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

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Short 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

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*. Inside 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.

Key Words: Consciousness, Neural Correlates of Consciousness, Subjective Experience, Voluntary Action, Unconscious Processing.

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

What does consciousness contribute to the functioning of 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 (Grossberg, 1987). Thus, 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. As outlined below, 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’; cf., Block, 2010), 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’ (J. A. 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 comprising 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; 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 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). Thus, 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; J. A. 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). Thus, 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 J. A. 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; N. E. 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, Lanska, Berger, & Gazzaley, 2009b), whereby one can, for instance, 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 comprising 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 primary 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, Faivre, & Koch, 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 instead 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.¹

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. As outlined below, 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; Section 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 last four decades, there is a growing *Subset Consensus*—that consciousness is associated with only a subset of all of the processes and regions of the nervous system² (Aru, Bachmann, Singer, & Melloni, 2012; Crick & Koch, 1995, 2003; Dehaene & Naccache, 2001; J. A. Gray, 2004; Grossberg, 1999; Koch, 2004; Koch & Greenfield, 2007; Logothetis & Schall, 1989; Merker, 2007, 2013a; Penfield & Jasper, 1954; Weiskrantz, 1992; Zeki & Bartels 1999). This subset seems to be qualitatively distinct—in terms of its functioning, physical make-up/organization, or mode of activity—from that of its unconscious counterparts in the brain (Bleuler, 1924; Coenen, 1998; Edelman & Tononi, 2000; Goodale & Milner, 2004; J. A. Gray, 2004; Llinás, Ribary, Contreras, & Pedroarena, 1998; Merker, 2007; Ojemann, 1986).

Consistent with the Subset Consensus, many aspects of nervous function are unconscious.³ 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 below). 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.⁴ In summary, it seems that much in the nervous system is achieved unconsciously. This insight from the Subset Consensus leads one to the 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; A. R. Damasio, 1989; Dehaene & Naccache, 2001; Del Cul, Baillet, & Dehaene, 2007; Doesburg, Green, McDonald, & Ward, 2009; Edelman & Tononi, 2000; Freeman, 1991; Koch, 2012; Kriegel, 2007; Llinás & Ribary, 2001; Merker, 2007; Ortinski & Meador, 2004; Sergent & Dehaene, 2004; Srinivasan, Russel, Edelman, & Tononi, 1999; Tallon-Baudry, 2012; Tononi, 2012; Tononi & Edelman, 1988; Uhlhaas et al., 2009; Varela, Lachaux, Rodriguez, & Martinerie, 2001; Zeki & Bartels, 1999) proposes that consciousness integrates neural activities and information-processing structures that would otherwise be independent. Most of the hypotheses comprising 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 present purposes, we construe the contents occupying such a workspace as comprising the conscious field (defined above).

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,

Hudetz, & Tononi, 2008; Boveroux et al., 2010; Långsjö et al., 2012; Lee, Kim, Noh, Choi, Hwang, & Mashour, 2009; Lewis et al., 2012; Schroter et al., 2012; Shrouff et al., 2011), and unresponsive states (e.g., coma or vegetative state; Laureys, 2005). Regarding perception research, it has been proposed that, during binocular rivalry,⁵ 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. 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). Consistent with the consensus, conscious actions involve more widespread activations in the brain than do similar but unconscious actions (Kern, Jaradeh, Arndorfer, & Shaker, 2001; McKay, Evans, Frackowiak, & Corfield, 2003; Ortinski & Meador, 2004).

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.⁶ Progress regarding the neurophysiology of conscious processes depends on progress 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 & Logothetis [2002], Dehaene [2014], Koch [2004], Lamme & 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; Panagiotaropoulos et al., 2013) or lower-order regions (Aru et al., 2012; Friedman-Hill, Robertson, & Treisman, 1995; Lamme, 2001; Liu, Paradis, Yahia-Cherif, & Tallon-Baudry, 2012; Robertson, 2003; Tallon-Baudry, 2012; Tong, 2003). Moreover, as noted in Footnote 2, whether cortical matter is necessary for consciousness remains controversial.

Theorists focusing on vision have proposed that, while 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, 2013a). This has led to the *cortical-subcortical controversy* (Morsella, Berger, & Krieger, 2011). While data from studies on patients with profound disorders of consciousness (e.g., vegetative state) suggest that signals from 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, Pace-Schott, & Hobson, 2002), suggest 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 Section 3.5). Clearly, more investigation is needed regarding the neural correlates of consciousness, for 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, 2013b).

