Neural correlates of the essence of conscious conflict: fMRI of sustaining incompatible intentions

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Abstract The study of intrapsychic conflict has long been central to many key theories about the control of behavior. More recently, by focusing on the nature of conflicting processes in the brain, investigators have revealed great insights about controlled versus automatic processes and the nature of self-control. Despite these advances, many theories of cognitive control or self-control remain agnostic about the function of subjective awareness (i.e., basic consciousness). Why people consciously experience some conflicts in the nervous system but not others remains a mystery. One hypothesis is that people become conscious only of conflicts involving competition for the control of skeletal muscle. To test one aspect of this larger hypothesis, in the present study, 14 participants were trained to introspect the feeling of conflict (the urge to make an error during a Stroop color-word interference task) and then were asked to introspect in the same way while sustaining simple compatible and incompatible intentions during fMRI scanning (to move a finger left or right). As predicted, merely sustaining incompatible skeletomotor intentions prior to their execution produced stronger systematic changes in subjective experience than sustaining compatible intentions, as indicated by self-report ratings obtained in the scanner. Similar ratings held for a modified Stroop-like task when contrasting incompatible versus compatible trials also during fMRI scanning. We use subjective ratings as the basis of parametric analyses of fMRI data, focusing a priori on the brain regions involved in action-related urges (e.g., parietal cortex) and cognitive control (e.g., dorsal anterior cingulate cortex, lateral PFC). The results showed that subjective conflict from sustaining incompatible intentions was consistently related to activity in the left post-central gyrus.

Introduction

In the history of psychology, the study of intrapsychic conflict was central to the development of many frameworks on the control of behavior, including Freud's (1938) intrapsychic conflicts between the ego and the id, Lewin's (1935) motivational conflicts (e.g., *approach–approach* conflict), Festinger's (1957) cognitive dissonance, Hull's (1943) conflicting drives (e.g., curbing an action-related impulse), and Neal Miller's (1959) examination of competing inclinations in animal models. More recently, by focusing on conflicting processes in the brain, investigators in the field of *cognitive control* have reached insights regarding (a) controlled, conscious processing, (b) automatic and unconscious processing, and (c) the nature of self-control (Botvinick 2007; Cohen et al. 1990; Curtis and D'Esposito

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2003, 2009; Gazzaley and Nobre 2011; Mayr 2004; Metcalfe and Mischel 1999; van Veen and Carter 2006).

For example, much has been learned about the nature of action control from laboratory *response interference* (RI) *paradigms*, which often involve conflict. In these paradigms, the mere presence of incidental action-related stimuli can activate processes that influence intended responses to a target stimulus (cf., Hubbard et al. 2011; Morsella and Miozzo 2002; Wilson et al. 2011). Such "distractor" stimuli can systematically facilitate or interfere with intended responses to a target. In the Stroop task (Stroop 1935), for instance, one must name the color in which a word is written. When the word and color are incongruous (e.g., RED in blue), response conflict leads to interference. Presumably, the conflict is between the automatic action plan of word-reading and the weaker plan of color-naming (Cohen et al. 1990; Eidels et al. 2010; Roelofs 2010). (See reviews of findings from the Stroop task in MacLeod 1991 and MacLeod and MacDonald 2000.) This interference during incongruent trials is manifested as increased error rates, response times (RTs), and participants' self-reported urges to make a mistake ("urges to err," for short; Morsella et al. 2009a). Such urges to err are considered a subjective aspect of processing. To record these subjective effects, participants are asked after each trial a question (e.g., "How strong was your urge to make a mistake?") and respond using a Likert scale, as explained below. When the color matches the word (e.g., RED in red) or is presented on a neutral stimulus (e.g., XXXX), there is little or no such interference.

Similarly, in the flanker task (Eriksen and Eriksen 1974), one must respond to a visual target and disregard flanking distractors. In one version of the task (Eriksen and Schultz 1979), during *flanker training*, participants are first trained to press one button with one finger when presented with the letter S or M and to press another button with another finger when presented with the letters P or H. After training, participants are instructed to respond to the stimulus presented in the center of an array and to disregard the flanking distractors. Interference (e.g., increased RTs and urges to err) is stronger when distractors and targets are associated with different actions (*response interference* [RI]), such as SSPSS, than when distractors and targets look different but are associated with the same response (*perceptual interference* [PI]; Morsella et al. 2009b), such as SSMSS. (Shortest RTs occur in the *Identical* condition [e.g., SSSSS].)

RI differs from PI in terms of both subjective effects and the underlying neural processing. Evidence suggests that, unlike perceptual interference, response interference stems primarily from the automatic, "stimulus-triggered" activation of target-incompatible action plans by distractors (DeSoto et al. 2001). Accordingly, psychophysiological research shows that RI competition involves simultaneous activation of the brain areas associated with the target- and distractor-related responses (DeSoto et al. 2001; Mattler 2005). Moreover, neuroimaging studies reveal that, though both RI and PI are associated with differences in performance, only the former is related to activations in the anterior cingulate cortex (van Veen et al. 2001), a brain region important in cognitive control that is located on the medial surface of the frontal lobe and is interconnected with many motor areas.

Conflicts involving primordial urges, too, activate this region (see review in Morsella et al. 2011a), and in the Stroop task, this region has been shown to be most active in contrasts between incongruent and neutral conditions (Botvinick et al. 2001; MacLeod and MacDonald 2000; Mayr 2004). There is a consensus that activation in the anterior cingulate cortex is often followed by ramped up activation in frontal control regions of the brain, such as the dorsolateral prefrontal cortex (DLPFC), which leads to increased cognitive control and improved performance (Cohen et al. 1990). Specifically, set-related top-down activation from prefrontal cortex increases the activation of posterior brain areas (e.g., visual association cortex) that are associated with task-relevant dimensions (e.g., color in the Stroop task; Enger and Hirsch 2005; Gazzaley et al. 2005; Gazzaley and D'Esposito 2007). It seems that much of the control-related processes occurring in frontal cortex may be transpiring unconsciously (Crick and Koch 2000; Suhler and Churchland 2009).

