improving future prediction accuracy and movement control. Thus, any discrepancies between the predicted and observed consequences of an action are used to increase or maintain the accuracy of forward models.

Reinforcement learning also involves the evaluation of the outcomes that follow an action. Computational models of reinforcement learning propose that learning can be based upon internal models of the state transitions and action outcomes within an environment, or based upon model-free learning mechanisms (Dayan & Niv, 2008). Model-free reinforcement learning involves learning to estimate or predict the likely outcome (value or reward) of a given action (state) given an appropriate action-selection policy. This kind of learning is associated with the formation of “habitual” responses (Graybiel, 2008) and has been particularly linked to the operation of the ventral striatum, the neurotransmitter dopamine acting as a reinforcement signal that codes for reward “prediction error” (Schultz,

Dayan, & Montague, 1997). By contrast, model-based reinforcement learning has been associated with goal-directed action in which the efficacy of candidate actions is evaluated with reference to an internal model of the task or state space. A key concept associated with this type of learning is that the selection of an appropriate action may involve a “mental simulation” of potential outcomes (Dayan & Niv, 2008). We suggest that the formation of “urges-for-action” is probably linked to the operation of the habit-learning system, whereas the formation of “desires-for-action” is probably associated with goal-directed, action-planning mechanisms.

A QUANTITATIVE META-ANALYSIS OF REWARD PREDICTION

In this paper, we have speculated that the insular cortex may accumulate evidence on the outcomes of an action and determine whether the conditions giving rise to the urge for action have been resolved. Within the computational framework offered by the forward model literature, this process might involve a comparison of a “next state estimate” (the output of a forward “sensory” model that provides an estimate of the sensory consequences of a planned action) with afferent sensory information that signals the sensory outcomes of the executed action. Within the computational framework offered by model-free reinforcement learning, this process would involve predicting or representing the likely outcome (value or reward) of an action.

To examine whether the insular cortex plays a key role in the representation of the reward estimates for planned actions, we carried out an ALE meta-analysis of functional brain-imaging studies that have investigated the anticipation or expectation of rewards. Full methodological information is provided in detail in the online supplementary material.

Studies were initially chosen by the following keywords: “reward,” “prediction,” “prediction error,” “fMRI” and “prediction,” “prediction error,” “expectation,” and “anticipation.” The reward modalities used in the studies reported here were monetary or pleasurable taste rewards. Studies were further refined according to the following criteria.

First, events used in the fMRI contrasts should occur *prior* to the onset of the reward to reflect the outcome of anticipatory processes rather than the processes in response to the actual receipt of a reward.

Second, the contrasts should reflect events in which participants hold an expectation of reward versus a control event such as the expectation of non-rewarding stimuli, or the expectation of loss. The study might

include, however, contrasts of high reward probability versus low reward probability. Thus, results that reveal activations by association with the reward probability were explicitly included in the analysis.

Third, participants should expect primary rewards or secondary rewards. Studies that investigated the prediction of non-rewarding events were excluded from this analysis. As a result of these selection criteria, eight studies were included in the meta-analysis. Full details of these studies are provided in the online supplementary material.

The results of the ALE meta-analysis are illustrated in Figure 8. They show that the following brain areas were significantly activated for contrasts associated with the prediction or expectation of rewards across the set of fMRI studies included in the analysis: the left ventral anterior insula cortex, the ventral striatum bilaterally, the globus pallidus bilaterally, and the dorsal cingulate cortex.

The above analyses implicate the input and output nuclei of the basal ganglia together with the anterior insula and the dorsal cingulate cortex in the representation of reward estimates. These findings are consistent with recent proposals that the basal ganglia nuclei modulate movement execution according to motivational factors, specifically context-specific cost/reward estimates (Turner & Desmurget, 2010); that the anterior insular cortex may represent expectations of both positive and negative action outcomes (e.g., Preusschoff, Quartz, & Bossaerts, 2008); and that the anterior cingulate cortex plays a fundamental role in relating actions to their outcomes, and functions, together with the ventral striatum, to mediate cost-benefit decisions over the selection of action (Behrens, Woolrich, Walton, & Rushworth, 2007; Rushworth, Mars, & Summerfield, 2009; Rushworth, Walton, Kennerley, & Bannerman, 2004).

These findings are also consistent with the proposal being advanced here that the anterior insular cortex and the dorsal cingulate motor areas, along with the ventral striatum and thalamus, form core nodes in a motivation-for-action system. Specifically, we propose that pleasant or unpleasant somatosensory or visceral sensations—for instance, the premonitory sensations that precede the occurrence of tics in TS—are represented within the SII, and in the posterior and mid-insular cortex, and that these sensations will often elicit habitual, overlearned, actions. We also propose that awareness of these bodily sensations, often perceived as an *urge for action*, is associated more specifically with the activity of the anterior insula cortex. Signals associated with such bodily sensations are relayed from the insula to cingulate motor areas that, together with the ventral striatum, may participate