Faced with this challenge, we propose that, because of the intimate liaison between *function* and *structure* in the nervous system (Cohen & Dennett, 2011; Merker, 2013a), 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, J. R. Gray, Krieger, & Bargh, 2009a), as can another form of integration known as *efference binding* (Haggard, Aschersleben, Gehrke, & W. Prinz, 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, Weidema, Eenshuistra, Hommel, & Gruber, 2008). Learned forms of efference binding can be expressed unconsciously (Fehrer & Biederman, 1962; Fehrer & Raab, 1962; Hallett, 2007; J. L. Taylor & McCloskey, 1990, 1996). For example, subjects can select the correct 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” (J. L. Taylor & McCloskey, 1996, p. 62; see review in Hallett, 2007). We return to the topic efference binding when discussing how conscious contents influence action (Section 3.2).

In contrast to these unconscious forms of integration, people tend to be very much aware of some integrations, as when one holds one’s breath while underwater or experiences an approach-avoidance conflict (Lewin, 1935; N. E. Miller, 1959). In the former, one experiences the inclinations to both inhale and to not inhale. Similar, 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.⁷ This form of integration has been distinguished from unconscious integrations/conflicts, such as the McGurk effect and smooth muscle conflicts (e.g., 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* (‘skeletal motor,’ for short) *output system* (Morsella, 2005). The skeletal motor output system contains the unconscious motor plans that are necessary to enact one skeletal motor act versus another (Bizzi & Mussa-Ivaldi, 2004; Rizzolatti, Fogassi, & Gallese, 2004; Rosenbaum, 2002). It stores, for example, the unconscious articulatory plans that are necessary for speech production (Buchsbaum, 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 skeletal motor 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 skeletal motor plans.⁸ 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).

Thus, 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).⁹ From this standpoint, the conscious field is unnecessary to integrate

perceptual-level processes (as in feature binding or intersensory conflicts), smooth muscle processes (Morsella et al., 2009a), or processes associated with motor control (discussed below). 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 below, 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 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. 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., due to 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.) Thus, 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. Thus, 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, Jantz, & Morsella, 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, but 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’ one 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. Thus, 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 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 manner that is understandable by the unconscious, action-related mechanisms comprising the skeletomotor output system (Morsella & Bargh, 2010a).

The three tenets presented below 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*¹⁰ of conscious content are usually about the world, about the body, or about action-related inclinations (Brentano, 1874; Chomsky, 1988; Fodor, 1980, 1998; J. A. Gray, 1995, 2004; Hume, 1888; Koch, 2004; Schopenhauer, 1818; 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 these claims, 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, 2013a; J. Prinz, 2007; W. Prinz, 2003). In everyday life, when speaking about this level of representation of external objects, we use the term ‘percept’ (J. A. Gray, 1995), but 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 (W. 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 body, but 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, Gazzaley, & Morsella, 2013; Goodale & Milner, 2004; Harleß,

1861; J. A. Gray, 2004; Grossberg, 1999; 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, Chua, Franks, & Enns, 2001; Fournier & Jeannerod, 1998; J. A. Gray, 2004; Gottlieb & Mazzoni, 2004; Heath, Neely, Yakimishyn, & Binsted, 2008; Liu, Chua, & Enns, 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).¹¹ It seems that we do not have direct, conscious access to motor programs, to syntax, to aspects of executive control (Crick, 1995; Suhler & Churchland, 2009; Tallon-Baudry, 2012; van Gaal et al., 2008), or to other kinds of ‘efference generators’ (Grossberg, 1999; Morsella & Bargh, 2010a; Rosenbaum, 2002), including those for emotional systems (e.g., the amygdala; Anderson, & Phelps, 2002; LeDoux, 1996; Öhman, Carlsson, Lundqvist, & Ingvar, 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, 2010a; Rizzolatti, Sinigaglia, & Anderson, 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 only of 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 instance, in the phonological loop, it is the phonological representation, and not, say, the motor-related, ‘articulatory code’ (Ford, M. Gray, Faustman, Heinks, & Mathalon, 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’).