Through interference paradigms, much has been learned about the nature of RI and action control (Morsella 2009). However, it remains unspecified why conscious awareness is associated with some aspects of action control but not others. (Henceforth, "conscious awareness," "consciousness," and "awareness" refer to a basic form of consciousness, which, for present purposes, is defined operationally as any subjective state that the subject can self-report about.) One must consider that much of the complex processing associated with RI occurs unconsciously, as in the case of the unintentional activation of reading plans in the incongruent condition of the Stroop task (cf., Morsella and Miozzo 2002). How and why is consciousness associated with only some aspects of action control?

Supramodular interaction theory

To address this question, research focusing on action control and on the findings reviewed above has begun to reveal not only the behavioral and neural aspects of RI, but how these aspects are systematically associated with consciousness. For instance, one "action-based" framework, *Supramodular Interaction Theory* (SIT; Morsella 2005), attempts to explain which aspects of action control must trigger changes in consciousness. Building on the *integration*

consensus (e.g., Baars 2002; Dehaene and Naccache 2001; Merker 2007), which posits that the primary function of conscious processing is to integrate information/processes that would otherwise be independent (see review in Godwin et al., in press), SIT proposes that, for the adaptive control of action, consciousness integrates neural activities and information-processing structures that would otherwise be independent, but the framework also specifies which kinds of integration require consciousness and which kinds do not. For example, the framework reveals that conscious processing seems unnecessary for integrations across different sensory modalities (e.g., as in intersensory conflicts and multimodal integration) or integrations involving smooth muscle effectors (e.g., integrations in the pupillary reflex; Morsella et al. 2009a, b). These integrations/conflicts can transpire unconsciously. In contrast, people are likely to be aware of conflicts involving competition for control of the skeletal muscle output system. These *conscious conflicts* (Morsella 2005) are triggered by incompatible skeletomotor plans, as when one holds one's breath while underwater, suppresses uttering something, or inhibits a prepotent response in a laboratory RI paradigm. On the basis of this and other evidence (cf., Morsella 2005), SIT proposes that the primary function of consciousness is to integrate incompatible skeletomotor intentions for adaptive action (e.g., holding one's breath).

From this standpoint, in the nervous system, there are three distinct kinds of integrations or "bindings" (Morsella and Bargh 2011). *Afference binding* is the binding of perceptual processes and representations. This occurs in feature binding (e.g., the binding of shape to color; Zeki and Bartels 1999) and *intersensory* binding, as in the McGurk effect (McGurk and MacDonald 1976). (This effect involves interactions between visual and auditory processes: An observer views a speaker mouthing "ga" while presented with the sound "ba." Surprisingly, the observer is unaware of any intersensory interaction, perceiving only "da.") Afference binding can occur unconsciously. Another form of binding, linking perceptual processing to action/motor processing, is known as *efference binding* (Haggard et al. 2002). This kind of stimulus–response binding allows one to press a button when presented with a cue. Observation of reflexes and of many laboratory experiments has shown that responding on the basis of efference binding can occur unconsciously. For example, Taylor and McCloskey (1990, 1996) demonstrated that, in a choice RT task, participants could select the correct motor response (one of two button presses) when confronted with subliminal stimuli (Hallett 2007). The third kind of binding, *efference-efference binding*, occurs when two streams of efference binding are trying to influence skeletomotor action simultaneously (Morsella and Bargh 2011). This occurs when one holds one's breath, suppresses uttering something,

voluntarily breathes faster for some reward, or suppresses a prepotent response in a RI paradigm such as the Stroop task. According to SIT, it is the instantiation of conflicting efference–efference binding that requires consciousness. Consciousness is the "crosstalk" medium that allows conflicting action processes to influence action collectively, leading to *integrated actions* (Morsella and Bargh 2011) such as holding one's breath. Absent consciousness, behavior can be influenced by only one of the efference streams, leading to *un-integrated actions* such as unconsciously inhaling while underwater or reflexively removing one's hand from a hot object.

The essence of conscious conflict

From this standpoint, the activation of incompatible action plans (e.g., to look left *and* right) is the essence of conscious conflict (Morsella et al. 2009a) and leads to the subjective effects associated with the RI conditions of interference paradigms (e.g., the incongruent Stroop condition and RI flanker condition). In support of this hypothesis based on SIT, experiments have revealed that incompatible skeletomotor intentions (e.g., to point right *and* left, to inhale *and* not inhale) produce strong, systematic intrusions into consciousness, but no such changes accompany smooth muscle conflicts or conflicts occurring at perceptual stages of processing (e.g., intersensory processing; see meta-analysis of evidence in Morsella et al. 2011a). Accordingly, of the many conditions in interference paradigms, the strongest perturbations in consciousness (e.g., urges to err) are produced by RI. The effects are unlikely to be an artifact of the participant observing his or her own RTs, because they arise even when RTs are statistically taken into account or when participants are in a motionless state in which no response is emitted, as when participants are instructed to "prime" incompatible actions (to point left *and* right) but perform no action (Morsella et al. 2009a, 2011a). Conversely, when distinct processes lead to *harmonious* action plans, as when a congruent Stroop stimulus activates harmonious word-reading and color-naming plans, there are few such perturbations in consciousness, and participants may even be unaware that more than one cognitive process led to a particular overt action plan (e.g., uttering "red"). (This phenomenon, called *synchrony blindness* [Molapour et al. 2011], is perhaps more striking in the congruent ["pro-saccade"] condition of the *anti-saccade task*, in which distinct brain regions/processes indicate that the eyes should move in the same direction [cf., Morsella et al. 2011b].)