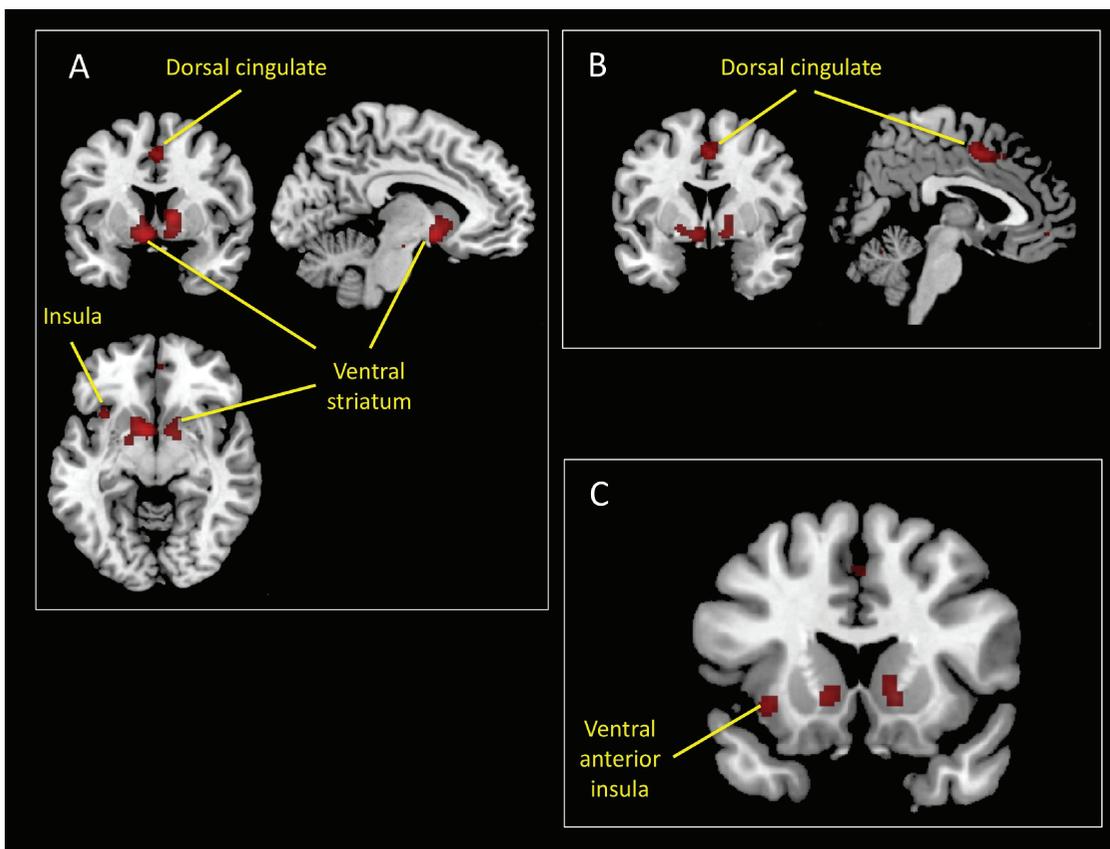


Figure 8. Main results of an ALE meta-analysis of neuroimaging studies of reward expectation (see the online supplementary material for additional information). This analysis revealed a number of activation foci that survived conservative statistical correction ($p < .05$ corrected for false discovery rate). Among these were activations within the insular cortex (A and C) and the dorsal mid-cingulate cortex (B).

in the selection of a particular action based upon a cost–benefit analysis of the likely “value” of an action given the organism’s previous history of action outcomes.

Finally, as illustrated in Figure 9, we propose that an estimate of the predicted sensory consequences (outcome) of the selected action is then returned to the insula and inferior frontal cortex, where it may be used to determine whether the sensations giving rise to the urge for action are predicted to alter as a result of the intended action, and, if appropriate, to generate a sense that the urge for action has been satisfied. This last proposal is consistent with recent demonstrations that signals from the cingulate motor area participate in the attenuation of somatosensory activity in SII ahead of voluntary movements (Parkinson et al., 2011). Such sensory cancellation is thought to be a key function of “forward models” (Wolpert, 1997; Wolpert & Ghahramani, 2000), and it is suggested that the predicted sensory consequences of self-generated movements can be attenuated in favor of unpredictable, exafferent, somatosensory input (i.e., sensory signals produced by the environment).