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 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; W. Prinz, 2003). With this in mind, one would expect that the nature of representations involved in consciousness are 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 above 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, 2010a; Morsella et al., 2009b).¹² 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). Thus, 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 of the conscious field (because they have access to all the contents in the conscious field), but they do possess *processing specificity* (for 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, Müsseler, Aschersleben, & W. Prinz, 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. Thus, 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 the case also 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. Thus, 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 influence 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 mismatch (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, Dunbar, & McClelland, 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, Gratton, Bashore, Eriksen, & Donchin, 1985; Eriksen & Schultz, 1979; DeSoto, Fabiani, Geary, & Gratton, 2001; Mattler, 2005; McClelland, 1979; van Veen, Cohen, Botvinick, Stenger, & Carter, 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.¹³ 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; W. Prinz, Aschersleben, & Koch, 2009). In this framework, conscious representations of one’s finger flexing, for instance, 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 (E. K. Miller, 2000), compete for the

control of action. Such competition between action-related representations is evident in the aforementioned Stroop Task (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 leads 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, while 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 valuable constraints on theorizing regarding the neural structures underlying of 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 only *inclined* to act a certain way. Again, such inclinations could be construed as action options. As discussed below, 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, Yamaguchi, Schall, & Palmeri, 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 who 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 (Figure 1).

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 afference* (information arising from the world that affects sensory-perceptual systems; Sherrington, 1906) and *corollary discharges* (e.g., when subvocalizing; cf. Chambon, Wenke, Fleming, W. Prinz, & Haggard, 2013; Christensen et al., 2007; Jordan, 2009; Obhi, Planetta, & Scantlebury, 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; J. A. Gray, 1995, 2004; Hume, 1888; Koch, 2004; Schopenhauer, 1818; Sergent & Dehaene, 2004), then it is parsimonious to propose that *the regions responsible for processing that content must be part of the neural correlate of consciousness for that content*. Thus, 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 region 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.

Consistent with the Sensorium Hypothesis, the majority of studies involving brain stimulation and consciousness have found that stimulation of perceptual (e.g., posterior) brain areas lead 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 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 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 feedback (e.g., corollary discharge) that is then ‘perceived’ by perceptual areas (Chambon et al., 2013; Farrer et al., 2008; Iacoboni, 2005; Iacoboni & Dapretto, 2006; Lau, Rogers, & Passingham, 2007; Melcher et al., 2013; Scott, 2013), which would be consistent with the Sensorium Hypothesis. One strong hypothesis from this 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 and Ideomotor hypotheses, 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 (J. R. Gray, Bargh, & Morsella, 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 the cortical, subcortical (e.g., thalamic), and thalamocortical accounts of consciousness mentioned above. Thus, 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 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 above, 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, Godwin, Geisler, & Morsella, 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 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, Shedlack, & Eckmann, 1980; Slotnick & Risser, 1990; Tham, Stevenson, & L. A. Miller, 2011), olfactory identification, and olfactory hedonics (Sela et al., 2009), as well as in more general cognitive processes including memory (Markowitsch, 1982), learning (Mitchell, Baxter, & Gaffan, 2007), and attentional processes (Tham et al., 2009; Tham et al., 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, Howard, Gitelman, & Gottfried, 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 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, Carmichael, Carnes, Clugnet, Kuroda, & Ray, 1991). In light of (a) this information, (b) the conclusions presented above about the MDNT, and (c) theories in which thalamic structures play an important role in consciousness (e.g., Llinás & Ribary, 2001; Llinás, Ribary, Contreras, & Pedroarena, 1998; Joliot, Ribary, & Llinás, 1994; 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 the 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, Simmons, Gitelman, and Small (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 A. R. Damasio, H. Damasio, & Tranel, 2012; Philippi et al., 2012; Tranel & Welsh-Bohmer, 2012).

Taken together, the neuroanatomical evidence presented above 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., A. 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 proven 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., 2010c) 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. Thus, for our purposes, the creation of a conscious olfactory content is a true ‘addition’ to the conscious field in that, not only does it involve the introduction of information about a particular stimulus, but it involves the addition, from one moment to the next, of an entire modality. (See additional advantages of studying olfactory consciousness in Footnote 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, Kapoor, Logothetis, & Panagiotaropoulos, 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 the *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 just bottom-up afference, but 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) proposed that reflex-like 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 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 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 unconscious 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. Thus, 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 is overt behavior (Allen, Wilkins, Gazzaley, & Morsella, 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, Judge, & Sanghera, 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 et al. (1977) 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, Vohs, DeWall, & Zhang, 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 encapsulated perceptual contents (Firestone & Scholl, 2014; Pylyshyn, 1984). Such ‘cross-contamination’ across contents would compromise the critical influence of such incentive/motivational states on behavior.