In synthesis, the SIT framework has been successful in homing in on the component processes of action production that are associated with intrusions in consciousness. For present purposes, we will focus only on a key hypothesis

from this approach that may illuminate the essence of conscious conflict—*that the mere activation of incompatible skeletomotor intentions in-and-of-itself must trigger strong changes in subjective experience, because the primary function of consciousness is to integrate such intentions for adaptive skeletomotor output.* The hypothesis predicts in a parsimonious fashion why both response conflicts and "hot" (Metcalfe and Mischel 1999) action conflicts yield subjective effects. For the latter, there is a skeletomotor plan associated with each goal participating in the conflict, and the plans of one goal are incompatible with those of the other goal. In the delay of gratification, for example, the plan of eating is incompatible with that of not eating; while holding one's breath underwater, the plan of inhaling is incompatible with that of not inhaling. Similarly, in the Stroop task, incompatible intentions are manifest when word stimuli activate conflicting word-reading and color-naming plans (Cohen et al. 1990).

However, substantially less research has focused on the neural correlates of the theoretically predicted conscious aspects of action production. Our primary goal is to identify the neural correlates of the aforementioned (and theoretically specified) aspects of action production that should be associated with intrusions in consciousness, namely the activation of incompatible action plans. Such an identification would advance the understanding of action and consciousness while illuminating the aspects of the problem of the neural correlates of consciousness, one of the greatest challenges in science.

Overview of the experimental approach

Participants were first trained to introspect about the subjective dimension of interest, and they then introspected about subjective states while sustaining compatible and incompatible action intentions. We examined the neural correlates of these two conditions. First, following the procedures of Morsella et al. (2009a), we trained participants to introspect about the subjective dimension of interest by having them rate their urge-to-err during the Stroop task. During this *introspection training*, participants named the colors in which stimulus words were written. We assumed that, when measuring this urge, participants presumably introspected and reported on the subjective experience associated with the conflict between the dominant word-naming and weaker color-naming responses (Cohen et al. 1990), though one cannot rule out that these judgments are influenced by arousal or a sense of effort from managing response conflict (see "General Discussion"). Based on theory (Morsella 2005) and previous findings (Morsella et al. 2011a), we predicted that the greatest urges to err would be reported in the incongruent condition (in part because this condition invokes incompatible action plans)

and that the weakest urges to err would be reported in the congruent condition (in part because this condition does not involve incompatible plans).

Following training, participants were informed that, when estimating their urge-to-err, what they were "looking inside their minds and measuring" was a psychological state known as "activity." To minimize experimental demand effects, we defined the concept of *activity* only in terms of the participant's Stroop task experience and offered no further information about the concept (see below). Thus, participants learned to introspect, not the general tendency to err on a task, but the specific urge or feeling that happens to be associated with interference on the Stroop task, in which incompatible plans play a role (Cohen et al. 1990). They were then told that they would later be asked to measure, not their urge-to-err, but specifically this kind of "activity" in a novel task.

Subsequently, in a *sustained intentions* task, participants rated activity while sustaining basic identical, compatible, or incompatible intentions. Based on Morsella et al. (2009a), compatible intentions consisted of pressing a button with a finger and "wiggling and hovering." The action intentions were deemed to be compatible because, in principle, one could satisfy the action goal of wiggling one's finger while reaching the button simultaneously. Based on piloting and behavioral evidence (see Morsella et al. 2009a), the action goals are regarded as thus being co-expressible. In contrast, incompatible intentions consisted of using a single finger to press separate buttons. We predicted that participants would report more activity while sustaining incompatible as compared to compatible or identical intentions. For the sake of comparison, we also measured this kind of subjective activity in the *multi-source interference task* (MSIT; Bush et al. 2003), described below.

Predictions about neural correlates of action-related urges

As mentioned above, much of the control-related processing in frontal cortex may be unconscious. It seems that we do not have direct, conscious access to motor programs or other kinds of "efference generators" (Grossberg 1999; Morsella and Bargh 2010; Rosenbaum 2002), including those for language (Levelt 1989), emotional systems (e.g., the amygdala; Anderson and Phelps 2002; Öhman et al. 2007), or executive control (Crick 1995; Suhler and Churchland 2009). The notion that efference generation is largely unconscious illuminates why, when speaking, one often does not know exactly which words one will utter next until the words are uttered or subvocalized following word retrieval (Levelt 1989; Slevc and Ferreira 2006).

Regarding the neural correlates of action-related urges, there is evidence implicating, not frontal areas, but

posterior perceptual regions as the key regions responsible for conscious states (see review in Godwin et al., in press). (Relevant to this hypothesis is research on the phenomenon of *sensory neglect*; cf., Graziano 2001; Heilman et al. 2003.) For example, in a study involving seven patients undergoing awake brain surgery, direct electrical stimulation of parietal areas of the brain gave rise to the subjectively experienced will to perform an action (that is, an "urge"), and increased activation made subjects believe that they actually executed the corresponding action, even though no action was performed (Desmurget et al. 2009; Desmurget and Sirigu 2010). Activating motor areas (e.g., in premotor areas) resulted in the performance of the actual action, but subjects believed that they did not perform any action (see also Fried et al. 1991): "Stimulation of the premotor region triggered overt mouth and contralateral limb movements. Yet, patients firmly denied that they had moved" (Desmurget et al. 2009, p. 811).

