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Homing in on Consciousness in the Nervous System:  
An Action-Based Synthesis

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**Short Abstract**

**Abstract:** The primary function of consciousness in the nervous system remains mysterious. *Passive frame theory*, a synthesis of empirically supported hypotheses from diverse fields of investigation, reveals that consciousness serves as a frame that constrains and directs skeletal muscle output, thereby yielding adaptive behavior. How consciousness achieves this is more counterintuitive, “low level,” and passive than the kinds of functions that theorists have attributed to consciousness. From this unique, action-based perspective, consciousness is in the service of the *somatic nervous system*. The framework begins to isolate the neuroanatomical, cognitive-mechanistic, and representational processes associated with consciousness.

## Long Abstract

**Abstract:** What is the primary function of consciousness in the nervous system? The answer to this question remains enigmatic, not so much because of a lack of relevant data, but because of the lack of a conceptual framework with which to interpret the data. To this end, we developed *passive frame theory*, an internally coherent framework that, from an action-based perspective, synthesizes empirically supported hypotheses from diverse fields of investigation. The theory proposes that the primary function of consciousness is well circumscribed, serving the *somatic nervous system*. For this system, consciousness serves as a frame that constrains and directs skeletal muscle output, thereby yielding adaptive behavior. The mechanism by which consciousness achieves this is more counterintuitive, passive, and “low level” than the kinds of functions that theorists have previously attributed to consciousness. Passive frame theory begins to illuminate (a) what consciousness contributes to nervous function, (b) how consciousness achieves this function, and (c) the neuroanatomical substrates of conscious processes. Our untraditional, action-based perspective focuses on olfaction instead of on vision and is *descriptive* (describing the products of nature as they evolved to be) rather than *normative* (construing processes in terms of how they should function). Passive frame theory begins to isolate the neuroanatomical, cognitive-mechanistic, and representational (e.g., conscious contents) processes associated with consciousness.

**Keywords:** Consciousness; neural correlates of consciousness; subjective experience; unconscious processing; voluntary action

### Introduction

What does consciousness contribute to the functioning of the nervous system? What is the primary role of this elusive phenomenon? The answers to these questions remain enigmatic, not so much because of a lack of relevant data, but because of the lack of a conceptual, internally coherent framework with which to interpret the data (Grossberg 1987). Hence, we developed *passive frame theory*, a framework that, from an action-based perspective, synthesizes empirically supported hypotheses from diverse fields of investigation. The framework begins to illuminate (a) what consciousness contributes to nervous function, (b) how consciousness achieves this function, and (c) the neuroanatomical substrates of conscious processes. Passive frame theory proposes that the primary function of consciousness is well circumscribed, serving the *somatic nervous system*. For this system, it serves as a frame that constrains and directs skeletal muscle output, thereby yielding adaptive behavior. The mechanism by which consciousness achieves this is more counterintuitive, passive, and “low level” than the kinds of functions that theorists have attributed to consciousness.

Our unique perspective and conclusions provide a comprehensive approach to the enigma of the primary function of consciousness. To solve this puzzle, an overarching coherent framework is a necessary first step to the development of more concrete advances (e.g., hypotheses for the derivation of experiment-specific predictions). Before discussing the hypotheses that serve as the tenets of passive frame theory, it is necessary to define some terms and describe the nature of our untraditional approach.

## 1. Purview, terms, and assumptions

### 1.1. *The scientific approach should focus on the most basic form of consciousness*

We believe that, to advance the study of consciousness, one should focus not on high forms of consciousness (e.g., “self-consciousness”), but on the most basic forms of consciousness (e.g., the experience of a smell, visual afterimages, tooth pain, or urges to scratch an itch). This form of consciousness has fallen under the rubrics of “sentience” (Pinker 1997), “primary consciousness” (Edelman 1989), “phenomenal consciousness” (Block 1995), “qualia” (Gray 2004), “phenomenal states” (Tye 1999), and “subjective experience.” In our framework, we refer to a thing of which one is conscious (e.g., an afterimage) as a *conscious content* (Merker 2007; Seth 2007). All the contents of which one is conscious at one time can be construed as composing the *conscious field* (Freeman 2004; Köhler 1947; Searle 2000). The contents of the conscious field change over time.

### 1.2. *The approach should be descriptive, non-normative*

We believe that the approach to consciousness should be a *descriptive*, naturalistically based one (which describes the products of nature as they evolved to be) rather than a *normative* one (which construes processes in terms of how they should function). Nervous mechanisms have been fashioned by the happenstance and tinkering process of evolution, whose products can be counterintuitive and suboptimal (de Waal 2002; Gould 1977; Lorenz 1963; Marcus 2008; Roe & Simpson 1958; Simpson 1949), far unlike the kinds of things humans design into machines (Arkin 1998). Hence, the ethologist Lorenz (1963) cautions, “To the biologist who knows the ways in which selection works and who is also aware of its limitations it is in no way surprising to find, in its constructions, some details which are unnecessary or even detrimental to survival” (p. 260). Similarly, when speaking about the *reverse engineering* of biological products, the roboticist concludes, “Biological systems bring a large amount of evolutionary baggage unnecessary to support intelligent behavior in their silicon based counterparts” (Arkin 1998, p. 32). The difference between the products of evolution and human artifacts is obvious when one considers the stark contrast between human locomotion and artificial locomotion – legs versus wheels (Morsella & Poehlman 2013).

When adopting a descriptive standpoint, even the most cursory examination of the brain reveals a contrast between conscious and unconscious processes (cf. Bleuler 1924). Hence, in every field of inquiry, there is the *de facto* distinction between the two kinds of processes, though often without mention of the taboo term “consciousness.” For example, in perception research, there exists the distinction between *supra-* versus *subliminal*. In memory research, there is the distinction between “declarative” (explicit) processes and “procedural” (implicit) processes (Schacter 1996; Squire 1987). In motor and language research, the conscious aspects of voluntary action or of speech production are contrasted with the unconscious aspects of, say, motor programming (Levelt 1989; Rosenbaum 2002; Taylor & Ivry 2013). Various fields also contrast “controlled” processing (which

tends to be conscious) and “automatic” processing (which is often unconscious; Lieberman 2007). In summary, from a descriptive approach, the contrast between conscious and unconscious processes in the brain is somewhat inevitable (Morsella & Poehlman 2013).

### **1.3. The approach should be minimalistic, focusing on simple cases**

When attempting to unravel a phenomenon as perplexing as consciousness, it is important to adopt a strategy in which scientific inquiry begins with the examination of the most basic, elemental instantiation of the phenomenon of interest (Panksepp 2007). Such a strategy proved fruitful in the development of physics (Einstein & Infeld 1967). Hence, in our approach, we focus on the actions of a hypothetical, simplified, human-like mammal that, though conscious (for a treatment of consciousness in mammals, see Gray [2004]), is not equipped with many of the complicated abilities/states associated with adult humans (e.g., syntax and music appreciation). Capable of having *approach-avoidance* conflicts (Lewin 1935; Miller 1959), this hypothetical organism is occupied only with basic operations (e.g., breathing, locomoting, and avoiding tissue damage) rather than with higher-level phenomena (e.g., mental rotation and sustained, directed thinking). This organism is also incapable of *indirect cognitive control* (Morsella et al. 2009b), whereby one can, for example, make oneself hungry or scared by deliberately imagining the kinds of things that would induce these states. Such higher-level phenomena are more likely to be predicated upon (a) extensive learning, (b) cultural influences, (c) intricate interactions among more elemental conscious processes, and (d) adaptations that are less phylogenetically primitive than those of the basic operations of interest (Morsella 2005).

In our “simple case,” this hypothetical organism is resting in a warm enclosure (e.g., a cave). It can consciously perceive an opening from which it could exit. For hours, the organism performs no notable locomotive act toward the opening nor to anything else, but then it perceives a noxious smell (e.g., smoke) from within the enclosure. Because of this new conscious content, it now exits hesitantly through the opening, even though it was inclined to remain within the warm enclosure. To illuminate the nature of consciousness, we will revisit this “creature in the cave” scenario throughout our treatise. We refer to the first events composing the scenario (e.g., the percept of the opening and the warmth) as stage 1 and the subsequent events (e.g., the smell and the inclination to stay in the cave) as stage 2.

In contrast to our strategy, descriptive accounts of consciousness have tended to focus on high-level functions, leading to conclusions such as that the function of consciousness pertains to social interaction (Frith 2010; Prinz 2012), language (Banks 1995; Carlson 1994; Macphail 1998), “theory of mind” (Stuss & Anderson 2004), the formation of the self (Greenwald & Pratkanis 1984), semantic processing (Kouider & Dupoux 2004; Mudrik et al. 2014; Thagard & Stewart 2014), the meaningful interpretation of situations (Roser & Gazzaniga 2004), and simulations of behavior and perception (Hesslow 2002). It is worth noting that, for good reasons, it has also been proposed that, contrary to the present account, consciousness *does not* contribute to

ongoing action (Hommel 2013; Jackson 1986; Kinsbourne 1996; 2000; Masicampo & Baumeister 2013; Pinker 1997).

#### **1.4. Overview of present, untraditional approach**

Our approach is untraditional in several ways. First, instead of focusing on the relationship between consciousness and perception, which has been the dominant approach (Crick & Koch 2003; Rosenbaum 2005), we focus on the relationship between consciousness and overt action. Second, unlike traditional *stimulus* → *response* approaches, we “work backward” from overt action to the underlying processes responsible for it (Sperry 1952). Thus, from our untraditional, action-based approach, we subscribe to an uncommon theoretical position – that the nature of consciousness is best understood by examining the requirements of adaptive (efferent) action control rather than the needs of perceptual analysis. From this unconventional approach to consciousness, one can appreciate that the requirements of adaptive skeletomotor action reveal much about the nature of both the conscious field and the generation of conscious contents. Third, building on Morsella and Bargh (2007), instead of focusing on vision to understand consciousness (which has been the prevalent approach; Crick & Koch 2003), we focus on the (possibly) more tractable system of olfaction, as illustrated in our “creature in the cave” example. The olfactory system possesses several features that render it a fruitful system in which to study consciousness.<sup>1</sup>

To summarize, our approach is *elemental, action-based, simple, and evolutionary-based* (or, for short, EASE, meaning “to make something less difficult”). We believe that an EASE perspective provides the most fruitful approach to the perplexing problem of consciousness and the brain. Whenever in our enterprise we encountered an obstacle for theoretical progress (e.g., the neural regions associated with consciousness), it was through our EASE perspective that progress was made. In the next three sections, we discuss from an EASE perspective the empirically supported hypotheses that serve as the tenets of passive frame theory. Through the process, we begin to isolate the neuroanatomical, cognitive-mechanistic, and representational (e.g., conscious contents; sect. 3) processes associated with consciousness.

