Précis of

Leveraging Multisensory Neurons, Circuits, Brains, and Bodies to Study Consciousness: From the Outside-In and the Inside-Out

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Chapters 1 & 2: Developing a science of multisensory perceptual awareness

(Adapted from Noel et al., 2015, Current Biology)

The study of perceptual awareness is one of the ultimate frontiers in contemporary neuroscience and, as a young field of empirical study, it draws heavily from insights in cognitive psychology, philosophy, and computer science. In turn, a wide array of theoretical frameworks exist; from those emphasizing a functional role of consciousness in cognitive processes (Baars, 1988 - cognitive psychology), to those equating consciousness with meta-cognition and second-order representations (Rosenthal, 2005; Lau & Rosenthal, 2011 – cognitive neuroscience/philosophy), and those conceiving of consciousness as an emergent property in highly complex and intertwined information processing devices (biological or not; Oizumi et al., 2014 – computer science, complexity theory). More broadly, it may be argued that the different theories are rooted in opposing views as to where they conceive the burden of explanation to lie. Some frameworks, such as Dehaene's Global Neuronal Workspace (GNW; Dehaene & Changeux, 2011) are "outside-in", in that they consider that sensory energies hit sensory periphery, these signals are then transduced and translated up the neuroaxis, and ultimately lead to perception. The challenge is in understanding the nature of the (admittedly non-linear and recurrent) transformation of energy in the external milieu up the cognitive hierarchy. Others, such as Blanke & Metzinger (2009) minimal phenomenal selfhood (MPS) approach, are "outside-in" theories in that they more faithfully reflect von Helmholtz's (1867) "perception as inference" vision. Namely, these latter theories argue that perception is imposed onto the world given prior experience, bodily representations, and/or motor affordances (Gibson, 1978).

Interestingly, a commonality to many of these theories – in fact, of those lying at the extreme of the outside-in/inside-out spectrum – is the central role they ascribe to *integration*. For instance, Baars' and Dehaene's Global Workspace Theory (Baars, 1988; Dehaene & Changeux, 2011) claim that consciousness enables *integration* across distinct cognitive modules (i.e., memory, language, and decision-making), while Tononi's Integrated Information Theory (IIT; Tononi et al., 2016) posits an identity relation between information *integration* and wakefulness. On the other extreme of the "outside-in"/"inside-out" spectrum, Blanke & Metzinger's (2009) MPS approach is rooted in the philosophical argument that for there to be a subjective experience there has to be an entity to be subject, and thus, perceptual awareness must be scaffolded on a pre-reflective bodily self-consciousness (Legrand, 2006). This bodily proto-self dictating exteroceptive perception is thought to be scaffolded on the process of multisensory *integration*.

Given these diverse frameworks and the wide spectrum of existent theories of consciousness, my dissertation departed from the dominant vision-centric study of consciousness (~ 75-80% of perceptual awareness studies are in fact studies of *visual* awareness; Faivre et al., 2017) and instead focused on developing a science of *multisensory* perceptual awareness. The motivation behind this aim was twofold. First, the alluded observation that a majority of theories posit integration as a central tenet in their model and the fact that integration is a *de facto* and well-defined process within the study of multisensory integration (Murray & Wallace, 2012). Secondly, our phenomenological experience of the world is multisensory – and not a cacophony of unisensory percepts – and thus the study of multisensory perceptual awareness re-aligns empirical investigation with subjective experience (Deroy et al., 2016). Further, by studying multisensory awareness we can novelty question whether Crick and Koch's (1990) assumption that all forms of consciousness follow similar organizational principles holds or not, and hence we can examine whether the existent theories and empirical studies of consciousness address visual awareness specifically, or perceptual awareness generally.

The dissertation is divided in two parts. The first section (Chapters 3-5; "Consciousness from the outside-in") examines "outside-in" theories of consciousness and questions whether insights derived from studies of visual awareness may be borrowed in the study of multisensory perceptual awareness (Chapter 3), or contrarily, whether the study of multisensory processes can inform existent theories of consciousness (Chapters 4 & 5).

The second section (Chapters 6-9; "Consciousness from the inside-out") more precisely tests Blanke's (Blanke, 2012; Blanke et al., 2015) hypothesis that body-related multisensory integration occurs within the peri-personal space (PPS; Chapter 6) – the space immediately adjacent to and surrounding your body (di Pellegrino et al., 1997) – and that this integrative process scaffolds bodily self-consciousness (Chapters 7 & 8). Further, in a translational effort I examine whether mapping of PPS may be utilized in diagnosing patients with disorders of consciousness (Chapter 9). The conjunction of Sections 1 & 2 highlights the utility in examining multisensory perceptual awareness, in that this science is not only in line with phenomenological experience, but also can be leveraged to probe theories of consciousness all along the "outside-in"/"inside-out" spectrum (Chapter 10).