Thus, each 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 over-arching goals or current task demands (e.g., Banerjee, Chatterjee, & Sinha, 2012; Bhalla & Proffitt, 1999; Bruner, 1973; Bruner & Postman, 1949; Dehaene, 2014; Meier, Robinson, Crawford, & Ahlvers, 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, for 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, that content is gone from the conscious field and no other module can ‘step in’ to supplant that content (Kosslyn, Ganis, & Thompson, 2001). As Merker notes, in constructing the conscious field, modules can send, not 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 , for a content cannot be segregated from the process by which it was engendered, as stated above.

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 the question, 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. Thus, 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.) Thus, 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; 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 which leads to the activation of other modules, that representation becomes conscious only after

feedback activation from the other modules returns to X and Y (Di Lollo, Enns, & Rensink, 2000; Fahrenfort, Scholte, & Lamme, 2007; Goodhew, Dux, Lipp, & Visser, 2012; Hamker, 2003; Kriegel, 2007; Lamme, 2001; Grossberg, 1999; Lee et al., 2009; Llinás, Ribary, Contreras, & Pedroarena, 1998; Pascual-Leone & Walsh, 2001; Tong, 2003). Reentrant processing may instantiate a kind of ‘check-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 be part of the conscious field and be well-crafted, it may require the concurrent activation from both feedforward 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; Schopenhauer, 1818; Merker, 2012). 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, 2013a). Thus, most conscious contents appear *as if* from a first-person perspective (Gibson, 1979; Merker, 2013a; J. Prinz, 2007). 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. The conscious field is imbued with a 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).¹⁴ 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, each of which is well-crafted and unambiguous (Dietrich & Markman, 2003; Freeman, 2004; Köhler, 1947; Merker, 2012; Scholl, 2001). The content generators cannot directly influence each other¹⁵ nor duplicate the generative abilities of each other. Thus, the resultant contents from these modules are encapsulated from each other, rendering the field to be *combinatorial*. 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. Thus, the refresh must occur more rapidly than the rate at which the fastest actions (e.g., saccades)

can be emitted (Merker, 2013a). (For theorizing regarding the temporal properties of such an updating process, see Libet, 2004; Merker, 2012, p. 56; Merker, 2013a, 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 comprising the skeletomotor output system. Thus, 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 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 of 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 for a lack of data, but from a lack of a suitable framework with which to interpret extant data (Grossberg, 1987). To provide such a framework, we now synthesize all our tenets.

Consciousness is a phenomenon serving the somatic nervous system; it is in the service of adaptive skeletomotor function (Subset Consensus and PRISM; Figure 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 either 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 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, but, 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 comprising the skeletomotor output system (Sensorium Hypothesis). Again, conscious contents are sampled only by unconscious action systems. Unconscious mechanisms such as unconscious inferences and corollary discharges from activated action plans (e.g., in the phonological loop; Scott, 2013) can trigger these contents. These contents can be construed as ‘action options.’ 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. Absent conflict, these action options activate unconscious efferences to the skeletomotor output system (Ideomotor Theory).

For the selection of any skeletomotor plan to be adaptive, selection must transpire in the frame of the other conscious contents comprising 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, 2013a). Hence, *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. As mentioned above, frame checks must occur more rapidly than the rate at which the fastest actions (e.g., saccades) can be emitted (Merker, 2013). 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 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). Again, 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). During the frame check, the content about the potential action 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. 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. Importantly, first, the conscious field permits for the contents about the smell *and* about the opening to influence action collectively, but this is only one component of all that is transpiring within the mental apparatus as a whole. 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 cave) be, in terms of their functional consequences for action selection, the same kind of thing—comparable tokens existing in the same decision space.

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 comprising 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 the other conscious contents at that moment in time. Thus, the conscious field permits for the response to one content to be made in light of the other contents (Tsushima, Sasaki, & Watanabe, 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 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 contributes only one function (albeit an essential function) to a wide range of processes, much as the internet plays the same critical role to 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 versus 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, for action systems, the outputs of dedicated memory systems and of executive processes, respectively.)