## **2. The circumscribed role of consciousness in the nervous system**

### **2.1. Tenet: Consciousness is associated with only a subset of nervous function**

Based on developments of the past four decades, there is a growing *subset consensus* – that consciousness is associated with only a subset of all the processes and regions of the nervous system<sup>2</sup> (Aru et al. 2012; Crick & Koch 1995; 2003; Dehaene & Naccache 2001; Gray 2004; Grossberg 1999; Koch 2004; Koch & Greenfield 2007; Logothetis & Schall 1989; Merker 2007; 2013b; Penfield & Jasper 1954; Weiskrantz 1992; Zeki & Bartels 1999). This subset seems to be qualitatively distinct – in terms of its functioning, physical makeup/organization, or mode of activity – from that of its unconscious counterparts in the brain (Bleuler 1924; Coenen 1998; Edelman & Tononi 2000; Goodale & Milner 2004; Gray 2004; Llinás et al. 1998; Merker 2007; Ojemann 1986).

Consistent with the subset consensus, many aspects of nervous function are unconscious.<sup>3</sup> Complex processes of an unconscious nature can be found at all stages of processing (Velmans 1991), including low-level perceptual analysis (e.g., motion detection, color detection, auditory analysis; Zeki & Bartels 1999), semantic-conceptual processing (Harley 1993; Lucas 2000), and motor programming (discussed in sect. 3.1). Evidence for the complexity of unconscious processing is found in cases in which the entire stimulus-response arc is mediated unconsciously, as in the case of unconsciously mediated actions (e.g., automatisms). There is a plethora of evidence that action plans can be activated, selected, and even expressed unconsciously.<sup>4</sup> In summary, it seems that much in the nervous system is achieved unconsciously. This insight from the subset consensus leads one to the following question: What does consciousness contribute to nervous function?

## **2.2. Tenet: The conscious field serves an integrative role**

The *integration consensus* (Baars 1988; 1998; 2002; 2005; Boly et al. 2011; Clark 2002; Damasio 1989; Dehaene & Naccache 2001; Del Cul et al. 2007; Doesburg et al. 2009; Edelman & Tononi 2000; Freeman 1991; Koch 2012; Kriegel 2007; Llinás & Ribary 2001; Merker 2007; Ortinski & Meador 2004; Sergent & Dehaene 2004; Srinivasan et al. 1999; Tallon-Baudry 2012; Tononi 2012; Tononi & Edelman 1988; Uhlhaas et al. 2009; Varela et al. 2001; Zeki & Bartels 1999) proposes that consciousness integrates neural activities and information-processing structures that would otherwise be independent. Most of the hypotheses composing this consensus speak of conscious information as being available “globally,” in some kind of workspace, as in Baars’s (1988) influential *global workspace theory*. For the present purposes, we construe the contents occupying such a workspace as composing the conscious field (defined in sect. 1.1).

Consistent with the integration consensus, the conscious processing of a percept involves a wider and more diverse network of regions than does the subliminal (unconscious) processing of the same percept (Singer 2011; Uhlhaas et al. 2009). The latter is subjected only to “local” processing. This evidence stemmed initially from research on perception (Del Cul et al. 2007; Uhlhaas et al. 2009), anesthesia (Alkire et al. 2008; Boveroux et al. 2010; Långsjö et al. 2012; Lee et al. 2009; Lewis et al. 2012; Schroter et al. 2012; Shrouff et al. 2011), and unresponsive states (e.g., coma or vegetative states; Laureys 2005). Regarding perception research, it has been proposed that, during binocular rivalry,<sup>5</sup> the neural processing of the conscious percept requires special interactions between both perceptual regions and other, traditionally non-perceptual regions (e.g., frontal cortex; Doesburg et al. 2009). This supports the view that some mode of interaction between widespread brain areas is important for consciousness (Buzsáki 2006; Doesburg et al. 2009; Fries 2005; Hummel & Gerloff 2005).

Evidence for the integration consensus is found also in action-based research. Conscious actions involve more widespread activations in the brain than do similar but unconscious actions (Kern et al. 2001; McKay et al. 2003; Ortinski & Meador 2004). Moreover, when actions are decoupled from consciousness (e.g., in neurological disorders), the actions often appear impulsive or inappropriate, as if they are not

adequately influenced by the kinds of information by which they should be influenced (Morsella & Bargh 2011).

### **2.3. Advances regarding the physiological processes engendering consciousness depend on advances regarding the neuroanatomy of consciousness**

The nature of the neuroanatomical network engendering the physiological processes (e.g., neural oscillations) proposed to be associated with consciousness remains controversial.<sup>6</sup> Progress regarding the neurophysiology of consciousness depends on advances regarding the identification of the neuroanatomical substrates of this state (Aru et al. 2012). Regarding neuroanatomy, when attempting to isolate the anatomical underpinnings of consciousness, investigators have followed Crick and Koch's (2003) recommendation and have focused on vision. (See reviews of neural correlates of visual consciousness in Blake and Logothetis [2002], Dehaene [2014], Koch [2004], Lamme and Spekreijse [2000], Metzinger [2000], and Tong [2003].) In vision research, controversy remains regarding whether consciousness depends on higher-order perceptual regions (Crick & Koch 1995; 1998; Panagiotaropoulos et al. 2012; 2013) or lower-order regions (Aru et al. 2012; Damasio, 2010; Friedman-Hill et al. 1995; Lamme 2001; Liu et al. 2012; Robertson 2003; Tallon-Baudry 2012; Tong 2003). Moreover, as noted in Note 2, whether cortical matter is necessary for consciousness remains controversial.

Theorists focusing on vision have proposed that, although the cortex may elaborate the contents of consciousness, consciousness is primarily a function of subcortical structures (Merker 2007; Penfield & Jasper 1954; Ward 2011). Penfield and Jasper (1954) based this hypothesis on their studies involving both the direct stimulation of, and ablation of, cortical regions. Based on these and other findings (e.g., observations of patients with anencephaly; Merker 2007), it has been proposed that consciousness is associated with subcortical areas (e.g., Merker 2007; 2013b). This has led to the *cortical-subcortical controversy* (Morsella et al. 2011). Although data from studies on patients with profound disorders of consciousness (e.g., vegetative state) suggest that signals from the frontal cortex may be critical for the instantiation of any form of consciousness (Boly et al. 2011; Dehaene & Naccache 2001; Lau 2008; Panagiotaropoulos et al. 2012; Velly et al. 2007), research on the psychophysiology of dream consciousness, which involves prefrontal deactivations (Muzur et al. 2002), suggests that, although the prefrontal lobes are involved in cognitive control, they may not be essential for the generation of basic consciousness (Aru et al. 2012; Merker 2007; Ward 2011). Regarding the necessity of the integrity of the frontal lobes for consciousness, it is important to consider that the surgical procedure of frontal lobotomy, once a common neurosurgical intervention for the treatment of psychiatric disorders, was never reported to render patients incapable of sustaining consciousness (see also Aleman & Merker 2014).

The role of subcortical structures in the production of consciousness, and the amount of cortex that may be necessary for the production of consciousness, remains to be elucidated (see further discussion in sect. 3.5). Clearly, more investigation is needed regarding the neural correlates of consciousness because controversy continues to surround not only the neurophysiological processes underlying consciousness, but even

the identification of the gross, *neuroanatomical* regions that are responsible for this peculiar form of processing (see treatment in Merker 2007; 2013a).

Faced with this challenge, we propose that, because of the intimate liaison between *function* and *structure* in the nervous system (Cohen & Dennett 2011; Merker 2013b), progress can be made regarding the neural underpinnings of consciousness by having a more precise understanding of the role of consciousness in nervous function (Lamme & Spekreijse 2000). With this in mind, one can reason as follows. If the consensus is that consciousness serves an integrative role, then, from an EASE perspective, what is the most basic form of integration that requires consciousness? Addressing this question allows one to better isolate consciousness within the nervous system, which could, in turn, resolve controversies regarding the neural correlates of consciousness.

#### **2.4. Tenet: The conscious field is for a specific kind of integration, involving the skeletal muscle output system**

One limitation of the integration consensus is that it fails to specify which kinds of integrations require consciousness and which kinds do not. Consciousness seems unnecessary for various kinds of integrations in the nervous system. For example, integrations across different sensory modalities, as in the case of *afference binding* (Morsella & Bargh 2011), can occur unconsciously. This form of integration occurs in feature binding (e.g., the binding of shape to color; Zeki & Bartels 1999) and in intersensory binding (Vroomen & de Gelder 2003), as in the ventriloquism and McGurk effects (McGurk & MacDonald 1976). (The latter 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.”) (See list of many kinds of unconscious afference binding in Morsella [2005], Appendix A.) Integrations involving smooth muscle effectors (e.g., in peristalsis or in the pupillary reflex), too, can occur unconsciously (Morsella et al. 2009a), as can another form of integration known as *efference binding* (Haggard et al. 2002).

Efference binding links perceptual processing to action/motor processing. This kind of stimulus-response binding is mediated unconsciously in actions such as reflexive pain withdrawal or reflexive inhalation. In learned behavior, efference binding allows one to press a button when presented with an arbitrary cue. Such a form of binding can be learned quickly (e.g., from a few trials of stimulus-response mapping; Hommel & Elsner 2009) and with little effort (Cohen-Kadosh & Meiran 2009; Melcher et al. 2008). Learned forms of efference binding can be expressed unconsciously (Fehrer & Biederman 1962; Fehrer & Raab 1962; Hallett 2007; Taylor & McCloskey 1990; 1996). For example, subjects can select the right motor response (one of two button presses) when confronted with subliminal stimuli, suggesting that “appropriate programs for two separate movements can be simultaneously held ready for use, and that either one can be executed when triggered by specific stimuli without subjective awareness” (Taylor & McCloskey 1996, p. 62; see review in Hallett 2007). We return to the topic of efference binding when discussing how conscious contents influence action (sect. 3.2).



In contrast to these unconscious forms of integration, people tend to be very much aware of some integrations, such as when one holds one's breath while underwater or experiences an approach-avoidance conflict (Lewin 1935; Miller 1959). In the former, one experiences the inclinations to both inhale and to not inhale. Similarly, when carrying a hot dish of food, one experiences the inclinations to drop the dish and to not drop the dish (Morsella 2005). Unlike unconscious integrations, such *conscious conflicts* (Morsella 2005) reflect a form of integration that is associated not with perceptual processing, but rather with action selection.<sup>7</sup> This form of integration has been distinguished from unconscious integrations/conflicts, such as the McGurk effect and smooth muscle conflicts (e.g., in the pupillary reflex). In short, conflicts at the stage of processing of action selection are experienced consciously, whereas conflicts at perceptual stages of processing are unconscious. It has been proposed that, unlike unconscious integrations, these integrations involve competition for control of the *skeletal muscle* ("skeletomotor," for short) *output system* (Morsella 2005). The skeletomotor output system contains the unconscious motor plans that are necessary to enact one skeletomotor act versus another (Bizzi & Mussa-Ivaldi 2004; Rizzolatti et al. 2004; Rosenbaum 2002). It stores, for example, the unconscious articulatory plans that are necessary for speech production (Buchsbbaum 2013) and the plans for blinking (Graziano 2008). When these plans are stimulated sufficiently, overt actions arise.