This is consistent with the age-old *Sensorium Hypothesis* (Gray 2004; Godwin et al., in press; James 1890; Müller 1843) that action/motor processes are largely unconscious (Gray 2004; Grossberg 1999; Goodale and Milner 2004) and that the contents of consciousness are influenced primarily by perceptual-based (and not action-based) events and processes (Gray 1995). Accordingly, it has been proposed that, in terms of stages of processing, that which characterizes conscious content is the notion of *perceptual afference* (information arising from the world that affects sensory-perceptual systems) or *perceptual re-afference*, such as the proprioceptive information generated during action production. Sherrington (1906) aptly referred to these two similar kinds of information as *exafference*, when the source of information stems from the external world, and *reafference*, when the source is feedback from overt actions. There is also similar feedback from the activation of internal, action plans (e.g., information arising from "corollary discharges" or "efference copies" of our own action plans; Chambon et al. 2013; Christensen et al. 2007; Jordan 2009; Miall 2003; Obhi et al. 2009).

The hypothesis that perceptual brain areas (e.g., parietal cortex) should be associated with action-related urges is supported by hypotheses and frameworks other than the age-old sensorium hypothesis. For example, such a notion is consistent with recent approaches focusing on *ideomotor theory*, *mirror neurons* (see review in Rizzolatti et al. 2008), reafference in action control, and working memory. We now discuss in brief each of these approaches.

In ideomotor theory (Harleß 1861; James 1890; Lotze 1852), the perceptual consequences of a given action, which Harleß (1861) referred to as the "Effektbild," automatically activate the unconscious motor programs responsible for enacting that action. In this way, voluntary action is guided by perceptual-like representations of what can

be construed as action effects. These effects include bodily states (e.g., a flexed finger) or "remote" effects in the external world, such as the change in position of a light switch (Hommel 1998; Hommel and Elsner 2009; Jordan 2009). From this standpoint, and consistent with the current hypothesis, intentional action depends in part on activation of perceptual-like representations, representations which are presumably associated primarily with post-central cortex. (For contemporary ideomotor accounts, see Hommel 2009; Hommel et al. 2001; Jordan 2009.) Contemporary ideomotor models go on to propose that perceptual action effects and action codes share the same representational format; hence, these accounts have been described as "common code" theories of perception-and-action (Hommel 2009).

Contemporary research on the mechanisms underlying mimicry, including "mirror neurons" (Rizzolatti et al. 2008), similarly suggests that there is overlap in the neural networks involved in (a) the perception of actions (e.g., the perception of the actions of others) and (b) the execution of one's own actions. From this standpoint, perceptual processing is an inextricable part of action control (Iacoboni 2005; Jordan 2009; Miall 2003). Consistent with this perspective, Desmurget et al. (2009) concluded in their brain stimulation study that action intentions in perceptual regions may be processed in terms of the perceptual consequences of the intended action (see review of convergent evidence in Jordan 2009; Miall 2003). Complementing these findings is research on the role of reafference in action control. This research reveals that a key component of the control of intentional action is reafference to perceptual areas of the brain (Berti and Pia 2006; Chambon et al. 2013; Iacoboni 2005; Miall 2003; Tallon-Baudry 2012).

Last, these conscious contents (e.g., urges and perceptual representations) are similar to (or perhaps one and the same with) the contents that occupy the "buffers" in working memory, a large-scale mechanism that is used to sustain the activation of content-based representations in mind (e.g., for information manipulation) and is intimately related to both consciousness and action production (Baddeley 2007; Fuster 2003). Recent developments reveal that working memory is intimately related to both action control and consciousness (LeDoux 2008), as is evident in the title and contents of a treatise on working memory— *Working Memory, Thought, and Action* (Baddeley 2007). Indeed, perhaps no mental operation is as consistently coupled with conscious processing as is working memory (LeDoux 2008). When trying to hold in mind action-related information, a person's consciousness is consumed by this goal (James 1890). For instance, when holding a to-be-dialed telephone number in mind (or when gargling with mouthwash for 30 s), action-related mental imagery occupies one's consciousness during the delayed action phase.

Similarly, before making an important toast (or, more dramatically, making the toast in an unmastered language), a person has conscious imagery regarding the words to be uttered, much as when an actor rehearses lines for an upcoming scene. The buffers storing information in working memory tend to involve perceptual regions (Baddeley 2007; Gazzaley et al. 2005). In this way, before an act, the mind is occupied with perception-like representations of what that act is to be, as James (1890) stated: "In perfectly simple voluntary acts there is nothing else in the mind but the kinesthetic idea… of what the act is to be" (James 1890, p. 771). Thus, voluntary action control often occupies both working memory and perceptual consciousness.

It is clear that there are several contemporary accounts that are consistent with the age-old hypothesis that the urges associated with intentional action should involve regions of the brain that have historically been associated with perceptual processing. In summary, we predict that the neural correlate of urges will involve perceptual areas (e.g., parietal cortex), including, in addition, perceptual areas that may constitute the buffers of working memory (cf., Buchsbaum and D'Esposito 2008).

Method

Participants

Participants had to be between the ages of 18 and 35, right-handed, native speakers of English, and had to have no history of brain damage. Fourteen participants participated for $20 per hour and gave informed consent under the auspices of the Yale University Human Investigation Committee.

Procedures

Participants were run individually at the Yale Magnetic Resonance Research Center. Introspection training, action training, and MSIT training occurred outside of the scanner, in a room near the scanner and before participants began the scanning session. For these training sessions, stimuli were presented on the screen of an Apple Power-Book (12″), and stimulus presentation and data recording were controlled by the software program PsyScope (Cohen et al. 1993). We will now describe the three training sessions in the order in which participants experienced them.