CONCLUSION

In this paper, we have begun to consider the nature and the functional anatomy of “urges-for-action,” both in the context of everyday behaviors such as yawning, swallowing, and micturition, and in relation to clinical disorders such as TS, where urges-for-action are considered pathological, and interfere with activities of daily living. We began by reviewing previous frameworks for thinking about behavioral urges, such as Davenport, Sapienza, and Bolser’s (2002) motivation-for-action framework that had been formulated in the context of the urge to cough. While it contains several important insights, we took the view that a core aspect of this framework—that actions depend upon the conversion of an urge-for-action into a conscious desire-for-action—was very likely incorrect. We felt that this was particularly true in the case of individuals with TS, in whom urges-for-action were associated with the occurrence of motor and vocal tics that the individuals found both embarrassing and distressing. In this instance, it is difficult to reconcile such actions with the notion that



Figure 9. (A) GCM effective connectivity analyses of fMRI BOLD activations of yawning revealed a reciprocal pattern of effective connectivity between the anterior insula, the cingulate motor area, and the mid-insula. (B) On the likely function of these connections, we propose that the anterior insula may represent the urge-for-action, that the cingulate motor region may participate in the selection of an appropriate action following a cost-benefit analysis based upon the organism's past action-outcome history, and that the mid-insular cortex may evaluate, based upon a prediction of the likely outcome of the selected action, whether the conditions giving rise to the urge have been resolved, and, if appropriate, may generate a sense that the urge-for-action has been satisfied. CMA: cingulate motor area.

they spring from a conscious desire for action. Instead we took the view that such actions may be habitual, and as such were highly overlearned and automatic, and could in some cases be executed with very little or no conscious awareness of the sensory stimulation that triggered the action. Importantly, we distinguished between reflex actions and the urge-for-action, which, we argued, occurred when bodily signals gave rise to an action that must be suppressed or deferred.

Then, using quantitative ALE meta-analytic techniques, we investigated the functional anatomy of the urge-for-action in the context of swallowing and micturition, and demonstrated that brain activations associated with these behaviors overlapped in two regions of the brain; the right insula and the dorsal anterior cingulate cortex. Furthermore, we showed that functional activations associated with the urge to tic in individuals with TS and the urge to yawn in neurologically healthy individuals also overlapped within these same two brain areas. These two areas have been conceptualized as the

limbic sensory and motor areas respectively (Craig, 2002, 2009), and based upon the effective connectivity analyses of our yawning fMRI data, we proposed that they are central in representing the urge-for-action, and together form a neural circuit that represents bodily sensations, generates an urge-for-action (which may or may not reach awareness), selects a particular action based upon a cost-benefit analysis of the likely "value" of that action, accumulates evidence on the outcomes of that action, determines whether the conditions giving rise to the urge have been resolved, and, if appropriate, generates a sense that the urge has been satisfied. Finally, we argue that this circuit is anatomically separate and largely independent of the neural system responsible for the preparation and execution of intentional, goal-directed, actions, although it is possible that these systems may overlap partially with respect to the sense of agency that accompanies intentional action, which has been associated with the activity of the insular cortex of the right hemisphere.

Commentaries

The urge for self and species preservation

Alice Mado Proverbio

Department of Psychology, University of Milano-Bicocca, Milan, Italy

E-mail: mado.proverbio@unimib.it

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Abstract: Besides sneezing, yawning, and scratching, other types of more complex behaviors can be considered urges for action, in that they are both compelling and can be overtly inhibited. Many behaviors increasing the survival rate of self and species have this instinctual (although not compulsory) nature. We feel a terrible urge to catch a newborn falling from a table, although we could choose not to do so. The hypothesis is advanced that both insula and cingulate cortex participate in social behaviors such as contagious yawning, laughing, and crying, but are not necessarily involved in the urge to cough, for example.

Jackson and coauthors state that motor reflexes (as in recoiling from fire) are different from urge-for-action in that they cannot be cortically inhibited (or temporally postponed). They also characterize urges for actions as different from desires because of their highly implicit and not overly conscious nature. These characterizations are insightful and correct in principle, but the authors focus on very specific and peculiar urge-for-action types, such as the urge of urination, and of yawning and scratching, which are far from homogeneous.

The urge to urinate is one of the many signals that originate in the brain upon hypothalamic impulses and that are involved in the homeostatic regulation of physiological parameters (such as blood oxygen, delta sleep-inducing peptide levels, and plasma concentration of glucose (Burdakov, Luckman, & Verkhatsky, 2005). In this view, the urge to eat in a person with very low glucose levels cannot be considered a reflex (it can be cortically guided, inhibited, or deferred) and is not necessarily a conscious desire (e.g., as with someone who is working and is very concentrated); therefore, it can be legitimately considered an urge-for-action. Similarly, the urge to breathe when there is a lack of

oxygen (at high altitude, or in badly air-conditioned places), or, again, the urge to lie down when cerebral blood pressure is low and we feel faint; the urge to quickly undress when it is too hot, or to wrap up when it is freezing; the urge to move arms and legs when we are drowning; and the urge to cough if we are suffocating can all legitimately be considered types of urges-for-action.

We are not sure that insula and mid-cingulate cortex are crucially involved in all these behaviors. It is possible that contagious yawning might share more similarities with other human behaviors reflecting the processing of social information (such as contagious crying and laughing). Indeed, we know that both insula and cingulate cortex play a very important role in empathy, in response to crying (Lang, Yu, Markl, Mü & Kotchoubey, 2011; Sander, Frome, & Scheich, 2007) or to the sight of suffering people (Proverbio, Adorni, Zani, & Trestianu, 2009). Possibly, these structures are responsible for other urges-for-actions such as those regulating instinctual parental behavior (catching a baby falling from a table, for example), aimed at increasing the survival rate of individuals (brushing an insect away from a child) or of the species.