Involving urges and other action-related inclinations, conscious conflicts occur when two streams of efference binding are trying to influence skeletomotor action simultaneously (Morsella & Bargh 2011). For example, conscious conflicts occur when one holds one's breath, suppresses uttering something, suppresses a prepotent response in a response interference paradigm, or voluntarily breathes faster for some reward. (The last example illustrates that not all cases of this kind of integration involve suppression.) These conscious conflicts appear to be triggered into existence by the activation of incompatible skeletomotor plans.<sup>8</sup> In our "creature in the cave" scenario, this form of integration occurs when the organism is inclined to both exit the enclosure (because of the smoke) but remain within it (because of the warmth).

Hence, Morsella (2005) proposes that the primary function of consciousness is to integrate information, but only certain kinds of information – the kinds involving incompatible skeletal muscle intentions for adaptive action (e.g., holding one's breath while underwater).<sup>9</sup> From this standpoint, the conscious field is unnecessary to integrate perceptual-level processes (as in feature binding or intersensory conflicts), smooth muscle processes (e.g., pupillary reflex; Morsella et al. 2009a), or processes associated with motor control (discussed in sect. 3.1). Instead, the conscious field is necessary to integrate what appear to be multiple inclinations toward the skeletomotor output system, as captured by the principle of *parallel responses into skeletal muscle* (PRISM; Morsella 2005). From this perspective, and as fleshed out in the next section, it is this third kind of binding that is the most basic form of integration that requires consciousness. PRISM explains why, phenomenologically, a wink is different from a reflexive blink and from the dilation of a pupil.

## **2.5. Tenet: The conscious field is for adaptive voluntary action**

In colloquial terms, one can conclude that consciousness is for adaptive “voluntary” action. Scientifically, consciousness can be construed as the medium that allows action processes to influence skeletomotor action collectively, leading to *integrated actions* (Morsella & Bargh 2011), such as holding one’s breath. Just as a prism combines different colors to yield a single hue, the conscious field permits for multiple response tendencies to yield a single, integrated action. Absent consciousness, skeletomotor behavior can be influenced by only one of the efference streams, leading to *unintegrated actions* (Morsella & Bargh 2011), such as unconsciously inhaling while underwater or reflexively removing one’s hand from a hot object. Reflecting a lack of integration, unintegrated actions appear as if they are not influenced by all the kinds of information by which they should be influenced. If a conscious content is not in the field, then it cannot influence voluntary action. For example, if the knowledge representations necessary for, say, “reality monitoring,” are not in the field (e.g., because of fever), then nothing else can assume the functional influence of these contents. (This is evident in action selection in dreams, which are often irrational, and in disorders of awareness, such as sensory neglect and anosognosia.) Hence, in voluntary action, when the appropriate contents are absent, there is no independent system or repository of knowledge that can step in to fill their role. Therefore, the conscious field wholly and exclusively determines what in everyday life is called voluntary behavior. Conversely, for every voluntary action, the organism can report a conscious content responsible for that action, regardless of the veracity of the introspection (Poehlman et al. 2012).

These conclusions also reveal that it is no accident that, historically, skeletal muscle has been described as “voluntary” muscle. Since at least the nineteenth century, it has been known that, though often functioning unconsciously (as in the frequent actions of breathing and blinking), skeletal muscle is the only bodily effector that can be consciously controlled; however, why this is so has never been addressed theoretically. PRISM introduces a systematic reinterpretation of this age-old fact (Morsella 2005): Skeletomotor actions are at times “consciously mediated” because they are directed by multiple systems that require consciousness to influence action collectively – what we refer to as *collective influence*.

Regarding the skeletomotor output system, one must consider that all processes trying to influence skeletomotor behavior must, in a sense, “go through it.” Each system giving rise to inclinations has its peculiar operating principles and phylogenetic origins (Allman 2000): One system “protests” an exploratory act while another system reinforces that act (Morsella 2005). Because each skeletomotor effector can usually perform only one act at a time (e.g., one can utter only one word at a time; Lashley 1951; Wundt 1900), there must be a way in which the inclinations from the many heterogeneous systems can be “understood” and processed collectively by the skeletomotor output system. To yield adaptive action, this process must also integrate information about other things (e.g., the physical environment). To a degree greater than that of any other effector system (e.g., smooth muscle), distinct regions/systems of the brain are trying to control the skeletomotor output system in different and often opposing ways. All inclinations toward

it, from primitive plans about basic needs to complex plans associated with language, must engage this system. Hence, the skeletomotor output system is the “final common path” for processes capable of influencing skeletomotor function (McFarland & Sibly 1975; Sherrington 1906). Figuratively speaking, the skeletomotor output system is akin to a single steering wheel that is controlled by multiple drivers (Morsella 2005).

### 3. Conscious contents

If one accepts that consciousness is in the service of voluntary action, then, from an EASE perspective and by working backward from overt action to central processing, one can ask the following question: What kinds of information and knowledge representation (Markman 1999) render voluntary action adaptive? To answer this question, one must examine the nature of conscious contents while appreciating that the varied inputs to the skeletomotor output system must (a) represent information that is essential for adaptive skeletomotor action and (b) be formatted in a manner that is understandable by the unconscious, action-related mechanisms composing the skeletomotor output system (Morsella & Bargh 2010b).

The three tenets presented in sects. 3.1 through 3.3 suggest that our “creature in the cave” is conscious of things such as external objects and the urge to eat or to affiliate (or to do other things that reflect the inclinations of the many “hot” affective/incentive systems; Metcalfe & Mischel 1999), because these things should influence the skeletomotor output system. For this creature, it is clear that *additions*<sup>10</sup> of conscious content are usually about the world, the body, or action-related inclinations (Brentano 1874; Chomsky 1988; Fodor 1980; 1998; Gray 1995; 2004; Hume 1739/1888; Koch 2004; Schopenhauer 1818/1819; Sergent & Dehaene 2004).

#### 3.1. Tenet: Conscious contents must be “perceptual-like” in nature

We propose that the cognitive and neural processes associated with the contents of our “creature in the cave” should be perceptual-like in nature. When making this claim, we acknowledge that conscious contents are neither purely sensorial nor purely motor related; instead, they represent well-crafted representations occurring at a stage of processing between sensory analysis and motor programming (Jackendoff 1990; Lashley 1956; Merker 2013b; Prinz 2003; 2007). In everyday life, when speaking about this level of representation of external objects, we use the term *percept* (Gray 1995); however, this level of representation is more precisely construed as an intermediate representational format (e.g., the color red or the illusion of “da” in the McGurk effect) that links perception to action (Prinz 2003). (To not introduce more jargon, we will continue to use the term *percept* to refer to conscious contents about the external world or the body; however, we do so mindful that the term, because of its sensory connotation, can be misleading.)

The proposal that contents are perceptual-like is based on the synthesis of conclusions from diverse areas of study. First, according to the age-old *sensorium hypothesis* (Godwin et al. 2013; Goodale & Milner 2004; Gray 2004; Grossberg 1999; Harleß 1861; James 1890; Müller 1843; Woodworth 1915), the contents of consciousness

are influenced primarily by perceptual-based (and not motor-based) events and processes, because motor processes are largely unconscious. There is substantial phenomenological evidence for this hypothesis. During action, for example, one is unconscious of the efference to the muscles that dictates which fibers should be activated at which time (Rosenbaum 2002). Although one is unconscious of these complex programs (Johnson & Haggard 2005), one *is* often aware of their proprioceptive and perceptual consequences (e.g., perceiving the hand grasping; Fecteau et al. 2001; Fournieret & Jeannerod 1998; Gottlieb & Mazzone 2004; Gray 2004; Heath et al. 2008; Liu et al. 2008; Rossetti 2001). These images tend to be perceptual-like images of action outcomes (Hommel 2009; Jeannerod 2006; Pacherie 2008): “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).<sup>11</sup> It seems that we do not have direct, conscious access to motor programs, syntax, aspects of executive control (Crick 1995; Suhlert & Churchland 2009; Tallon-Baudry 2012; van Gaal et al. 2008), or of other kinds of “efference generators” (Grossberg 1999; Morsella & Bargh 2010b; Rosenbaum 2002), including those for emotional systems (e.g., the amygdala; Anderson & Phelps 2002; LeDoux 1996; Öhman et al. 2007; Olsson & Phelps 2004). (Unconscious executive control from activated action sets exemplifies what has been historically referred to as “imageless,” *determining tendencies* [Ach 1905/1951].)

In line with the sensorium hypothesis, examination of the liaison between action and consciousness reveals an isomorphism regarding that which one is conscious of when one is (a) observing one’s own action, (b) anticipating an action effect, (c) dreaming, and (d) observing the behaviors of others (Graziano 2010). In every case, it is the same, perceptual-like dimension of the experience that constitutes that which is consciously available (Farrer et al. 2008; Melcher et al. 2013; Morsella & Bargh 2010b; Rizzolatti et al. 2008; Sperry 1952). Speech processing provides a compelling example. Consider the argument by Levelt (1989) that, of all the processes involved in language production, one is conscious of only a subset of the processes, whether when speaking aloud or subvocalizing. (Language reveals that mechanisms in action production can be complex but unconscious, as in the case of syntax.) It is for this reason that, when speaking, one often does not know exactly which words one will utter next until the words are uttered or subvocalized following lexical retrieval (Levelt 1989; Slevc & Ferreira 2006). For example, in the phonological loop, it is the phonological representation and not, say, the motor-related, “articulatory code” (Ford et al. 2005) that one is conscious of during spoken or subvocalized speech (Buchsbaum & D’Esposito 2008; Fodor 1998; Rizzolatti et al. 2008). It is for this reason that Buchsbaum (2013) concluded that in the phonological loop, the “inner voice” (i.e., the articulatory code) cannot hear itself. Although there has been substantial debate regarding the nature of conscious representations (e.g., whether they are “analogical” or “propositional”; Markman 1999), few would argue about the isomorphism among the conscious contents experienced while acting (e.g., saying “hello”), dreaming (e.g., saying “hello” in a dream), or observing the action of another (e.g., hearing “hello”).

### **3.1.1. Perceptual-like contents as the lingua franca of action systems**

Building on the sensorium hypothesis, we encountered a second reason why conscious contents must be perceptual-like. This reason pertains to the nature of the representational

format. Regarding collective influence, the format of conscious contents must permit the contents to influence action systems (Freeman 2004) if there is to be perception-to-action translations (Merker 2012; Prinz 2003). With this in mind, one would expect that the nature of representations involved in consciousness would be capable of being received and “understood” (i.e., to be *access general*; Barrett 2005) by multiple action systems in the brain. The perceptual-like representations discussed in sect. 3.1 happen to meet this criterion. It has been proposed a priori, and for reasons having nothing to do with the current theorizing, that the representations that are the most “broadcastable” (i.e., received and understood by the most brain systems) happen to be perceptual in nature (Fodor 1983; Morsella & Bargh 2010b; Morsella et al. 2009b).<sup>12</sup> Moreover, one could argue that, if contents are aimed at influencing the complex and unconscious action mechanisms of the skeletomotor output system, it makes sense that the format of these contents would be the format to which the skeletomotor output system evolved to respond (i.e., perceptual stimuli). Accordingly, the phylogenetically old response systems in the skeletomotor output system (e.g., allowing for a spider stimulus to trigger a startle response; Rakison & Derringer 2008) are likely to have evolved to deal with this kind of representation (i.e., one reflecting external objects; Bargh & Morsella 2008; LeDoux 1996). Hence, perceptual-like representations can be construed as a kind of (domain general) lingua franca that can lead to content-driven activations in the skeletomotor output system. In other words, the mechanisms in the skeletomotor output system do not possess *access specificity* to contents in the conscious field (because they have access to all the contents in the conscious field), but they do possess *processing specificity* (because each action mechanism can be activated by only some contents; Barrett 2005).