SECTION I: CONSCIOUNESS FROM THE OUTSIDE-IN

Chapter 3: Is a science of multisensory perceptual awareness necessary?

(Adapted from Noel et al., 2018, Journal of Cognitive Neuroscience)

This first experimental chapter aimed at directly questioning whether a science of multisensory perceptual awareness is necessary, or conversely whether we could simply extrapolate findings from visual neuroscience to other domains; auditory awareness, tactile awareness, audio-visual awareness, etc. Continuous high-density electroencephalography (EEG) was recorded from participants, as they were presented with auditory (A), visual (V), or audio-visual (AV) stimuli at the threshold for detection. Participants were asked to report detection of stimuli via button press. As illustrated in Figure 1A (top panels), albeit stimuli being presented with the same intensity, when participants reported perceiving the cue strong evoked potentials were observed (blue = A; red = V; green = AV), but this was not the case when stimuli were not perceived. Importantly, therefore, according to average evoked potentials, the presence of strong and sustained neural responses differentiates between perceptual states (i.e., perceived vs. non-perceived) regardless of the modality of the stimuli (i.e., visual vs. auditory) and across the unisensory and multisensory divide. Interestingly, this conclusion did not generalized to other (arguably more sophisticated) measures. Namely, the reproducibility of evoked potentials (Figure 1B; McIntosh et al., 2008) was unaltered across perceptual states for AV presentations, but did change for A and V stimuli. Similarly, while the neural complexity (akin to within-trial noisiness; Casali et al., 2013) of responses differentiated between perceived states for auditory and visual trials, it did not do so for audio-visual presentations (Figure 3C).

Taken together, the findings indicated that while some metrics of consciousness may apply across sensory modalities and the combination thereof (i.e., the presence of late and sustained evoked potentials), other more sophisticated metrics such as reproducibility and complexity may not. Further, the presence of late and sustained responses have recently been demonstrated to most closely index report, which was required within the current study in detecting any sensory stimuli regardless of modality, and not phenomenological awareness itself (Tsuchiya et al., 2015). In sum, therefore, it appears that insights derived from visual awareness may not be straightforwardly applied to the multisensory case, and hence we ought to develop a science of *multisensory perceptual awareness*. Lastly, and as a corollary, we compared multisensory evoked potentials to the sum of unisensory responses as a function of perceptual state. Performing this contrast – multisensory pair vs. unisensory sum – is a well-established approach in indexing true multisensory integration (linear summation indicating multisensory convergence but not integration), and the results here suggested that multisensory integration occurs when stimuli were consciousness perceived, but not when stimuli were not detected (Figure 1A, bottom panels). Hence, in addition to questioning Crick and Koch's (1990) assumption that all forms of consciousness follow similar organizational principles, the current results support Baars' (1988) conjecture that integration may not occur outside of awareness.