Finally, I would make a distinction between spontaneous yawning and contagious yawning. Spontaneous yawning is thought to have the important function of increasing oxygen blood levels, by expanding the lungs and stretching the muscles (Thompson, 2011). It is also known to lower brain temperature, thus favoring increase in sleepiness and passage to the sleep stage (Gallup & Gallup, 2007). Overall, yawning is probably involved in the circadian and homeostatic control of sleep and wakefulness. Contagious yawning, on the other hand, is thought to be based on the activity of mirror neurons, with the purpose of synchronizing and regulating the behavior of cohabitant individuals, similarly to contagious laughing and crying (Geangu, Benga, Stahl, & Striano, 2010). In this view, the urge to yawn when another does so would stimulate regions involved in theory of mind and empathy, such as the cingulate cortex (Platek, Mohamed, & Gallup, 2005), as was found by Jackson and coauthors.

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Similarities and differences between normal urges and the urge to tic

Beth A. Belluscio, Sule Tinaz,
and Mark Hallett

Human Motor Control Section, National Institute of
Neurological Disorders and Stroke, Bethesda, MD,
USA

E-mail: belluscb@ninds.nih.gov

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Abstract: Investigations into the neurobiological substrates underlying urge are important for developing better understanding and treatment for impulse-control disorders. We characterize the phenomenon based on normal bodily (interoceptive) urges. Features include the following: a preceding awareness of an uncomfortable bodily sensation, a sense of urgency that action must be taken, rising distress when action is delayed, a temporary (e.g., a few minutes in length) ability to suppress or manifest the action voluntarily, subsequent relief once action is taken, association with an action that is necessary to survival. We compare and contrast these characteristics with those described by Tourette syndrome patients as the urge to tic, and highlight several unknowns which merit further investigation.

Understanding the anatomical and physiological basis of “urges” is important not only because they occur in disease states, such as Tourette syndrome, but also because they are closely related to impulses that, when uncontrolled, can wreak havoc on individuals and societies. Problems with impulse control include substance abuse, domestic violence, sexual deviancy, and pathological gambling. In this context, it is important to clearly define what is meant by “urge,” to delineate what distinguishes normal from pathological urges, and to clarify how urges differ from other modes of action selection. Study of the underlying functional anatomy, as reviewed by Jackson et al., can then lead to a greater understanding and better treatment of impulse-control disorders.

The elementary components of brain function can be divided into sensory input, processing, and motor output. Urge is one mode of processing. Although it exists within a continuum of modes including reflex, desire, and intention, in which boundaries are somewhat artificial, defining the phenomenon helps unify

research efforts. Sensory input that leads to urge can come from within the body (interoceptive) or from outside the body (exteroceptive). We characterize urge based on examples of common bodily urges: to urinate, yawn, cough, blink, and sleep. In each, sensory input can trigger the action out of awareness, in which case there is no urge and the action is perceived as occurring involuntarily. If, however, the action is delayed, the sensation reaches awareness and the urge to act develops. Urge is separate from the sensation. The sensation that our bladder is full is distinct from the *need* (urge) to empty it. Bodily sensations that trigger urge are uncomfortable and, as they mount in intensity, lead to a feeling of distress. This is probably because the actions to which urges lead are those that are essential to our survival. During a brief period, we can control the action by either suppressing it or executing it, but at some point it occurs without our will. In this way, the actions driven by urges are neither truly involuntary nor truly voluntary. Because of the short time frame in which action must be taken, there is a sense of urgency with urge, differentiating it from desire. Once the action is taken, the sensation is eliminated and there is an experience of relief.

In many ways, Tourette patients experience a parallel series of events (Bliss, 1980). Their tics can occur completely out of awareness, and, in these instances, would be described as involuntary. Often, however, patients describe an uncomfortable bodily sensation that triggers the urge to tic: a feeling that the action *must* be done. When tics are suppressed, the sensation and urge increase in intensity, leading to mounting distress. Patients state that they voluntarily make tics occur in response to the urge (Lang, 1990), causing a reduction in the bothersome sensation and a feeling of relief. With prolonged suppression, the urge becomes overwhelming and tics occur beyond patients' control. Thus, tics reside in that gray zone between involuntary and voluntary, and have been called “un-voluntary.”

However, there are some key distinctions between normal interoception-related urges and those associated with tics. First, we do not yet know what type of sensory input generates the uncomfortable bodily sensations that trigger the urge to tic. Although patients sometimes describe these sensations as coming from muscles or joints, it has never been demonstrated experimentally that sensory activity initiated in the periphery is the origin of their sensory experience. Second, tics are not key to survival. It is an important aspect of the pathology

in Tourette syndrome that patients experience such distress in relation to actions that are not only nonessential but also nonproductive. We do not yet understand when or how this association is made. Third, following the tic, the bothersome sensation is not eliminated, but only reduced in intensity. Finally it is not clear why tics must be performed in a particular way in order to achieve relief and diminishment of the bothersome sensations. Continued research into the circuitry that mediates both normal and pathological urges, as described by Jackson et al., will help our understanding and treatment of Tourette syndrome and other impulse-control disorders.