### **3.2. Tenet: Conscious contents can directly activate action processes in the skeletal muscle output system**

According to *ideomotor theory* (Greenwald 1970; Harleß 1861; Hommel 2009; Hommel et al. 2001; James 1890; Lotze 1852), the perceptual representations identified by the sensorium hypothesis provide a mechanism for goal-directed action control. In this theory, the mental image of the (perceptual-like) *action effects* (in the body or in the world) of an instrumental action leads to the execution of that action, with the motor programming involved being unconscious. (It is noteworthy that contemporary ideomotor accounts are agnostic regarding the role of consciousness in action control [e.g., Hommel 2013].)

In ideomotor accounts, action selection is thus driven by the selection of the representation of the perceptual consequences of a motoric act. Hence, the many conscious contents about the world and the body can be construed as “action options” for the skeletomotor output system. From this standpoint, the urge to move the arm leftward is isomorphic to the perceptual consequences of what would be observed if the act were performed. This is also the case for the “higher” abilities, such as language. For example, before making an important toast (or making a toast in an unmastered language), a person has conscious imagery regarding the words to be uttered. Hence, action selection is concerned with achieving a final end state (e.g., flicking a switch or saying “hello”), which can be realized in multiple ways, as in the case of *motor equivalence* (Lashley

1942), in which several different behaviors can lead to the same end state. The unconscious motor programs realizing these end states are complex and context sensitive, as in the case of co-articulation in speech (Levelt 1989; see also Zhang & Rosenbaum 2008).

According to ideomotor theory, there is a direct link between activation of action-related perceptual processes and (unconscious) action systems. Such a link is consistent with overwhelming evidence demonstrating that the presentation of action-related perceptual stimuli automatically and systematically influences action processing (see reviews of evidence in Ellis 2009; Hommel & Elsner 2009). This is evident in classic paradigms such as the flanker (Eriksen & Eriksen 1974) and Stroop tasks (Stroop 1935). In the latter, participants must name the color in which words are written. When the color and word name do not match (e.g., RED in blue font), response interference arises because the automatic (and unintentional) word-reading plan competes with the weaker (and intended) color-naming plan (Cohen et al. 1990). Behavioral and psychophysiological evidence reveals that, during such response interference, competition involves simultaneous activation of the brain processes associated with both the target- and distracter-related responses (Coles et al. 1985; DeSoto et al. 2001; Eriksen & Schultz 1979; Mattler 2005; McClelland 1979; van Veen et al. 2001). Additional evidence stems from neurological conditions (see review in Morsella & Bargh 2011) and in the aforementioned research on unconscious efference binding, in which subliminal stimuli influence motor responses (Hallett 2007).

### **3.3. Tenet: Action selection as the result of inter-representational dynamics**

From an ideomotor standpoint, once an action goal (e.g., pressing a button) is selected, unconscious motor efference enacts the action directly.<sup>13</sup> From this standpoint, that which prevents the activation of an action goal representation from directly influencing overt action is only the activation of an incompatible action goal (James 1890; Prinz et al. 2009). In this framework, conscious representations of one's finger flexing, for example, automatically lead to the flexing of one's finger, unless representations of incompatible action effects (e.g., the finger *not* flexing; James 1890) happen to be activated. It is important to note that the incompatibility regarding these two action effects resides not in the conscious field, in which both action effects could be represented simultaneously, but rather in the simultaneous execution of the two action plans.

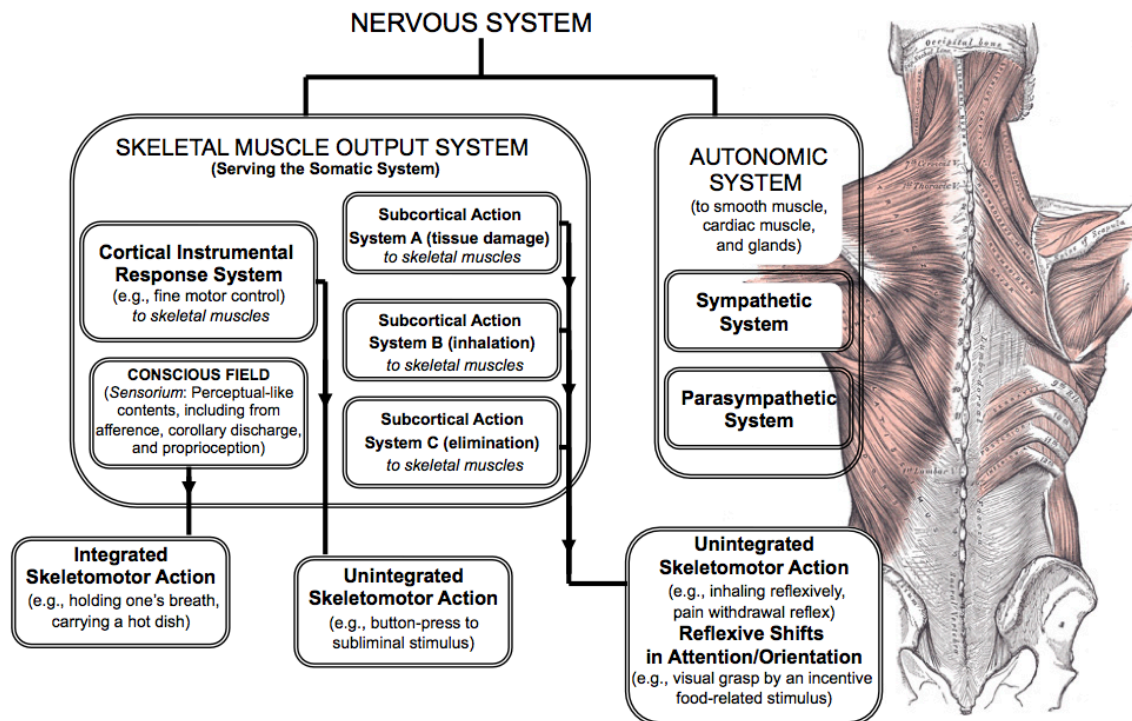
Consistent with this view of action conflicts, in one scenario, a conflict may involve representations *A* and *B* (associated with neural correlates  $A_{NC}$  and  $B_{NC}$ ), and then, at a later time and in a different context, a conflict may involve representations *C* and *D* (associated with neural correlates  $C_{NC}$  and  $D_{NC}$ ; Curtis & D'Esposito 2009). Importantly, the two conflicts involve separate cognitive and neural processes, suggesting that "no single area of the brain is specialized for inhibiting all unwanted actions" (Curtis & D'Esposito 2009, p. 72). Instead, representations, including those of action sets (Fuster 2003; Grafman & Krueger 2009) and rules (Miller 2000) compete for the control of action. Such competition between action-related representations is evident in the aforementioned Stroop task (Stroop 1935).

In our approach, this arrangement in which the contents of the conscious field lead to the activation of multiple (and often competing) action plans causes one to appreciate that, in the skeletomotor output system, there must be a (unconscious) mechanism by which one action plan can influence behavior more than other activated action plans. Such a mechanism would ensure that when holding one's breath while underwater, for example, the action plan to refrain from inhaling would influence behavior more than that of inhaling, although the conscious field would represent both inclinations. Appreciation of such potential "bottlenecks" in action selection can serve as a valuable constraint on theorizing regarding the neural structures underlying consciousness.

Importantly, in the perception-to-action loop, consciousness represents conflicts and not necessarily the representations associated with the resolution of such conflicts, should such representations exist (Morsella 2005). This peculiar property of consciousness arises because consciousness is about a stage of processing reflecting action options and not the mechanisms that, should they exist, represent conflict resolution. This illuminates why Chomsky (1988) observes that humans, unlike machines, are not only *compelled* to act one way or another but can also be *inclined* to act a certain way. Again, such inclinations could be construed as action options. The resolution of conflict depends not on some general property of consciousness, but on the peculiarities (e.g., relative strengths) of the systems that happen to be in conflict (Skinner 1953). Consciousness only permits that conflicts occur; it does not aim to resolve them (Morsella 2005). Each conflict is idiosyncratic and, if it is to be resolved, must require post-conscious, content-specific algorithms (e.g., one in which overt behavior is influenced most by prepotent action plans; Gold & Shadlen 2007; Logan et al. 2015). Hence, it is challenging to arrive at general principles for predicting the outcomes of conflicts involving different systems (Campbell & Misanin 1969; see model of countermanding in Logan et al. [2015]). The Internet provides a good analogy for the role of consciousness in conflict: The Internet permits two people from different cities to debate, but it cannot resolve conflicts between them. Another analogy would be an interpreter that translates for two parties that are in conflict about some issue. The interpreter is necessary for the instantiation of the conflict and for its potential resolution; the interpreter, however, cannot resolve the conflict.

In summary, to advance the identification of the neural substrates of consciousness, it is essential to keep in mind that consciousness is a phenomenon associated with perceptual-like processing and interfacing with the somatic nervous system (Fig. 1).

**Figure 1.** *The divisions of the nervous system and place of consciousness within the system (based on Poehlman et al. 2012), including the major divisions of the somatic and autonomic systems. Afferece binding within systems can be unconscious. Although response systems can influence action directly, as in the case of unintegrated actions, only in virtue of consciousness can multiple response systems influence action collectively, as when one holds one's breath while underwater.*



### 3.4. Neural evidence supports the sensorium hypothesis

The sensorium hypothesis and ideomotor theory reveal that, in terms of stages of processing, that which characterizes conscious content is the notion of *perceptual afferece* (information arising from the world that affects sensory-perceptual systems; Sherrington 1906) and *corollary discharges* (e.g., when subvocalizing; cf. Chambon et al. 2013; Christensen et al. 2007; Jordan 2009; Obhi et al. 2009; Scott 2013), both of which are cases of perceptual-like content. This hypothesizing is consistent with the idea that, insofar as consciousness must always contain some content (Brentano 1874; Fodor 1980; 1998; Gray 1995; 2004; Hume 1739/1888; Koch 2004; Schopenhauer 1818/1819; Sergent & Dehaene 2004), then it is parsimonious to propose that *the neural regions responsible for processing that content must be part of the neural correlate of consciousness for that content*. Hence, if content *X* is in consciousness, then the circuits processing content *X* must be part of a neural correlate of consciousness (e.g., at least of *X*). (Of course, within such an arrangement, it may be that the region[s] processing the particular content need not be the region[s] in which that content becomes associated with the conscious field; content processing could arise in one locus of the network, but



the participation of contents in the conscious field could arise at another locus of the network.) With this notion in mind, we turn to the neural evidence regarding conscious contents.