Introspection training

Based on the procedures of Morsella et al. (2009a), participants performed 24 Stroop trials, in which they had to utter the color name in which stimulus words were presented as quickly and as accurately as possible. Following

each response, participants were asked "How strong was the urge to make a mistake?", which they rated on an 8-point scale, in which 1 signified "almost no urge" and 8 signified "extremely strong urge." Training consisted of 24 Stroop trials having 8 congruent (e.g., RED written in red), 8 incongruent (e.g., RED in blue), and 8 control (e.g., HOUSE in green) stimuli in random order. In the incongruent condition, targets (colors) and distractors (words) were re-paired systematically (e.g., if RED was written in blue, then BLUE was written in red). Participants were instructed to name the color in which the word was written as quickly and as accurately as possible.

On each trial, following a blank screen (500 ms), a ready prompt (question mark) appeared onscreen until participants indicated that they were ready to proceed by pressing the space bar. Thereafter, a fixation point (+) was shown at the center of the screen for 1.5 s. It was followed by a blank screen (700 ms), after which time a randomly selected Stroop stimulus appeared (48-point Helvetica), remaining onscreen for 850 ms. The experimenter observed how each participant responded to each stimulus word. After the response and 700 ms, participants were asked about their urge to err (see above). Thereafter, the next trial began after 500 ms. Of the 24 trials, 8 were congruent; 8 were control; and 8 were incongruent.

Immediately following the 24th trial, participants were told the following. "What you were measuring inside your mind when estimating your urge to make a mistake is a psychological state called 'activity.' When your urge to make a mistake on this task was high, activity was high; when your urge to make a mistake on this task was low, activity was low. Which of the following is associated with more 'activity'? RED written in black or BLACK written in black?" No participant had difficulty understanding the concept of activity: All participants responded in the affirmative to the question, "Do you understand the concept of activity?" It is important to note that we could have just as well called this dimension of interest something as arbitrary as "J5" or "Wundt Energy," for the construct was defined only by the participant's own experience. We selected the term "activity" only because it is unbiased and intuitive.

Action training

Following introspection training, participants learned throughout the course of 15 trials about the nature of the simple motor acts that comprised our critical, sustained intentions task. During resting position, the finger depressed the central of three buttons of a standard fMRI button box. Depending on the color of a cue (two colored squares; Fig. 1), participants (a) released the central button, slid their finger leftward (3 cm), and clicked the button on the left (action for the red cue), (b) clicked the
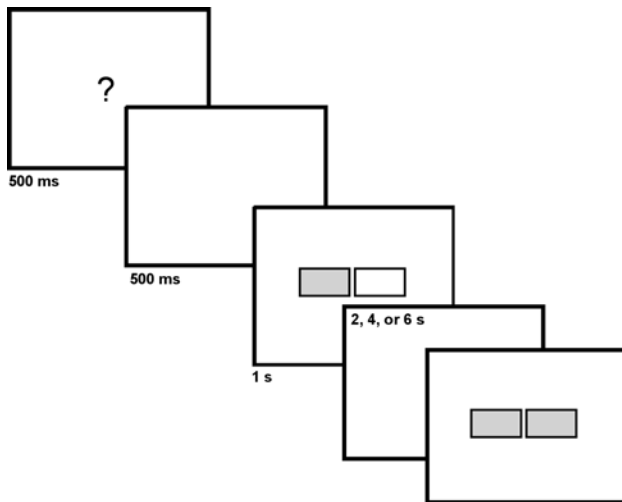
Fig. 1 Schematic of trial events across time

button on the right (3 cm) with a similar motion (action for green cue), or (c) released the central button and "hovered and slightly wiggled" their index finger over the box (action for the yellow cue). For this action, participants were instructed, "Release the central button by slightly lifting your left index finger; then hover and slightly wiggle or vibrate the finger." The vibration was more of an up and down motion, spanning roughly 3 s. The experimenter verified that each participant could perform each of the actions accurately.

Participants were told that, before an action cue (a color) would appear, they would see a color prompt to prime their response. They were instructed to not respond to this prompt but to respond only after seeing the subsequent cue. In the first 8 trials of training, the prompts unambiguously informed the participant about the nature of the required action. Each trial unfolded as follows. After a blank screen (700 ms), a ready prompt (a question mark, presented for 500 ms), and another blank screen (500 ms), a prompt was presented for 1 s. Following a variable delay of 2, 4, or 6 s, the action cue appeared onscreen till the participants performed the action or a timeout of 2 s. After the 8 identical trials, participants were told that the following trials would be similar to the first 8 except that prompts may be ambiguous (two different colors), signaling that each of the two cues is equiprobable as target and that they should prepare to perform either action as quickly as possible. Participants were encouraged to be in a state of readiness, with the instructions to mentally prepare to perform both actions and to respond to the target cue as fast as possible. There were trials in which the prompts were associated with actions that were co-expressible (2 trials of "yellow-green" compatible prompts and 2 trials of "yellow-red" compatible prompts), and trials in which the

prompted actions could not be co-expressed (2 "red-green" incompatible prompts).

MSIT training

Participants were informed how to perform the MSIT through instructions presented on the computer screen, which included the following critical directions. "The three labeled keys on the keyboard represent the digits 1, 2, and 3, from left to right. In this task, you will see sets of three digits appear in the center of the screen. These will change every few seconds. Your task is to press the key indicating which digit is numerically different from the other two. Some examples will make this clear." The participant was then shown examples of MSIT stimuli along with the correct response. It was emphasized to participants that, "on all trials, report which digit is numerically different, regardless of its position or relative size." There were 16 practice trials. On each trial, the MSIT stimulus was presented in the center of the screen for 1,750 ms, after a variable delay (250, 2,250, or 4,250 ms). Twelve trials were congruent, and 4 were incongruent.

Scanning

Scanning was performed on a 3T Siemens Trio, with a whole-brain TR of 2.0 s for functional runs. A localizer and T1 flash structural image were also obtained for each participant. There were six functional runs: 3 sustained intentions and 3 MSIT.