Features of normal and tic-related urges

| <i>Characteristic</i> | <i>Normal</i> | <i>Tic</i> |
|---|---------------|------------|
| Sensory input from bodily organs | Yes | ? |
| Sensation reaches awareness when action delayed | Yes | Yes |
| Sensation is uncomfortable | Yes | Yes |
| Experience urgency and need to take action | Yes | Yes |
| Action can be suppressed (minutes), and then must occur | Yes | Yes |
| Relief from discomfort with action taken | Yes | Some |
| Action is necessary to organism survival | Yes | No |

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The role of consciousness in the urge-for-action

Álvaro A. Rivera-Rei¹, Andrés Canales-Johnson¹, David Huepe¹, and Agustín Ibáñez^{1,2}

¹Laboratory of Cognitive and Social Neuroscience, Universidad Diego Portales, Santiago, Chile

²Institute of Cognitive Neurology (INECO), Favaloro University, and National Scientific and Technical Research Council (CONICET), Buenos Aires, Argentina

E-mail: aibanez@neurologiacognitiva.org

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Abstract: A neuroanatomical model of urge-for-action phenomena has been proposed based on the “motivation-for-action” network (e.g., insula and mid-cingulate cortex). Notwithstanding the sound evidence presented regarding the functional and anatomical correlates of this model, the nature

of the relationship between urges and conscious awareness remains to be addressed. Moreover, this model does not seem to explain (1) how a conscious access threshold is reached, and (2) the way in which the urges are related to more general contents of consciousness.

Jackson et al. have proposed a novel model of urge-for-action. This model considers the nature and functional anatomy of urge-for-action in the context of normal life and clinical disorders. Through a meta-analysis, the authors show that there is an overlap between limbic sensory and motor neural circuits related to urges of everyday behaviors such as swallowing and tics in Tourette syndrome. The primary merit of this work is unquestionable; the authors propose an empirical and theoretical model of urge-for-action incorporating actions that do not necessarily require conscious awareness of the sensory stimulation that triggered them. Nevertheless, there are important issues that this model does not explicitly incorporate.

First, it is not clear how urge-for-action, as defined in this paper, can be a fully unconscious phenomenon. If the momentary inhibition of the action is an integral part of the definition of these urges, then that inhibition should be unconscious as well. In this paper, we find a lack of evidence on this topic, perhaps reflecting more than a mere lack of interest on this matter. Having searched the literature on unconscious inhibition of action, we found several instances in which willed intention is involved (e.g., go/no go tests in Eimer & Schlaghecken, 2002, and van Gaal, Ridderinkhof, van den Wildenberg, & Lamme, 2009). It is hard to imagine a fully unconscious inhibition of the kinds of actions considered to be representative of urge-for-action (coughing, swallowing, yawning, etc.). As long as that inhibition plays an important role in this process, we should be consciously aware of our urge-for-action as opposed to our reflexes.

The second issue concerns the nature of the relationship between urges and conscious awareness. Jackson et al. explained that the intensity of physiological afferent stimulation relates directly to the awareness of the urge’s strength during a phenomenon such as swallowing, but it is not clear how this phenomenon could be explained by their proposed model.

Despite the straightforward relationship between insular cortex and interoceptive conscious awareness (e.g., Ibáñez, Gleichgerrcht, & Manes, 2010), this fact

is not explicitly taken into account in terms of the neuronal activity of the cortical and subcortical regions considered in this model. More importantly, even if we consider that urge-for-action could be an unconscious phenomenon, it remains unclear how this model could explain the transition between urges the subject is not conscious of and those of which the subject is consciously aware. Along these lines, is it the strength of activation of the right insular cortex, the anterior cingulate cortex (ACC), or the circuit between these regions that is responsible for setting the threshold between unconscious and conscious awareness of urges? This point is far from being addressed in Jackson et al.'s model.

Finally, how could the urge-for-action model of Jackson et al. be integrated with more general models of consciousness? Current models have determined the activation of widespread cortical regions during goal-directed visual awareness (e.g., Dehaene et al., 2001) and have specified some neuronal markers for reaching the threshold of conscious perception (e.g., Del Cul, Baillet, & Dehaene, 2007). How does this urge-for-action circuit interact with more general circuits of conscious perception? Interoceptive awareness is conceptualized as the capacity of being aware of some specific *content* of consciousness; that is, of visceral perception (Ibáñez et al., 2010). Therefore, the authors should clarify the way in which interoceptive awareness might be related to other contents of consciousness, such as goal-directed cortical circuits underlying more general conscious perception phenomena.