Consistent with the sensorium hypothesis, there is evidence implicating perceptual brain regions as the primary regions responsible for consciousness. For example, direct electrical stimulation of parietal areas gives rise to the conscious urge to perform an action, and increased activation makes subjects believe that they actually executed the corresponding action, even though no action was performed (Desmurget et al. 2009; Desmurget & Sirigu 2010; see also Farrer et al. 2008). However, activating motor areas (e.g., premotor regions) leads to the expression of the actual action, but subjects believe that they did not perform any action whatsoever (see also Fried et al. 1991). Importantly, consistent with our foregoing conclusions, the urge to perform a motor act is associated with activation of perceptual regions.

In accord with the sensorium hypothesis, the majority of studies involving brain stimulation and consciousness have found that stimulation of perceptual (e.g., posterior) brain areas leads to changes in consciousness (e.g., haptic hallucinations). This should not be surprising given that these regions were identified as “perceptual” in the first place by the use of self-report during brain stimulation (e.g., Penfield & Roberts 1959). Self-report usually involves consciousness (see discussion in Bayne 2013). In the literature, we found only one datum in which brain stimulation of a frontal (non-olfactory) area led to a conscious content. In this study (Fried et al. 1991, cited in Haggard 2008), weak electrical stimulation of the pre-supplementary motor area led to the experience of the urge to move a body part, with stronger stimulation leading to movement of the same body part. It has been proposed that such activation led to corollary discharge that was then “perceived” by perceptual areas (Chambon et al. 2013; Farrer et al. 2008; Iacoboni 2005; Iacoboni & Dapretto 2006; Lau et al. 2007; Melcher et al. 2013; Scott 2013), which would be consistent with the sensorium hypothesis. One strong hypothesis from this line of theorizing is that activations in regions that are non-perceptual or motor should never (independent of corollary discharge) influence the conscious field.

Consistent with the sensorium hypothesis and ideomotor theory, research reveals that a key component of the control of intentional action is feedback about ongoing action plans to perceptual areas of the brain, such as post-central cortex (Berti & Pia 2006; Chambon et al. 2013; Desmurget et al. 2009; Farrer et al. 2008; Iacoboni 2005; Miall 2003). With this information in mind, it has been proposed that consciousness is associated not with frontal or higher-order perceptual areas, but with lower-order perceptual areas (Gray et al. 2013; Liu et al. 2012; Tallon-Baudry 2012). However, it is important to qualify that though the sensorium hypothesis specifies that consciousness involves neural circuits that, traditionally, have been associated with perception, such circuits are widespread throughout the brain and exist within both cortical and subcortical regions (Merker 2012). Hence, the sensorium hypothesis is consistent with several neuroanatomical accounts of consciousness, including cortical, subcortical (e.g., thalamic), and thalamocortical accounts of consciousness. Hence, on the basis of the

sensorium hypothesis alone, it is premature to dismiss subcortical accounts of consciousness (e.g., Merker 2007; Penfield & Jasper 1954; Ward 2011).

In conclusion, at the present stage of understanding, the literature provides no clear answer regarding the neural substrates of any kind of conscious content (see treatment in Merker 2013a; 2013b). Based on the foregoing conclusions about conscious contents, we believe that, to illuminate this issue further, progress can be made by adopting an EASE perspective and focusing on a (relatively) tractable perceptual region – namely, that of the understudied olfactory system.

### ***3.5. Tenet: The olfactory system provides clues regarding the neural correlates of conscious perceptual content in the sensorium***

Our EASE perspective led us to the sensorium hypothesis. Now, with the same perspective, we focus on one kind of content in the sensorium. As noted in sect. 1.4, when attempting to isolate the substrates of a conscious content, researchers have followed Crick and Koch's (2003) recommendation and focused on vision. It is clear that isolating the neuroanatomical substrate of a visual conscious content remains controversial. From an EASE perspective, and based on previous research (Merrick et al. 2014; Morsella & Bargh 2007), we focus our attention instead on olfaction (see also Keller 2011), a phylogenetically old system whose circuitry appears to be more tractable and less widespread in the brain than that of vision or higher-level processing such as music perception. As Shepherd (2007) concludes, "The basic architecture of the neural basis of consciousness in mammals, including primates, should be sought in the olfactory system, with adaptations for the other sensory pathways reflecting their relative importance in the different species" (p. 93).

Several features of this system render it a fruitful arena in which to isolate the substrates of consciousness. First, olfaction involves a primary processing area that consists of paleocortex (which contains only half of the number of layers of neocortex) and primarily only one brain region (the frontal cortex; Shepherd 2007). In contrast, vision and audition often involve large-scale interactions between frontal cortex and parietal cortices. These observations reveal the relative simplicity of the anatomy of the olfactory system compared to that of other systems. Second, regarding the cortical-subcortical controversy, olfaction can reveal much about the contribution of thalamic nuclei in the generation of consciousness: Unlike most sensory modalities, afferents from the olfactory sensory system bypass the first-order, relay thalamus and directly target the cortex ipsilaterally (Shepherd & Greer 1998; Tham et al. 2009). This minimizes spread of circuitry, permitting one to draw conclusions about the necessity of first-order thalamic relays in (at least) this form of consciousness.

By studying olfaction, one can also draw some conclusions about second-order thalamic relays (e.g., the mediodorsal thalamic nucleus; MDNT). After cortical processing, the MDNT receives inputs from olfactory cortical regions (Haberly 1998). Although it is likely that the MDNT plays a significant role in olfactory discrimination (Eichenbaum et al. 1980; Slotnick & Risser 1990; Tham et al. 2011), olfactory

identification, and olfactory hedonics (Sela et al. 2009), as well as in more general cognitive processes including memory (Markowitsch 1982), learning (Mitchell et al. 2007), and attentional processes (Tham et al. 2009; 2011), we have found no evidence that a lack of olfactory consciousness results from lesions of any kind to the MDNT (see theorizing about this possibility in Plailly et al. [2008]). Regarding second-order thalamic relays such as the MDNT, one must keep in mind that, in terms of circuitry, these nuclei are similar in nature to first-order relays (Sherman & Guillery 2006), which are quite simple compared to, say, a cortical column.

Consistent with “cortical” theories of consciousness, Cicerone and Tanenbaum (1997) observed complete anosmia (the loss of the sense of smell) in a patient with a lesion to the left orbital gyrus of the frontal lobe. In addition, a patient with a right orbitofrontal cortex (OFC) lesion experienced complete anosmia (Li et al. 2010), suggesting that the OFC is necessary for olfactory consciousness. (It is worth mentioning that we are speaking of the OFC with respect to, not the high-level executive processes with which it has been associated, but, consistent with the sensorium hypothesis, its perceptual processing [i.e., olfactory perception].) Moreover, conscious aspects of odor discrimination have been attributed to the activities of the frontal and orbitofrontal cortices (Buck 2000). Keller (2011) concludes, “There are reasons to assume that the phenomenal neural correlate of olfactory consciousness is found in the neocortical orbitofrontal cortex” (p. 6; see also Mizobuchi et al. 1999). (According to Barr and Kiernan [1993], olfactory consciousness depends on the piriform cortex.) However, not all lesions of the OFC have resulted in anosmia: Zatorre and Jones-Gotman (1991) reported a study in which OFC lesions yielded severe deficits, yet all patients demonstrated normal olfactory detection.

Another output pathway from the piriform cortex projects to the insular cortex (Haberly 1998; Schoenbaum & Eichenbaum 1995), a structure that has anatomical connections to the ventral posteromedial (VPM) nucleus of the thalamus (Price et al. 1991). In light of (a) this information, (b) the conclusions presented previously about the MDNT, and (c) theories in which thalamic structures play an important role in consciousness (e.g., Joliot et al. 1994; Llinás & Ribary 2001; Llinás et al. 1998; Ward 2011), one could propose that olfactory consciousness depends on the integrity of the insula and thalamus. However, regarding the thalamus, it has been observed that though thalamic lesions can impair olfactory discrimination and complex olfactory learning (Eichenbaum et al. 1980; Martin 2013), such lesions, including those of the VPM, never result in anosmia (Martin 2013; Price 1985; Price et al. 1991; Sela et al. 2009). The lesion literature also reveals an additional important fact about olfactory consciousness. Olfactory consciousness does not require the involvement of any transthalamic pathway. In addition, for corticocortical connections, the olfactory system requires no “higher-order” (Sherman & Guillery 2006) thalamic relays (e.g., the MDNT or VPM; Gottfried 2006; Price 1985; Price et al. 1991). Considering these characteristics, Gottfried (2006) concludes, “The most parsimonious explanation for this anatomical variation is an evolutionary one: As primitive paleocortex, the olfactory circuitry simply developed long before the emergence of a thalamic module” (p. 53). These peculiar neuroanatomical characteristics are unique to olfactory consciousness.

Regarding the role of the insula in olfactory consciousness, after reviewing the literature, we concur with Mak et al. (2005) that there is no evidence that anosmia results from damage of any kind (e.g., unilateral or bilateral lesions) to the insular cortex: “There are no reports of olfactory deficits resulting from damage to the insula” (p. 1693; see also Damasio et al. 2012; Philippi et al. 2012; Tranel & Welsh-Bohmer 2012).

Taken together, the neuroanatomical evidence leads one to conclude that, in order to advance the current understanding of the neural underpinnings of consciousness, the next hypothesis to falsify is that *olfactory consciousness requires cortical processes*. This hypothesis is far from obvious, and it is falsifiable, because there are strong empirically based frameworks (e.g., Damasio 1999; Merker 2007; Panksepp 1998) proposing that consciousness is a function of subcortical processes. When these frameworks are integrated with our present treatment of the liaison between consciousness and olfactory circuits, our hypothesis could be proved to be inaccurate. For example, it might be that olfactory percepts are elaborated at a cortical level but become conscious only at some subcortical level (e.g., in the brainstem). Such a falsification of our hypothesis would advance our understanding of consciousness and the brain. Figuratively speaking, falsifying this particular “cortical” hypothesis provides the “lowest hanging fruit” for identifying the neural substrates of consciousness. In this way, the olfactory system can be used as a test bed for hypotheses stemming from the cortical-subcortical controversy.

Third, from an EASE perspective, there are phenomenological and cognitive/mechanistic properties that render this system a fruitful network in which to investigate consciousness. Regarding phenomenological properties, unlike what occurs with other modalities, olfaction regularly yields no subjective experience of any kind when the system is under-stimulated, as when odorants are in low concentration, or during sensory habituation. This “experiential nothingness” (Morsella et al. 2010) is more akin to the phenomenology of the blind spot than to what one experiences when visual stimulation is absent (darkness). In the latter case, there still exists a conscious, visual experience (e.g., that of a black field). The experiential nothingness associated with olfaction yields no conscious contents of any kind to such an extent that, absent memory, one in such a circumstance would not know that one possessed an olfactory system. Hence, for our purposes, the creation of a conscious olfactory content is a true “addition” to the conscious field in that it involves not only the introduction of information about a particular stimulus, but also the addition, from one moment to the next, of an entire modality. (See additional advantages of studying olfactory consciousness in Note 1.)