Sustained intentions task

Following the three stages of training, participants performed a basic form of the sustained intentions task (Morsella et al. 2009a) in the scanner (240 TRs). This task did not involve any rating of activity. Each trial proceeded as follows. Following a ready prompt (a question mark, 500 ms) and a blank screen (500 ms), the action prompt appeared for 1 s. This was followed by a variable duration time of 2, 4, or 6 s, after which a target appeared (2 s). There were 29 trials presented in random order. The trials consisted of "yellow-red" compatible prompts (5 trials), "yellow-green" compatible prompts (5 trials), "red-green" incompatible prompts (10 trials), and 9 identical trials, in which the prompts and subsequent cues were identical.

Sustained intentions task with introspection

Participants then performed two blocks of the sustained intentions task (300 TRs each). This time, the task involved introspections of "activity" following each trial. A rest period was included between the two blocks of trials. A trial
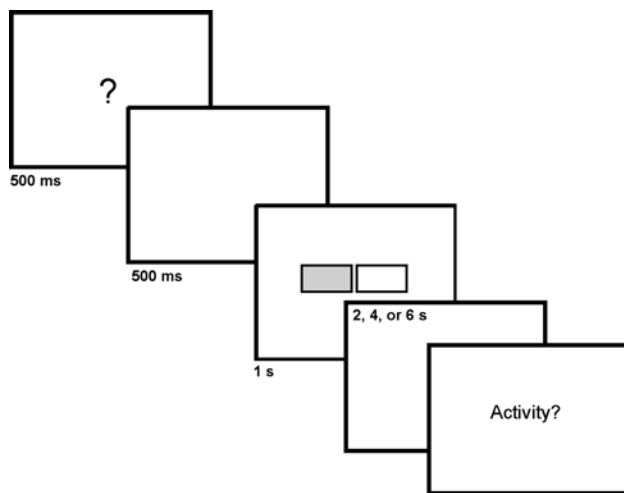
Fig. 2 Schematic of events across time during an introspection trial

proceeded as follows. Following a blank screen (700 ms), a ready prompt (a question mark, 500 ms), and another blank screen (500 ms), the action prompt was presented for 1 s. This was followed by a blank screen of variable duration (2, 4, or 6 s). As in the previous task, on half of the trials, an action cue was then presented (2 s); on the other half of the trials, however, participants were not cued to perform an action but were prompted to report their "activity" (Fig. 2). For this self-report, participants were presented with the word "Activity?" and a 1–8 scale on the screen. Participants were trained to navigate an arrow above the number on the scale that best represented their activity. Participants were able to provide their self-report of this rating through these means without difficulty. Whether a given trial was an introspection trial or a regular action trial was unknowable to the participant, as the two kinds of trials were presented an equal number of times and in pseudo-random order. The order was not fully random because we did not want the same color prompts to appear in adjacent trials.

For the introspection trials of Block A, there were 3 identical trials, 3 "yellow-red" compatible prompts, 3 "yellow-green" compatible prompts, and 6 "red-green" incompatible trials. The remaining trials did not involve introspection. Because of our constraint in creating the pseudo-random sequence of trials, in which we did not want the same prompt to appear in two adjacent trials, we could not balance perfectly the conditions of the non-introspection trials: 5 identical, 5 "yellow-green" compatible prompts, 3 "yellow-red" compatible trials, and 4 "red-green" incompatible trials. Interspersed among the trials were "fixation" trials of different durations (e.g., 3, 4, 6, or 18 s). Block B presented the same trial sequence, but in reverse order. The order of presentation of Blocks A and B was counterbalanced across participants.

MSIT

Following the three blocks of the sustained intentions task, participants performed a block of trials of the MSIT (183 TRs). For this block, participants did not report any subjective activity. Each trial of this block went as follows. Following a blank screen that was presented for a variable duration (10, 1,000, or 3,500 ms), participants responded to the presentation of one of the randomly selected MSIT stimuli (1,750 ms). The block of trials included 72 congruent trials and 24 incongruent trials.

MSIT with introspection of activity

Participants then performed two blocks of MSIT trials (273 TRs) in which, following each trial, participants rated the amount of activity associated with each response. The procedures for the MSIT were identical to that of the previous (non-introspection) block of trials except that participants now rated activity using the scale and arrow from the introspection trials of previous blocks. Each of the two blocks presented 32 congruent trials and 12 incongruent trials. The order of presentation of blocks was counterbalanced across trials.

Results

Behavioral analyses

During introspection trials in the scanner, participants' ratings of subjective activity were as expected for both the MSIT and the sustained intentions task; see Fig. 3. In the sustained intentions task, there was a main effect of condition, $F (2, 26) = 51.534$, $p < .0001$. In particular, participants rated their subjective activity as being highest on the incompatible trials and less so on the compatible trials, $t_{\text{paired}}(13) = 4.38$, $p < 0.001$; ratings in both conditions were higher than on identical trials, t's$(13) = 7.66$, 7.34, p's $< .0001$. This is what was found in Morsella et al. (2009a). In the MSIT, every subject rated the subjective activity as being higher on the incompatible trials than on the compatible trials, $t_{\text{paired}}(13) = 7.62$, $p < .0001$. In addition, every subject had longer RTs on incompatible trials than on compatible trials (the equivalent of the Stroop effect), $t_{\text{paired}}(13) = 12.46$, $p < .0001$.