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Urges, inhibition, and voluntary action

Parashkev Nachev

Institute of Neurology, University College London,
London, UK

E-mail: p.nachev@ion.ucl.ac.uk

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Abstract: It is constitutive of the notion of an urge that it must precede the action it urges. For the duration of an urge to be non-zero, some process must keep the action being urged in check. Urges therefore inevitably involve inhibition of action, and perhaps conflict between action and inaction. In

any event, they cannot form a critical part of the phenomenology that many argue must precede voluntary action, for if they play any part at all, it is only in situations where the action is to some degree inhibited.

The notion of “urge” has come to play a pivotal role in current conceptions of voluntary action. Curiously, it has done so without detailed exploration of the kinds of actions—involuntary or atypically voluntary—where the need to invoke it is arguably much greater, and where an understanding of its neural basis is far more plausibly within reach. And when one analyzes such actions—as Jackson and his colleagues lucidly and comprehensively do—the notion of urge that emerges is radically at odds with one that gives it a critical role in voluntary action. This is just as important a conclusion as the independent clarification of the neural substrate of urges itself.

It is surely right that urges must be dissociated from the sensations that in some cases prompt them. The urge to yawn, for example, is not plausibly any kind of sensation: One can only describe it with reference to the action it compels. What is minimally constitutive of the notion of an urge is that it is an urge *to do something*: it is both transitive and directed at a specific action. It is also true, as Jackson and his colleagues point out, that an urge must temporally *precede* the action: If it post-cedes it, we would not call it an urge, and if it parallels it in time, then it could not be an urge to perform the action because the action is already being performed. But the implication goes further. Since the urge is to perform the action, the necessary interval between it and the action during which the urge is experienced must involve *inhibition* of the action, for otherwise the action would be performed immediately. Inhibition is therefore an inevitable consequence of the notion of an urge.

Indeed, it is striking that the actions commonly associated with urges—both in the normal and in the pathological state—are usually of the kind that cannot be actively *chosen* but only *withheld*. One cannot actively choose to yawn or sneeze, and if one coughs or voids one's bladder voluntarily one tends to do so pre-emptively of the normal action. To the extent to which we have control over such actions, it is to keep them in check, to be released at the time when their performance is convenient. There are, of course, other comparably “automatic” actions, such as blinking, where urges play a much less prominent role, but it is notable that they tend to be of a kind one rarely has

reason to suppress. Equally, the actions associated with urges in movement disorders such as Gilles de la Tourette syndrome are perceived as unwanted; where no such strong perception exists—in many cases of chorea, for example—patients do not complain of urges.

An urge to act, then, cannot be empirically dissociated from the inhibition of the action, and presumably also from the conflict between action and inaction: this is so not because we lack the experimental tools but because inhibition is constitutive of the notion of an urge. This implies that the neural substrate Jackson and his colleague identify must also subservise these processes. More importantly, it casts further doubt on the notion that an urge is a signature of the phenomenology that is argued to precede voluntary action and to take part in its self-ascription. For if an urge signifies the inhibition of an action, it can hardly be thought of as the “idea” driving it. This also explains why urges are often reported during macrostimulation of the dorsomedial frontal cortex: The set of multiple neuronal pools inevitably severally activated at that scale of stimulation is bound to contain units that inhibit as well as drive active movement.

There are, of course, numerous unanswerable arguments against the ideomotor theories of action popularized by Libet’s work, but keeping the lid on that coffin is so extraordinarily difficult another nail can never go amiss.

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Unaware urges? Let’s not complicate matters further

Edward H. F. de Haan

Department of Psychology and Centre of Cognitive Sciences Amsterdam, University of Amsterdam, Amsterdam, The Netherlands
E-mail: e.h.f.dehaan@uva.nl

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Abstract: The model put forward for the neuroanatomical basis of urges-for-action is compelling. The arguments based on meta-analyses of existing neuroimaging data are elegant and convincing. However, I am not convinced by the suggestion

that there are conscious urges and urges that remain unaware. In my view, awareness is a defining feature of an urge.

Jackson et al. develop a convincing case for the existence of a neuroanatomical system that is responsible for the “urge-for-action.” The role of the (right) insula and the dorsal anterior cingulate cortex is inferred on the basis of a number of separate meta-analyses looking at associated brain activations in response to specific stimulation—in this case different triggers of urges. The idea that there are separate systems for “willed” or planned actions and “urged” actions makes sense and is clearly supported by the clinical and neuroimaging data.

The definition of “urges-for-action” proves more complicated. The beginning is relatively straightforward. These urges involve a limited set of actions that are habitual, standardized routines, such as scratching, yawning, or swallowing. They typically do not require feedback, and they are functional in that they alleviate specific negative or unpleasant bodily states. Things become tricky when we are offered the suggestion that we have conscious and unconscious urges (cf. Dijkerman & De Haan, 2007). We are told that urges and desires are not synonymous, and the main reason for this is that urges may also remain unaware to the person who “experiences” them. Indeed, we may find ourselves swallowing or yawning without having had a conscious urge, but it is not clear to me why this behavior cannot be classified as “reflexive.” Indeed, the Davenport, Sapienza, and Bolser (2002) study seems to indicate that we are dealing with a system where the intensity of the (negative) stimulation is directly related to strength of the perceived urge. This makes sense, the limbic system including the insula, registers the amount of bodily discomfort, and depending on the severity of this discomfort, a more or less “urgent” urge is felt.