For these reasons, olfaction provides the best portal for understanding the neural correlates of additions to the conscious field. In our “creature in the cave” example, the smell of smoke is an addition to the conscious field that influences skeletomotor responses toward *other* conscious contents (e.g., the visual percept of the opening). Examining the neural correlates of such an addition might provide more evidence for the integration consensus. For example, it has been hypothesized that one becomes conscious of an olfactory percept only when the representation is part of a wider network involving other systems (Cooney & Gazzaniga 2003), such as motor (Mainland & Sobel 2006) or

semantic-linguistic (Herz 2003) systems. (See review of the relationship between neural oscillations and olfactory consciousness in Merrick et al. [2014].)

In conclusion, regarding neuroanatomy, our primary hypothesis is that consciousness is associated with what has traditionally been regarded as “perceptual” regions of the brain, a hypothesis that challenges some accounts of consciousness in which consciousness is associated with executive processes in frontal cortex (e.g., Boly et al. 2011; Dehaene & Naccache 2001; Lau 2008; Panagiotaropoulos et al. 2012; Safavi et al. 2014; Velly et al. 2007). Our secondary hypothesis is that olfactory consciousness can be constituted entirely by cortical circuits.

#### **4. The generation of conscious contents and field dynamics**

##### **4.1. Tenet: Content generation is encapsulated**

In our “creature in the cave” example, the addition of an olfactory content to the conscious field just “happens,” without any noteworthy effort on the part of the organism (Mainland & Sobel 2006). The content arises from a particular configuration of afference (e.g., the unconscious visual and auditory afference in the McGurk effect) to what can be construed as a *content generator* (associated with a perceptual region). Traditionally, these content generators (e.g., for color) have been construed as “modules” (Fodor 1983). Such a configuration of afference may include not only bottom-up afference, but also afference from unconscious top-down processes from knowledge systems and from frontal control regions (Suhler & Churchland 2009; Tallon-Baudry 2012). Importantly, these generative processes that create conscious content are themselves context sensitive and unconscious (e.g., as in the McGurk effect; Lamme & Spekreijse 2000). Regarding context sensitivity, consider that the image of a snake on a television screen triggers little if any fear, but such is not the case in a natural context.

Usually, contents enter consciousness in a manner that is more automatic, and less driven by intentions of the experiencing “agent,” than appears to be the case in the everyday life of us pensive humans (Tallon-Baudry 2012; Vierkant 2013). Often, contents tend to “just happen” (Vierkant 2013). In line with these views, Helmholtz (1856/1925) proposed that unconscious processes can generate conscious content in a manner that resembles reflexes and other unintentional actions. When speaking about such “unconscious inferences,” Helmholtz was referring not only to the generation of the conscious contents associated with low-level perceptual processes such as depth perception, but also to higher-level, non-perceptual processes such as automatic word reading – an unnatural, intellectual process that requires years of training. Helmholtz noted that when one is confronted with an orthographic stimulus (e.g., HOUSE), the stimulus automatically triggers a conscious representation of the phonological form of the word (i.e., /haus/). Seldom in everyday life is it appreciated that, in this situation, the visual stimulus triggers a conscious content that is very different in nature from that of the environmental stimulation that brought the content into existence: The conscious representation of the phonological form of the word is associated not with the visual modality, but with audition (Levelt 1989).

Conscious content can be generated by unconscious inferences also in the case of action-related urges (e.g., from unconsciously generated corollary discharge). These urges are often triggered in a predictable and insuppressible manner. For example, when one holds one's breath while underwater or runs barefoot across the hot desert sand in order to reach water, one cannot help but consciously experience the inclinations to inhale or to avoid touching the hot sand, respectively (Morsella 2005). Regardless of the adaptiveness of the expressed actions, the conscious strife triggered by the external stimuli cannot be turned off voluntarily (Morsella 2005; Öhman & Mineka 2001). In these cases, the externally activated action-related urges are, in a sense, insulated, or "encapsulated" (Fodor 1983), from voluntary control. Hence, although inclinations triggered by external stimuli can be behaviorally suppressed, they often cannot be mentally suppressed (Bargh & Morsella 2008). One can think of many cases in which externally triggered conscious contents are more difficult to control than overt behavior (Allen et al. 2013).

It has been argued that it is adaptive for content generation to be encapsulated in this way and for conscious contents to be incapable of directly influencing each other in the conscious field (Firestone & Scholl 2014; Merrick et al. 2014; Rolls et al. 1977). From this standpoint, the conscious, perceptual representations for instrumental action should be unaffected by the organism's beliefs or motivational states (Bindra 1974; 1978). As Rolls and Treves (1998) conclude, "It would not be adaptive, for example, to become blind to the sight of food after we have eaten it to satiety" (p. 144). Similarly, it would not be adaptive for contents pertaining to incentive/motivational states to be influenced directly by other contents, such as desires and beliefs (Baumeister et al. 2007). For example, if one's beliefs could lead one to voluntarily "turn off" pain, guilt, or hunger, then these negative states would lose their adaptive value. Although motivation and beliefs may contaminate higher-order processes such as memory, they should have little influence over perceptual contents (Cooper, Sterling, Bacon, & Bridgeman, 2012; Firestone & Scholl 2014; Pylyshyn 1984; Pylyshyn, 1999). Such "cross-contamination" across contents would compromise the critical influence of such incentive/motivational states on behavior.

Hence, a given content is independent of other contents in the conscious field, whether the contents arise from environmental stimulation or from memory. Specifically, a conscious content (e.g., "da" in the McGurk effect) cannot directly influence the nature of other contents already in the conscious field (e.g., the smell of a rose, a toothache; Morsella 2005). (Of course, this is not to mean that the configuration of afference engendering one content cannot influence the generation of other contents – a form of context sensitivity in afference processing that occurs unconsciously [Lamme & Spekreijse 2000; Merker 2012].) Because of encapsulation, illusions persist despite one's knowledge regarding the actual nature of the stimuli (Firestone & Scholl 2014; Pylyshyn 1984).

It could be said that a given content does not "know" about its relevance to other contents (including high-level, knowledge-based contents) or to current action. When representing a food object, for example, the content does not know whether the food item

will be eaten or, instead, be thrown as a weapon. This view stands in contrast to several influential theoretical frameworks in which both the activation of, and nature of, conscious contents are influenced by what can be regarded as overarching goals or current task demands (e.g., Banerjee et al. 2012; Bhalla & Proffitt 1999; Bruner 1973; Bruner & Postman 1949; Dehaene 2014; Meier et al. 2007; Stefanucci & Geuss 2009). Because of the principle of encapsulation, conscious contents cannot influence each other either at the same time nor across time, which counters the everyday notion that one conscious thought can lead to another conscious thought.

In the present framework, not only do contents not influence each other in the conscious field, but as Merker (personal communication, June 30, 2012) concludes, content generators cannot communicate the content they generate to another content generator. For example, the generator charged with generating the color orange cannot communicate “orange” to any other content generator, because only this generator (a perceptual module) can, in a sense, understand and instantiate “orange.” Hence, if the module charged with a particular content is compromised, then that content is gone from the conscious field, and no other module can “step in” to supplant that content (Kosslyn et al. 2001). As Merker notes, in constructing the conscious field, modules cannot send messages with content, but only “activation” to each other (see also Lamme & Spekreijse 2000). This activation, in turn, influences whether the receiver module will generate not the kind of content generated by the module from which it received activation, but rather its own kind of content (e.g., a sound). Because messages of content cannot be transmitted to other content generators, the neural correlates of the content for  $X$  must include activation of the module that generates  $X$ , because a given content cannot be segregated from the process by which it was engendered, as stated previously.

#### ***4.2. Tenet: Field contents must meet multiple-constraint satisfaction, be unambiguous, and appear as if apprehended from a first-person perspective***

From an EASE perspective, one can ask, what does a conscious content require if it is to lead to adaptive action? To answer this question, one must first consider that in the case of object perception (such as the opening in our “creature in the cave” example), representations must be veridical to some extent in order to render action adaptive (Firestone & Scholl 2014). For example, during action selection, it would not be adaptive for a circular object to be represented with, say, straight lines and corners. Similarly, it would not be adaptive for an object on the left to be represented as if it were on the right. Hence, for the conscious field to afford adaptive action, it must represent with some veracity the spatial relation of those objects to the organism (Gibson 1979). Under normal circumstances, the contents of the conscious field at each moment are complete and unambiguous. Accordingly, Merker (2012) concludes that, because of the very nature of the constitution of the systems giving rise to conscious sensory representations, these systems are incapable of representing stimulus ambiguity (e.g., as in the Necker cube), at least at one moment in time. (However, such ambiguity could exist in unconscious perceptual processing [Merker 2012].) Hence, a given content emerges from polysensory configurations of afference, as in the McGurk effect, leading to the “global best estimate” of what that content should be (Helmholtz 1856/1925; Merker 2012).

Such well-constructed contents could stem from (a) the proposed, unconscious mechanisms of “multiple drafts” (Dennett 1991); (b) the interpretative processes of “apperception” (Wundt 1902/1904); or (c) “reentrant processing,” in which a module, in order to give rise to a conscious representation, must receive feedback activation from other modules about that representation (Lamme 2001; Pascual-Leone & Walsh 2001; Tong 2003). For example, if visual modules *X* and *Y* construct a representation that leads to the activation of other modules, then that representation becomes conscious only after feedback activation from the other modules returns to *X* and *Y* (Di Lollo et al. 2000; Fahrenfort et al. 2007; Goodhew et al. 2012; Grossberg 1999; Hamker 2003; Kriegel 2007; Lamme 2001; Lee et al. 2009; Llinás et al. 1998; Pascual-Leone & Walsh 2001; Tong 2003). Reentrant processing may instantiate a kind of “checks-and-balances” system for constructing accurate conscious contents that satisfy the criteria of multiple modules, a form of *multiple-constraint satisfaction* (Dennett 1991; Merker 2012). In addition, feedback of this sort may underlie the phenomenon of “contextual modulation” (e.g., in figure-ground effects; Lamme & Spekreijse 2000). More simply, this feedback may be necessary because conscious contents may require (a) high levels of activation (Kinsbourne 1996) or (b) sustained activation for a prolonged period (Lau 2009), both of which can be furnished by sustained reverberation (Hebb 1949). In summary, for a content generator to contribute to the conscious field and for its contents to be crafted well, it may require the concurrent activation from both feed-forward and feedback mechanisms (Lamme & Spekreijse 2000).

The conscious field of our “creature in the cave” includes representations of urges and external objects, which incorporate the relation between such things and the organism itself (Lehar 2003; Merker 2012; Yates 1985). More generally, contents are usually sensed to be different from, and separate from, the observing agent (Brentano 1874; Merker 2012; Schopenhauer 1818/1819). Insofar as the action selection process of the skeletomotor output system must take into account spatial distance from the organism as one of the many factors in adaptive selection, then all contents about the external world (including the body) must have a common, egocentric reference (Merker 2013b). It would be disadvantageous for this rule to be violated and for, again, an object on the left to be represented as if on the right. Hence, most conscious contents appear *as if* from a first-person perspective (Gibson 1979; Merker 2013b; Prinz 2007). The conscious field is imbued with this first-person perspective during waking, in dreaming, and for illusions in which, through clever experimental manipulations and the presentation of certain stimuli, the perspective is momentarily perceived as if from outside of the body (Ehrsson 2007).<sup>14</sup> From this standpoint, the demands of adaptive action selection require the creation of a first-person perspective, which is a primitive form of “self.”