Compared to the many functions attributed to consciousness, that 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. Thus, 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, 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 the identification of 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). Without an EASE perspective, one could imagine that that which consciousness contributes to the somatic system could be realized without anything like 'subjectivity,' but this would reflect more our human powers of imagination than what was selected in evolution for nervous function to yield adaptive behavior.

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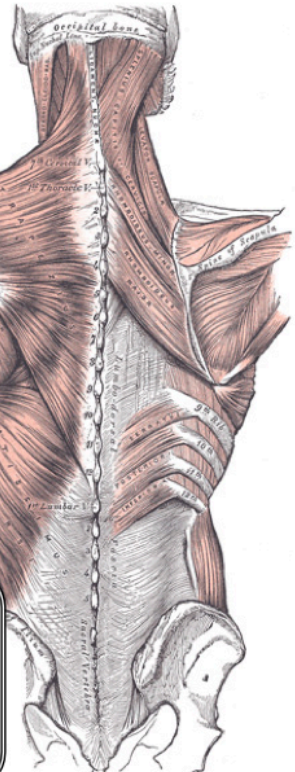
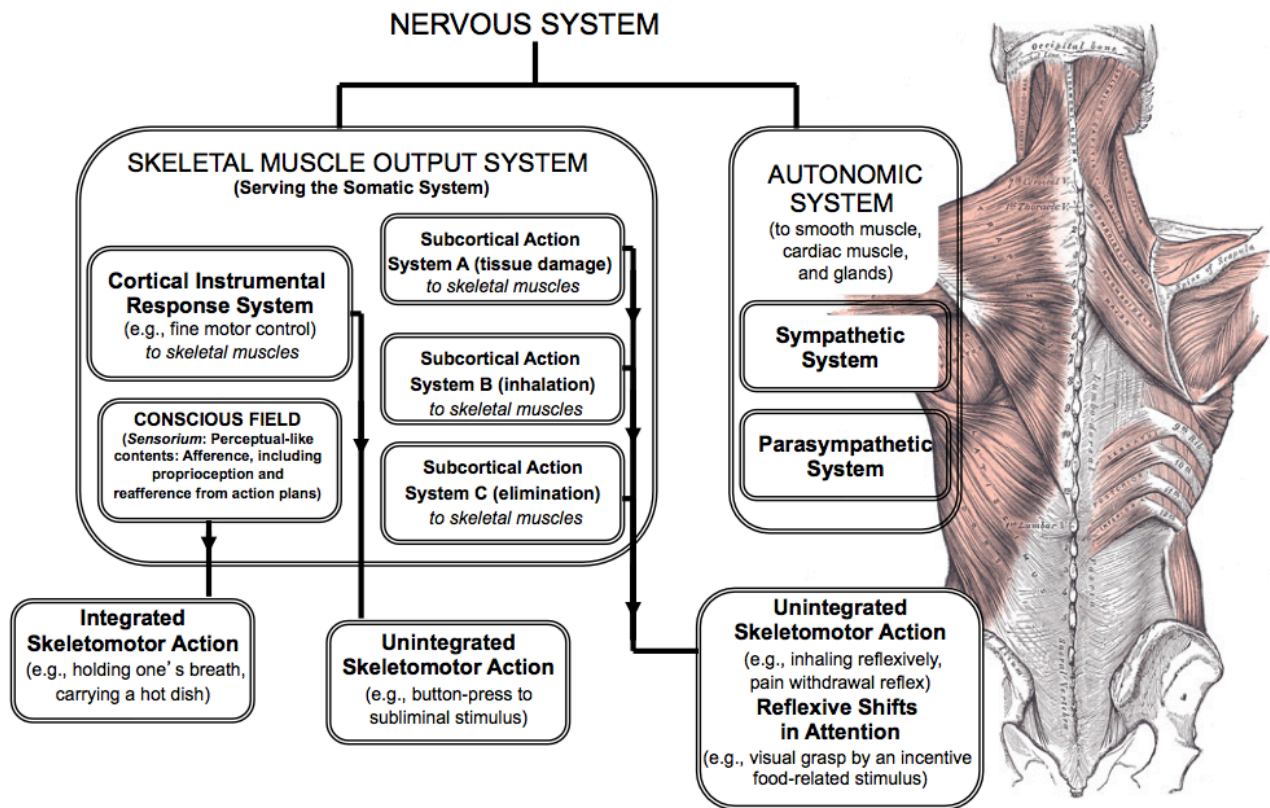
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Figure Caption

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. Afference 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.