I also agree with the authors that what distinguishes a reflex from an urge is the fact that a reflex—by definition—is immediate and proceeds without conscious interference. An urge, however, may need to be postponed as the execution of the required action is socially or emotionally compromising. Here I would like to suggest a different interpretation from the one put forward by Jackson et al. that an urge may be construed as an interrupted reflex. The reflex entails a complex sequence of detecting a specific negative

bodily state coupled to a proven alleviating motor action. The fact that this motor action is not socially or emotionally acceptable is in essence culturally defined, and therefore, is a learned response.

Thus, and this is my central thesis, the defining aspect of an urge is a learned interruption of a reflexive sequence. The result of this interruption is a conscious awareness of the pending action *and* the fact that this action is not acceptable in the current situation. In this view, an unconscious urge is a contradiction in terms, as an urge constitutes the awareness of the desire to perform an action coupled with the learned response to inhibit this action.

Jackson et al. state that it is “difficult to reconcile the concept of a ‘desire,’ which is often defined as ‘a longing or craving for something that brings satisfaction or enjoyment,’ with unwanted actions, the execution of which is experienced as unpleasant and distressing” (p. 229). I find this surprising and I cannot subscribe to this “difficulty” felt by the authors, as in my experience this is often exactly what patients with obsessive compulsive disorder or Gilles de la Tourette syndrome report. The simultaneous experience of the urge to carry out an action and the concurrent realization that this is not acceptable, socially or emotionally, could be posited as the hallmark of obsessive compulsive disorder. In fact, after the act has been performed, there is again a simultaneous experience but now one of relief (because the act has—somewhat—alleviated the negative bodily state) and shame (because the executed act was socially or emotionally unacceptable). Interestingly, when I was reading the article for the first time, I thought that, toward the end, the authors would propose a role for the right insula in becoming aware of an urge. They did not do so, and I am glad they did not, because it is not important for their main conclusion.

This review provides strong evidence for a separate network in the brain involved in the detection of well-defined negative bodily states and a set of habitual, standardized routines to alleviate the discomfort. When the required action is consciously flagged because of learned associations with negative social or emotional connotations, the execution of these actions is—temporarily—inhibited, and an “urge” is experienced.

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My urge, my tic – a missing link between urges and tic inhibition

C. Ganos¹ and F. C. Hummel²

¹Movement Disorders Research Group, Department of Neurology, University Medical Center Hamburg-Eppendorf (UKE), Hamburg, Germany

²Brain Imaging and Neurostimulation (BINS) Laboratory, Department of Neurology, University Medical Center Hamburg-Eppendorf (UKE), Hamburg, Germany

E-mail: f.hummel@uke.de

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Abstract: Despite the fact that premonitory urges precede most tics in patients with Gilles de la Tourette syndrome (GTS), the voluntariness of tic elicitation and its suppressibility as a response to these urges still remains unclear. Moreover, there are no systematic studies examining the association between urge intensity and the ability to suppress tics. As shown by behavioral, neurophysiological, and imaging data, sensorimotor networks in GTS exhibit altered patterns of organization modulated through interactions with frontomesial networks of volitional inhibition.

In their nice and elaborated review, Jackson et al. provide a functional basis for a distinction between reflexive behaviors and actions that come from urges helpful in daily life (such as the urge to yawn, urinate, and cough) and those possibly interfering with daily life (such as the urge to tic). They argue that the latter are associated with *unwanted actions*, principally as their *interoceptive gatekeepers*, allowing their conscious *suppression or deferment*. Particularly for Gilles de la Tourette syndrome (GTS), they propose that premonitory sensations are represented within the somatosensory (SII) and mid- and posterior insular cortices, leading to *habitual actions*. They argue that the urge for action is associated with activity of the anterior insular cortex, which is then relayed to the cingulum and the ventral striatum for reward-based prediction analysis, and then forwarded again to the insular and inferior frontal cortices, which in their turn satisfy or propagate the urge for action.

Examining the properties of the urge in GTS, and already before Leckmann’s seminal paper (Leckmann,

Walker, & Cohen, 1993) on the subject, Bliss, a clinician and GTS patient himself, published (Bliss, 1980) a thorough description of his own premonitory sensations and, as a result, argued for the voluntariness of tics. In the following years, systematic studies showed that more than 90% of patients with GTS report these urges and consider tics as, if at all, only partial involuntary. It has been consistently found that the development of the urge is reported with a lag of about 3 years after the onset of tics (Banashewski, Woerner, & Rothenberger, 2003; Kwak, Dat Vuong, & Jankovic, 2003; Leckmann et al., 1993). The delayed appearance of this phenomenon has led to a series of hypotheses: Is the association of urges and tics a compensatory evolutionary development as a basis for the option to suppress these phenomena, or are urges and tic suppressibility co-existing phenomena, as suggested by recent tic-suppression studies? (Banashewski et al., 2003; Conelea & Woods, 2008).