#### **4.3. Tenet: The conscious field serves as a frame that represents encapsulated contents for collective influence over, not itself, but the skeletal muscle output system**

It seems that the conscious field is like a mosaic of discrete, heterogeneous contents, rendering the field to be *combinatorial*. Each content is well-crafted and unambiguous



(Dietrich & Markman 2003; Freeman 2004; Köhler 1947; Merker 2012; Scholl 2001). The contents cannot directly influence each other,<sup>15</sup> and the content generators cannot duplicate the generative abilities of each other. Hence, the resultant contents from these modules are encapsulated from each other. These mosaic-like gestalts (i.e., the conscious field) arise in consciousness in a discontinuous manner, with each conscious moment, lasting for fractions of a second, having an updated version of all the contents in the conscious field. For action to be adaptive, the refresh rate of the entire field must be faster than the quickest rate at which voluntary actions can be produced. Hence, the refresh must occur more rapidly than the rate at which the fastest actions (e.g., saccades) can be emitted (Merker 2013b). (For theorizing regarding the temporal properties of such an updating process, see Libet [2004] and Merker [2012, p. 56; 2013b, p. 12].)

Importantly, the collective influence of the combination of contents in the conscious field is not toward the conscious field itself; instead, according to PRISM, the conscious field is apprehended by the (unconscious) mechanisms composing the skeletomotor output system. Hence, the conscious contents of blue, red, a smell, or the urge to blink are the tokens of a mysterious language understood, not by consciousness itself (nor by the physical world), but by the unconscious action mechanisms of the skeletomotor output system. Why do things appear the way they do in the field? Because, in order to benefit action selection, they must differentiate themselves from all other tokens in the field – across various modalities/systems but within the same decision space.

Although possessing elements of a “Cartesian Theater” (Dennett 1991), this arrangement does not introduce the “homunculus fallacy,” because, in the skeletomotor output system, there are many motor homunculi, each incapable of duplicating the functions of the system as a whole (Dennett 1991). Unlike the “workspace” models associated with the integration consensus (e.g., Baars 1988; Dehaene 2014), which propose that conscious representations are “broadcast” to modules engaged in both stimulus interpretation and content generation, in our framework (as in Merker 2007), the contents of the conscious field are directed only at response modules in the skeletomotor output system. In short, conscious contents are “sampled” only by unconscious action systems that are charged with (specifically) skeletal muscle control.

## 5. Passive frame theory: An action-based synthesis

No activity of mind is ever conscious.

— Lashley (1956, p. 4)

It is the *result* of thinking, not the process of thinking, that appears spontaneously in consciousness.

— George A. Miller (1962, p. 56)

To reiterate, progress on the study of consciousness and the brain has suffered not so much from a lack of data, but from a lack of a suitable, internally coherent framework with which to interpret extant data (Grossberg 1987). To provide such a framework, we now synthesize all of our tenets.

Consciousness is a phenomenon serving the somatic nervous system (subset consensus); it is in the service of adaptive skeletomotor function (PRISM; Fig. 1). At each moment, the conscious field is generated anew, with a new medley of contents. PRISM predicts the kinds of information that must become conscious contents. These kinds of information are about things (e.g., external objects and urges) that should influence the skeletomotor output system (the “steering wheel” associated with consciousness). To the organism, these unambiguous, well-crafted, and highly context-sensitive contents usually arise in an automatic, non-self-generated manner. The contents, which arise from configurations of afference (including top-down processes and unconscious intersensory interactions), are encapsulated from each other: One content does not “know” whether it is relevant to other contents or to ongoing action (encapsulation). Consciousness can thus be construed as a “continuous feed” system that is always “on,” even in the absence of conflict or of other forms of cross-system checking (Morsella 2005). In other words, the primary function of the conscious field is collective influence of otherwise encapsulated contents on the skeletomotor output system. Such an influence is essential especially under conditions of conflict; however, as a continuous feed system, this mechanism of collective influence persists even under conditions in which conflict is absent.

The contents (e.g., objects and urges) are “perceptual-like,” which is the “common format” apprehended by the action-related mechanisms composing the skeletomotor output system (sensorium hypothesis). Conscious contents are sampled only by unconscious action systems (PRISM). These contents can be construed as “action options.” Absent conflict, these action options activate unconscious efferences to the skeletomotor output system (ideomotor theory). Unconscious mechanisms such as unconscious inferences and corollary discharges from activated action plans (e.g., in the phonological loop; Scott 2013) can trigger conscious contents. We refer to the interdependence between unconscious and conscious mechanisms as the *conscious-unconscious cycle*.

The conscious field permits collective influence of all the heterogeneous contents upon the skeletomotor output system (PRISM). All influences on skeletomotor behavior, from the highest-level processes (e.g., language) to the lowest-level processes (e.g., pain withdrawal), must engage the skeletomotor output system. For the selection of any skeletomotor plan to be adaptive, selection must transpire in the frame of the other conscious contents composing the conscious field at that instant. We refer to this as a “frame check.” It is required for adaptive skeletomotor function and is essential for integrated actions in the context of conflict. Under certain circumstances (e.g., fast motor acts such as rapid eye gazes), frame checks must occur quickly, as last-minute changes to courses of action often arise in the face of new information (Merker 2013b). Hence, frame checks must occur more rapidly than the rate at which the fastest actions (e.g., saccades) can be emitted (Merker 2013b). During adaptive action selection, anticipated action effects, actual action effects, and information about the immediate environment must exist as comparable tokens in a common decision space. Although consciousness has historically been associated with the highest levels of processing, here it is revealed

that consciousness must occur at the level of processing that is shared with that of representations of the immediate external environment. Consciousness is associated only with frame checks and not with the more active aspects of the conscious-unconscious cycle (e.g., content generation, conflict resolution, motor programming).

With these conclusions in mind, we now return to our “creature in the cave” scenario. Because of encapsulation, the percept of the opening of the cave is consciously available even when the opening is not relevant to ongoing action (i.e., before detection of the smoke). Regarding neural events, the content addition of the olfactory stimulus involves a wide network of regions (integration consensus). To the organism, the olfactory content “just happens.” Before the content, there was no olfactory consciousness; hence, the smell of smoke is a “true addition.” Because messages of content cannot be transmitted, the olfactory content *must* involve perceptual areas of processing (sensorium hypothesis). The neuroanatomical correlates of such an olfactory content remain controversial (e.g., the cortical-subcortical controversy). We believe that progress regarding such controversies will stem from further examination of the cortical aspects of olfactory consciousness.

For our “creature in the cave,” the conscious content about the smell triggers a conscious content representing an avoidance tendency toward the smell. Specifically, this content about potential action is about the perceptual aspects of the to-be-produced action (sensorium hypothesis). Such a conscious content about an action can arise from activations in perceptual areas triggered by corollary discharges from unconscious, motor processes (Buchsbaum 2013; Chambon et al. 2013; Iacoboni 2005; Iacoboni & Dapretto 2006; Lau et al. 2007). Again, as with the case of (a) anticipated action effects, (b) actual action effects, and (c) information about the immediate environment, adaptive action selection requires that the conscious contents associated with both *stage 1* (e.g., the percept of the opening and the warmth) and *stage 2* (e.g., the smell and the inclination to stay in the cave) be, in terms of their functional consequences for action selection, the same kind of thing – comparable tokens existing in the same decision space. Thus, the conscious field permits for the contents about the smell *and* about the opening to influence action collectively.

During the frame check, the content about the potential action to exit conflicts with the content about the inclination to remain within the warm enclosure. In this case, the conflict between remaining in the enclosure and exiting is consciously experienced by the organism; however, this is only one component of all that is transpiring within the mental apparatus as a whole. Representations reflecting the outcome of the conflict (should they exist) reside outside of consciousness (which itself is primarily about action options). Such a resolution will reflect not any property of consciousness, but the peculiarities of the conflicting systems involved.

In terms of action selection, the conscious field could be construed as the evolutionary strategy for dealing with what the ethologists and behaviorists referred to as a *complex of multiple discriminative stimuli* (also known as a *compound discriminative stimulus*), in which the “stimulus control” from one discriminative stimulus depends

systematically on the nature of the other discriminative stimuli composing the scene (Spear & Campbell 1979). In collective influence, the response to one conscious content – and the “meaning” of that content for ongoing action selection – depends exclusively on the nature of itself and the other conscious contents at that moment in time. Hence, the conscious field permits for the response to one content to be made in light of the other contents (Tsushima et al. 2006), thereby yielding integrated behavior. In this process, the conscious field wholly and exclusively determines what in everyday life is called voluntary behavior.

We now apply these insights to a case involving a higher-level system (language). At Thanksgiving dinner, our simple organism (now equipped with language) perceives a stimulus that triggers (unintentionally and automatically) in consciousness the action option of uttering a famous saying. This perceptual-like subvocalized phonological content, which “just happens” in consciousness, could stem from complex processes, involving, perhaps, corollary discharge from unconscious motor centers (Mathalon & Ford 2008; Scott 2013). After a frame check, the organism does not utter the phrase, because, a moment after experiencing the subvocalization, the organism experienced another content (the smell of hot chocolate) that led to an action plan (drinking) that was incompatible with speaking. The foregoing example reveals how the reiterative cycle of conscious field construction, and the frame check that each construction affords, yields the collective influence that adaptive skeletomotor action demands.

## 6. Implications and concluding remarks

Passive frame theory reveals that the province of consciousness in nervous function is more low-level, circumscribed, counterintuitive, and passive than what theorists have proposed previously. Because conscious contents do not know their relevance to other contents nor to ongoing action, consciousness is less purposeful at one moment in time than what intuition suggests. It is not only less purposeful and “all-knowing” than expected, but also contributes only one function (albeit an essential function) to a wide range of processes, much as how the Internet plays the same critical role for a varied group of events (e.g., the sale of books or dissemination of news), and the human eye, though involved in various processes (e.g., hunting vs. locomoting), always performs the same function. Because consciousness contributes to a wide range of heterogeneous processes, it appears as being capable of doing more than it actually does.

Passive frame theory also reveals that the contribution of consciousness to nervous function is best understood from a passive, *structural*-based (instead of a *processing*-based) approach. Such a perspective is in contrast to contemporary approaches but is in accord with historical ways to describe how biological systems achieve their ends (Grafman & Krueger 2009). Figuratively speaking, at one moment in time, there are few “moving parts” in the conscious field. (The field itself has no memory and performs no symbol manipulation; for these high-level mechanisms, it only presents, to action systems, the outputs of dedicated memory systems and of executive processes, respectively.)