Figure 1



Footnotes

¹ First, unlike in vision, there are few executive functions (e.g., mental rotation, symbol manipulation) coupled with olfaction. Thus, 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, Kapoor, & Logothetis, 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, 1974; 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, Thompson, & Ganis, & 2006). Thus, 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 Section 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, Krieger, & Bargh, 2010c): Cerebellum (Schmahmann, 1998), amygdala (Anderson & Phelps, 2002; LeDoux, 1996), basal ganglia (Bellebaum, Koch, Schwarz, & Daum, 2008; Ho, Fitz, Chuang, & Geyer, 1993), mammillary bodies (Duprez, Serieh, & Raftopoulos, 2005; Tanaka, Miyazawa, Akaoka, & Yamada, 1997), insula (A. R. Damasio, 2011, as cited in Voss, 2011; see also A. R. Damasio, 2010), and hippocampus (Crick & Koch, 1990; Milner, 1966; Postle, 2009). In addition, investigations of ‘split-brain’ patients (O’Shea & Corballis, 2005; Wolford, M. B. Miller, & Gazzaniga, 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 Sections 2.3 and 3.5).

³ For 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, 2010b).

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, Jaradeh, Arndorfer, & Shaker, 2001; Klein, 1984; Laurey, 2005; Pilon & Sullivan, 1996) and epileptic seizures, in which *automatisms* arise while the actor appears to be unconscious. These unconscious automatisms include motor acts (Kutlu et al., 2005; Kokkinos, Zountsas, Kontogiannis, & Garganis, 2012), written and spoken

(nonsense) utterances (Blanken, Wallesch, & Papagno, 1990; Kececi, Degirmenci, & Gumus, 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 & Jedynek, 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 & Goodale, 1995; Weiskrantz, 1992, 1997; 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 (Section 2.4; Ansorge, Neumann, Becker, Kalberer, & Cruse, 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 regarding the role they have in the generation of consciousness. It has been proposed that cortical electroencephalography does not reflect conscious processing (Merker, 2013b). 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 (Llinás & Ribary, 2001; Llinás, Ribary, Contreras, & Pedroarena, 1998; Joliot, Ribary, & Llinás, 1994), and (c) cortico-cortical activity (Panagiotaropoulos et al., 2012; Schubert, Blankenburg, Lemm, Villringer, & Curio, 2006). (Regarding the role of oscillations in consciousness, see Aru & Bachmann 2009; Crick & Koch, 1990; Doesburg, Green, McDonald, & Ward, 2009; Doesburg, Kitajo, & Ward, 2005; Engel & Singer, 2001; Fries, 2005; Hameroff, 2010; Jung-Beeman et al., 2004; Meador, Ray, Echauz, Loring, & Vachtsevanos, 2002; Panagiotaropoulos, Deco, Kapoor, & Logothetis, 2012; Singer, 2011; Uhlhass et al., 2009; Wessel, Haider, & Rose, 2012).

⁷ Action selection, as when one presses one button versus another button or moves leftwards versus rightwards, is distinct from *motor control/motor programming* (Proctor & Vu, 2010), processes which are largely unconscious (discussed below).

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 (J. R. Gray, Bargh, & Morsella, 2013; Molapour, Berger, & Morsella, 2011; Morsella et al., 2009c), but no such changes accompany conflicts involving smooth muscle (Morsella et al., 2009a) or occurring 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, van Opstal, & van den Bussche, 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’ (Bleuler, 1924). 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 must always possess some content (Brentano, 1874; Fodor, 1980, 1998; J. A. Gray, 1995, 2004; Hume, 1888; Koch, 2004; Schopenhauer, 1818; 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. Thus, 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, not *enter* consciousness, but *become* conscious, thereby joining other conscious contents. Thus, 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, Visser, & Lipp, & Dux 2011). 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 (Section 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, Vosgerau, & Newen, 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, but this mechanism is beyond the abilities of our simple organism and, for present purposes, unnecessary for appreciating the primary role of consciousness.