fMRI analyses

All analyses of the functional data were conducted using FEAT 5.92, part of the FMRIB's Software Library (FSL). We included motion correction (MCFLIRT); smoothing with a gaussian kernel (5 mm FWHM); a high-pass filter
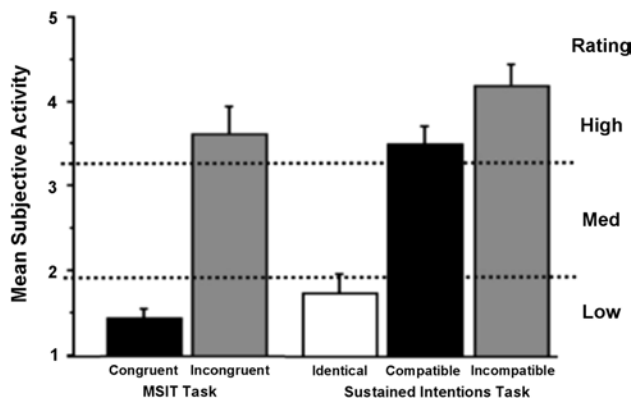
Fig. 3 Subjective activity ratings from introspection trials inside the scanner for both tasks, by task condition. The labels on the *right side* (*high*, *med*, *low*) show the cutoffs used to bin trials for a parametric analysis of the imaging data in terms of subjective activity as the parameter of interest

Fig. 4 SI task activity. An axial slice at $Z = +56$, showing thresholded maps, $p < .05$, corrected, of three different contrasts: *a* a linear contrast (high > medium > low) of subjective activity, shown in *red*, *b* Incompatible > Compatible > Identical trials, shown in *blue*, and *c* all task conditions > baseline. The *right side* of the brain is shown on the *left side* of the image

(100 s); registration to a high-resolution structural image (T1 flash); normalization to MNI space prior to group-level analyses; and a voxel-level threshold of $Z = 2.3$, with a minimum cluster-size criterion to achieve $p < .05$, whole-brain corrected (Worsley et al. 2001). The first 3 TRs (6.0 s) were discarded prior to analysis to allow for T1 stabilization. Analyses at the first level used a double-gamma HRF model and temporal derivative, with regressors orthogonalized against each other. Thirteen participants had usable fMRI data for the analyses of the sustained intentions task, and 12 had usable data for the analyses of the MSIT.

To test our key prediction, we conducted a parametric analysis of brain activity as related to the subjective activity ratings. To do so, for both tasks, we first binned the ratings made in the scanner as reflecting high, medium, or low subjective activity, in order to better equate the number of instances of a given rating in a given category (i.e., collapsing the numerical ratings onto what is effectively a 3-point scale).

For the sustained intentions task, we first modeled event-related task activation as greater than a fixation baseline at the first level (within scanning runs) and computed a linear contrast of subjective activity (high > medium > low). The group-level reliability of the linear contrasts was then assessed at a higher level using a mixed effects model (FLAME-1). This revealed two significant clusters: 713 voxels in left post-central gyrus centered at coordinates −40, −25, 57 (*x*, *y*, *z*) in MNI space, see Fig. 4; and 888 voxels in the right cerebellum centered at 15, −49, −20 in MNI space (not shown).

For the MSIT, we similarly modeled event-related activation at the first level by trial-type and computed a linear contrast on activity ratings (high > medium > low), all within scanning runs. We again used a mixed effects model
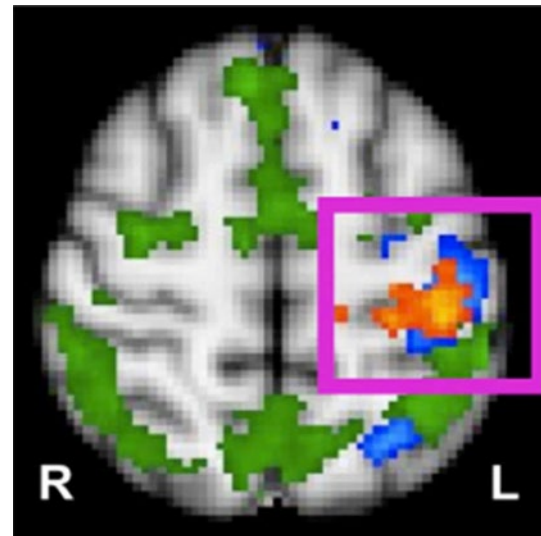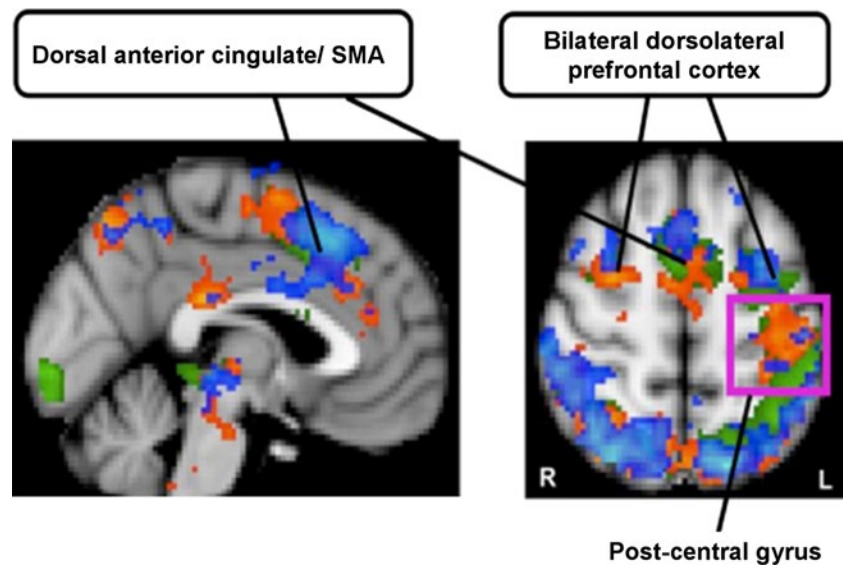
(FLAME-1) for higher-level analyses. This revealed 8 clusters, see Fig. 5. We note in particular the cluster in the left post-central gyrus: 612 voxels centered at −36, −25.6, 58 in MNI space. Clusters were also present in dorsal anterior cingulate cortex and bilateral PFC.