Compared to the many functions attributed to consciousness, that which is proposed here is by far the most basic, low-level function. Because consciousness integrates processes from various systems, this role is more apparent when studying consciousness across modalities than when studying it within only one modality. Hence, the province of consciousness is best appreciated from a “systems-level” approach to the brain. The conscious-unconscious cycle of our approach also reveals the interdependence between (passive) conscious and (active) unconscious processes. (Few approaches examine the interactions between the two kinds of processes.) Last, our approach reveals that the demands of adaptive action (e.g., heterogeneous action systems must use the same effector) and the limitations of the cognitive apparatus (e.g., action selection often must occur quickly) illuminate many of the properties of consciousness, including that of a basic form of the sense of self.

With our framework as a foundation, future investigations could lead to a consensus regarding, for example, the neural circuitry underlying consciousness. Because the identification of the dynamic, neural processes associated with consciousness depend in part on identification of the neuroanatomical correlates of consciousness, a consensus should first be reached regarding the latter, more tractable problem. The most feasible way to reach such an identification is for investigators to cooperate across fields and attempt to isolate the correlates of consciousness at multiple levels of analysis, with increased research activity devoted to regions (a) predicted a priori, by theory, to be associated with consciousness and (b) identified as being the most experimentally tractable, as in the case of olfactory circuits. Because consciousness serves as a special interface between sensory and motor processing, theory-based predictions regarding the relationship between conscious contents and the skeletomotor output system (e.g., the link between olfactory percepts and integrated skeletomotor behavior) may advance attempts to identify the substrates of consciousness. We hope that our framework serves as a useful foundation for such collective endeavors.

Together with our EASE perspective, passive frame theory provides a fecund and internally coherent framework for the study of consciousness. Based on hypotheses from diverse areas of investigation, our synthesis reveals how consciousness serves an essential, integrative role for the somatic nervous system, a role that is intimately related to adaptive functioning of skeletal muscle (one of many effector systems in the body). When not subscribing to an EASE perspective, one could imagine ways in which the proposed contribution of consciousness to the somatic system could be realized without anything like ‘subjectivity.’ However, these musings would reflect our human powers of imagination more than what was selected in evolution for nervous function to yield adaptive behavior.

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## NOTES

1. First, unlike in vision, there are few executive functions (e.g., mental rotation, symbol manipulation) coupled with olfaction. Hence, in olfaction, one is less likely to conflate the substrates of consciousness with those of high-level executive functions (see Aru et al. 2012; Panagiotaropoulos et al. 2013). Similarly, in vision and audition, imagery can be used to preserve information in working memory through active rehearsal (Baddeley 2007), but olfactory images are difficult to couple with such operations (Betts 1909; Brower 1947; Lawless 1997; Stevenson 2009). Second, olfactory experiences are less likely to occur in a self-generated, stochastic manner: Unlike with vision and audition, in which visually rich daydreaming or “ear worms” occur spontaneously during an experiment and can contaminate psychophysical measures (respectively), little if any self-generated olfactory experiences could contaminate measures. Last, olfaction is more segregated from the semantic system than is the most studied sensory system – vision. In the latter, there are deep, inextricable relationships among perception, conceptualization, and semantics (Barsalou 1999; Kosslyn et al. 2006). Hence, when isolating the neural substrates of olfactory consciousness, one is less likely to include higher-level processes (e.g., semantic processes) associated with more than just olfactory consciousness. (See additional advantages of studying olfactory consciousness in sect. 3.5.)

2. Consistent with this consensus, evidence reveals that consciousness of some kind persists with the nonparticipation (e.g., because of lesions) of several brain regions (Morsella et al. 2010): cerebellum (Schmahmann 1998), amygdala (Anderson & Phelps 2002; LeDoux 1996), basal ganglia (Bellebaum et al. 2008; Ho et al. 1993), mammillary bodies (Duprez et al. 2005; Tanaka et al. 1997), insula (Damasio 2011, as cited in Voss 2011; see also Damasio 2010), and hippocampus (Crick & Koch 1990; Milner 1966; Postle 2009). In addition, investigations of “split-brain” patients (O’Shea & Corballis 2005; Wolford et al. 2004) suggest that consciousness survives following the nonparticipation of the non-dominant (usually right) cerebral cortex or of the commissures linking the two cortices. Controversy surrounds the hypothesis that cortical matter is necessary for consciousness (discussed in sect. 2.3 and sect. 3.5).

3. For the present purposes, unconscious events are those processes that, though capable of systematically influencing behavior, cognition, motivation, and emotion, do not influence the organism’s subjective experience in such a way that the organism can directly detect, understand, or self-report the occurrence or nature of these events (Morsella & Bargh 2010a).

4. See review in Morsella and Bargh (2011). In brief, unconsciously mediated actions can be observed during unconscious states, including forms of coma/persistent vegetative

states (Kern et al. 2001; Klein 1984; Laureys 2005; Pilon & Sullivan 1996) and epileptic seizures, in which *automatisms* arise while the actor appears to be unconscious. These unconscious automatisms include motor acts (Kokkinos et al. 2012; Kutlu et al. 2005), written and spoken (nonsense) utterances (Blanken et al. 1990; Kececi et al. 2013), singing (Doherty et al. 2002; Enatsu et al. 2011), and rolling, pedaling, and jumping (Kaido et al. 2006). Similarly, in neurological conditions in which a general consciousness is spared but actions are decoupled from consciousness, as in *alien hand syndrome* (Bryon & Jedyak 1972; Chan & Ross 1997), *anarchic hand syndrome* (Marchetti & Della Sala 1998), and *utilization behavior syndrome* (Lhermitte 1983), hands and arms carry out complex actions autonomously. These actions include complex goal-directed behaviors such as object manipulations (Yamadori 1997). Often, the behaviors are unintentional (Marchetti & Della Sala 1998; Suzuki et al. 2012). (See other forms of unconscious action in Bindra [1974], Milner and Goodale [1995], Weiskrantz [1992, 1997], and Westwood [2009].) In addition, actions can arise from stimuli of which the actor is unaware, as in the case of subliminal stimuli that, though imperceptible, can influence action (sect. 2.4; Ansorge et al. 2007; Hallett 2007).

5. In binocular rivalry (Logothetis & Schall 1989), an observer is presented with different visual stimuli to each eye (e.g., an image of a house in one eye and of a face in the other). Surprisingly, however, an observer experiences seeing only one object at time (a house and then a face), even though both images are always present.

6. Regarding neural oscillations, for example, controversy remains about the role that they play in the generation of consciousness. It has been proposed that cortical electroencephalography does not reflect conscious processing (Merker 2013a). In addition, there is controversy concerning the regions that are responsible for these oscillations. Consciousness-related oscillations have been proposed to reflect primarily (a) thalamic activity (Ward 2011), (b) thalamocortical activity (Joliot et al. 1994; Llinás & Ribary 2001; Llinás et al. 1998), and (c) corticocortical activity (Panagiotaropoulos et al. 2012; Schubert et al. 2006). (Regarding the role of oscillations in consciousness, see Aru and Bachmann [2009], Crick and Koch [1990], Doesburg et al. [2005; 2009], Engel and Singer [2001], Fries [2005], Hameroff [2010], Jung-Beeman et al. [2004], Meador et al. [2002], Panagiotaropoulos et al. [2012], Singer [2011], Uhlhass et al. [2009], and Wessel et al. [2012].)

7. Action selection, as when one presses one button versus another button or moves leftward versus rightward, is distinct from *motor control/motor programming* (Proctor & Vu 2010), processes that are largely unconscious (discussed in sect. 3.1).

8. Experiments have revealed that incompatible skeletomotor intentions (e.g., to point right *and* left, to inhale *and* not inhale) produce systematic intrusions into consciousness (Gray et al. 2013; Molapour et al. 2011; Morsella et al. 2009c), but no such changes accompany conflicts involving smooth muscle (Morsella et al. 2009a) or occur at perceptual stages of processing (e.g., intersensory processing; see quantitative review of evidence from multiple paradigms in Morsella et al. [2011]). Additional evidence stems from the observation that consciousness is required to counteract the interference effects of conflict (Desender et al. 2014).

9. Bleuler (1924) proposed that that which transforms unconscious processes to conscious processes is more than just integration – the integration must involve the “ego complex.” We propose that this complex is related to volition and the skeletomotor output system.

10. It is important to specify the notion of an *addition* of content to the conscious field. It has been proposed that consciousness cannot be “content free” but must always possess some content (Brentano 1874; Fodor 1980; 1998; Gray 1995; 2004; Hume 1739/1888; Koch 2004; Schopenhauer 1818/1819; Sergent & Dehaene 2004), such as that of a perceptual object or an action-related urge. We adopt this assumption. However, it has also been stated that contents *enter* consciousness, as if consciousness were a bucket into which contents enter. Hence, there is a contradiction: According to one interpretation, there can be no bucket without contents, but, according to the other interpretation, consciousness (i.e., the bucket) could exist independent of contents. Perhaps it is more accurate and parsimonious to state that new contents do not *enter* consciousness but *become* conscious, thereby joining other conscious contents. Hence, when something becomes conscious (e.g., the smell of smoke), we regard it as an “addition” to the conscious field. If consciousness is capacity limited, then at times an addition may also be construed as a replacement, because the new content removes other content (see evidence in Goodhew et al. 2012). It is controversial whether contents in the conscious field actually constitute the field or modulate it. (For a treatment concerning whether the field is componential or unitary, see Searle [2000].) Importantly, in the present model, whether the field is componential or unitary leads to the same functional consequences, because of the encapsulation of conscious contents (sect. 4.1).

11. According to a minority of theorists (see list in James 1890, p. 772), one *is* conscious of the efference to the muscles (what Wundt called the *feeling of innervation*; see James 1890, p. 771). In contrast, James (1890) staunchly proclaimed, “There is no introspective evidence of the feeling of innervation” (p. 775). This efference was believed to be responsible for action control (see review in Sheerer 1984). (Wundt later abandoned the feeling-of-innervation hypothesis [Klein 1970].)

12. This proposal is based in part on the requirements of “isotropic information,” which are beyond the scope of the present discussion (see Fodor 1983). As noted by Fodor (2001), in order to solve the “input” (or “routing”) problem, in which the appropriate representations must be made available to the appropriate information-processing modules, the representations must be perceptual in nature (Barrett 2005; Barsalou 1999).

13. Perhaps, in addition to action selection, a “go signal” is required for action initiation (Bullock & Grossberg 1988). The need for such a mechanism is beyond the scope of the present framework.

14. From an EASE perspective, it is parsimonious to treat the *sense of agency*, too, as a conscious content that is experimentally manipulable. It is experienced when there is the perception of a lawful correspondence between *action intentions* and *action outcomes* (Wegner 2002) and depends in part on conceptual processing (Berti & Pia 2006; David et al. 2008; Haggard 2005; 2008; Jeannerod 2009; Synofzik et al. 2008).



15. In forms of metacognition (e.g., *indirect cognitive control*; Morsella et al. 2009b), there are cases in which, through top-down control, conscious contents can lead to the strategic activation of other contents; however, this mechanism is beyond the abilities of our simple organism and, for the present purposes, unnecessary for appreciating the primary role of consciousness.

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