As for the neurophysiology of tic generation, the zeitgeist led to the study of the correlates of the voluntariness of movement disorders, with the pioneering work of Obeso, Rothwell, and Marsden (1981), followed 14 years later by another work (Karp, Porter, Toro, & Hallett, 1996), which examined the presence of the Bereitschaftspotential (BP) in tics. The results were equivocal, with the first study showing that tics were not preceded by the BP, and the second demonstrating its presence in 2 out of 5 patients. This led to the hypothesis (Kwak et al., 2003) that only tics associated with a premonitory sensation—and therefore consciously perceived and voluntarily initiated—are preceded by the BP. This has been shown in three patients in the only study to date that addressed this question (Duggal & Nizamie, 2002). Additionally, and in accordance with the latter study, which, surprisingly, found a shorter than normal BP, Moretto showed that patients with GTS have a delayed experience of volition (Moretto, Schwingenschuh, Katschnig, Bhatia, & Haggard, 2011). This would imply that not only the formation of tics but also the formation of normal movements would necessitate an altered pattern of motor organization through fronto-striato-thalamo-cortical pathways, as supported by current findings (Heise et al., 2010; Roessner et al., 2011). Furthermore, in the absence of direct evidence to support the notion that the awareness of urges correlates positively with the ability to suppress tics—a suppression, which, according to Jackson et al., would lead to the propagation of the urge and further activation of the

anterior insula—the role of frontomesial networks of volitional inhibition (Kühn, Haggard, & Brass, 2009) and tic suppression has to be addressed in detail. These networks presumably influence the pre-supplementary motor area activity in a top-down fashion, as supported by a recent EEG experiment showing elevated inter-regional interactions between these and sensorimotor and prefrontal areas during tic inhibition, paralleled by an increasing urge to tic (Serrien, Orth, Evans, Lees, & Brown, 2005).

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An urge to act or an urge to suppress?

John C. Rothwell and Mark J. Edwards

Institute of Neurology, and Sobell Department of Motor Neuroscience and Movement Disorders, University College London, London, UK
E-mail: j.rothwell@ion.ucl.ac.uk

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Abstract: There is no doubt that there exist urges to act, but are these really the cause of the action or is an urge a shorthand term to describe the effort involved in suppressing an action that is triggered automatically by some other process?

There is no doubt that there exist urges to action—just think back to Zidane’s uncontrolled and badly timed urge to head-butt an opponent. But can we go quite as far as Jackson and colleagues in believing that they all arise from activity in the same anterior insular and caudal cingulate regions of the cortex? Furthermore, does activity in these regions then drive the premonitory sensations that are sometimes described by patients with Tourette’s syndrome prior to their tics? The argument of Jackson and colleagues is erudite and informed, but there seems to be a certain sleight of hand in the logical steps of the argument which lead to the definition of a “motivation for action” network.

The authors begin with the highly reasonable assertion that an urge to act is, at least in the majority of instances, an awareness of the effort involved in restraining the act. That is, some other factor (perhaps only dimly perceived) is the trigger for this latent action, and when we become aware of the impending

action, we are able to prevent it from being released by effort of will. Effectively, this seems to be saying that stimulus–response associations exist that can give rise to actions. Consistent with this idea, the authors point out that some actions that can be associated with urges on one occasion (e.g., yawning) can, on another occasion, emerge without the sensation of an urge. The rule seems to be that if the stimulus or impending action is perceived before the action occurs, and if the action is subsequently withheld, then we experience an urge to act (unless the stimulus disappears). We can feel an itch or a “desire” to scratch and we can decide to withhold the scratch; if the itch persists, then we may develop an urge to scratch. Paradoxically, an urge to act turns out to be an intention to suppress. The action itself is triggered by some other factor in an automatic fashion.

This seems to be a very simple and reasonable interpretation that involves two interacting processes: the basic stimulus–response coupling and a supervisory system with a power to withhold the response. However, the authors then seem to pursue quite a different interpretation about halfway through the article. The turning point comes after the analysis of the first set of imaging data. Here they find common

activation in anterior insula and caudal cingulate cortex during yawning and micturition. They then say that activity in these common areas is responsible for the urge to act and then causes the action, as illustrated in Figure 9. At this stage, we have lost the low-level stimulus–response coupling and all mention of inhibition. We are now told that inputs to the anterior insula produce an urge to act (not to suppress a prepotent action). This constitutes a feeling that we have to make a particular movement, which is then achieved via activation of caudal cingulate cortex.

We accept that it is difficult to decide which of these interpretations is true. What strikes us as odd is that the authors begin by emphasizing the importance of inhibition, yet end by talking about motivation to act. Would it not be simpler to suppose that stimulus–response associations exist at all levels of the sensorimotor system from spinal reflexes to striatal habits. These are all to a greater or lesser extent modifiable by a supervisory system we may equate with volitional control. An urge to act is an expression of the interaction between these systems, not a separate system itself.

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