General discussion

According to the theoretical developments about the role of consciousness in action production (e.g., SIT; Morsella 2005), the activation of incompatible skeletomotor plans should trigger notable and quantifiable changes in consciousness. Using three different paradigms (the Stroop, MSIT, and sustained intentions task), we were able to find such subjective effects from the coactivation of incompatible plans. The behavioral data from inside the scanner directly replicated the findings of Morsella et al. (2009a), giving us a good basis from which to investigate the neural correlates of this subjective effect.

Although action control under conditions of conflict (i.e., the activation of incompatible action plans) involved frontal brain regions that have been linked to cognitive control, the subjective effects experienced by participants were correlated with perceptual processing (left post-central gyrus), which is in line with research on the neural correlates of action-related urges (Desmurget et al. 2009; Desmurget and Sirigu 2010), the sensorium hypothesis, ideomotor theory (Gray 2004; Godwin et al., in press; James

Fig. 5 MSIT. Neural regions that show linear increase in activity across activity ratings in MSIT task (*red*), greater activation in incongruent trials than in congruent trials in MSIT task (*blue*), and all task-related regions (*green*). $z = +56$ (MNI space). In the axial slice ($Z = +56$), the *right side* of the brain is shown on the *left side* of the image

1890; Müller 1843), mirror neurons (Rizzolatti et al. 2008), reafference in action control (Berti and Pia 2006; Chambon et al. 2013; Iacoboni 2005; Miall 2003), and (during the MSIT, albeit not during the sustained intentions task) with working memory (Baddeley 2007; Buchsbaum and D'Esposito 2008; LeDoux 2008).

The present neuroimaging data, along with the sensorium hypothesis, are in accord with the notion that the urges from conflicting action intentions often intrude into consciousness in a concrete and corporeal manner. For example, when holding one's breath, one experiences, not only high-level thoughts about the ongoing conflict and situation, but intense corporeal sensations (e.g., tension in the chest region), perceptual events that are associated with somatosensory regions of the brain. Perhaps, if our task had involved actions that are more complicated than simple button presses, then we would have found activation of the parietal regions associated with higher levels of action monitoring (Miall 2003). At this stage of understanding, we remain agnostic regarding the activation of subcortical regions during our sustained intentions task, though there is a growing literature on the role of subcortical areas in action selection. (For a review of the thalamus in action selection, see Humphries and Gurney 2002.) In our task, we were most interested in the regions whose levels of activation covaried to some extent with the urge ratings.

Challenges and limitations of introspection-based approaches

The measure of a subject's urge-to-err (i.e., the urge to make a mistake when responding) is not a perfect measure of the subjective aspects associated with cognitive processing. However, for the kinds of tasks at hand, it seems to be the most reliable and practical measure. It is important to note that, in these kinds of introspection-based studies, due to the inherent limitations of language and communication, the experimenter is limited with respect to what can be learned from a subject's self-report (cf., Block 2007). For instance, because the average naïve subject will not understand what the experimenter means by "subjective experience" or "subjective modulation," it is only through commonly understood concepts and terms such as "urge to make a mistake" that an experimenter is able to infer any systematic changes in the subject's subjective experience. It is worth keeping in mind that these self-reports are only an index associated with what the experimenter is really concerned about—intrusions in the conscious field induced by, say, the activation of incompatible skeletomotor intentions.

Because of the limitations inherent in all introspection paradigms, we cannot rule out that judgments were based on self-observations involving RT performance (including metacognitions of mental processing speed) or on folk beliefs regarding how one should comport oneself in an experiment about cognitive control (cf., Morsella et al. 2009b). Regarding the former, data from other studies suggest that these trial-by-trial subjective effects are not due just to participants observing their own RTs. For example, these subjective effects are still robust in a Stroop-like interference paradigm in which participants are instructed to withhold responding for over a second (Morsella et al. 2009b), which eradicates RT effects (Eriksen and Schultz 1979). Moreover, as in the present study, similar subjective effects induced by conflicting action plans are present when participants sustain incompatible intentions (e.g., to point left and right) in a motionless state in which no response is required or emitted (Morsella et al. 2009a). In addition, though post-error corrections in interference paradigms

involve improved performance (e.g., faster RTs) on trials following a trial involving response interference (e.g., an incongruent trial), reported urges to err actually increase in such a trial, which has been explained as a difference between *implicit* measures of performance (e.g., RT) and *explicit* measures (e.g., self-reports about task difficulty; A. Etkin, personal communication, July 1, 2009; Etkin et al. 2010; Gyurak et al. 2011; Morsella et al. 2009b).

In addition, it may be that participants based their ratings on heuristics such as, "if the prompts are associated with different actions, then I will always report 6 as the rating." Although this cannot be fully ruled out by the present study, this alternative seems unlikely given that participants' ratings tended to vary across trials within each condition. For instance, for the incompatible condition of the MSIT, the first five ratings from a participant selected at random were *4*, *1*, *5*, *6*, and *6*. Of course, it may well be that participants were using a more sophisticated and nuanced heuristic when producing the current pattern of results.

Despite the limitations, we feel that, at this stage of understanding, our introspective measure reveals subjective effects that are systematic, measurable, reliable, and that, as outlined in the Introduction, arise in a theoretically predicted fashion. Because our research focuses on the relationship between consciousness and action—itself an underexplored area of research (Rosenbaum 2005)—we believe that the current approach provides a unique portal through which to study the nature of consciousness in the brain. We hope that these initial data will serve as a foundation for further explorations on the neural correlates of the subjective aspects of action control.

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