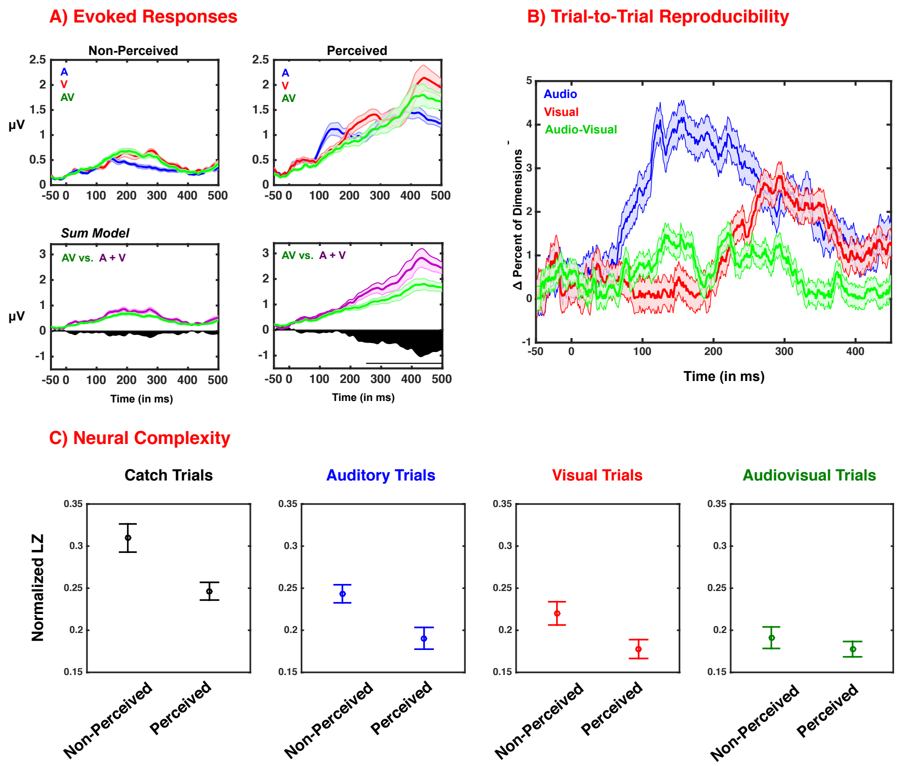

Figure 1. Neural Correlates of Perceptual Awareness as a Function of Sensory Modality. A) Evoked Potential. Perceived trials resulted in stronger neural responses (Global Field Power) regardless of sensory modality. Nonetheless, contrast of multisensory responses to the summative model indicated that multisensory integration did not occur unconscious **B) Reproducibility.** Increase in number of Principle Component Analysis (PCA) dimensions needed to account for 90% of trial-to-trial variance when stimuli were perceived vs. not **C) Neural Complexity.** Lempel-Ziv complexity corresponds to the size of a dictionary needed to account for all data in a lossless manner. This measure is proportional to the randomness in time-series data, and results here indicated that this measure could differentiate between perceptual states for unisensory conditions but not multisensory ones. Zero on the x-axis is time of stimuli onset; shaded areas/error bars are +/- 1 standard error or the mean.

Chapters 4 & 5: Can the study of multisensory awareness inform existent theories of consciousness?
(Adapted from Noel et al., Submitted, Neuron)

Given the findings from Chapter 3 indicating that results pertinent to multisensory perceptual awareness may not exactly mimic those of visual or auditory awareness, in Chapter 4 & 5 I asked whether to the contrary, multisensory contexts could be applied to inform existent (visually-derived) theories of consciousness.

Arguably the frontrunner theories of consciousness are Dehaene's Global Neuronal Workspace theory (GNW; Dehaene & Changeux, 2011) and Tononi's IIT (Tononi et al., 2016). As alluded to above, these theories possess their similarities – particularly in being "outside-in" theories of consciousness and ascribing a central (yet distinct) role to integration in consciousness. Nonetheless, they also possess their idiosyncrasies. In particular, the GNW posits that an external stimulus will evoke a conscious experience if its associated neural information is widely distributed across distinct brain areas and networks (i.e., integrated). Information becomes widely available throughout the neocortical mantle if the initial ascending sensory input crosses a minimum threshold and is subject to neural ignition – the non-linear transition whereby neural responses become all-or-none by engaging reverberant networks. On the other hand, the IIT is arguably more concerned with the structure of neural architectures, than with the neural dynamics occuring within them. Within the IIT framework, consciousness-level scales proportionally with the amount of integration information a particular network supports. That is, the larger the difference in information present in a network as a whole vs. in the subsystems of the network, the more conscious will that network be. Interestingly, the IIT is therefore a panpsychic theory of consciousness in that consciousness is graded and in principle a wide array of non-biological entities could possess a modicum of consciousness.

Given that the GNW and IIT disagree on whether consciousness is categorical or not, in Chapter 4 I attempted to inform the "all-or-none" (GNW) vs. graded (IIT) debate, by leveraging the process of multisensory integration. Fascinatingly, this debate has been halted by the difficulty in probing cases of partial consciousness. However, this issue becomes trivial under the multisensory context, where on occasions during audio-visual presentations participants will report the presence of solely the auditory or visual signal (Colavita et al., 1974). Hence, in a first step I developed neural networks that in light of the GNW should in principle support either no-consciousness, A-consciousness, V-consciousness, or AV-consciousness (given non-linear input-output functions and the presence of feedback connections establishing re-entrant network motifs). Surprisingly, modeling results suggested that even though the assemblage of the networks was in line with GNW, perceptual awareness and multisensory performance decoding from these networks suggested a linear relation between task performance and perceptual awareness. Comprehensive psychophysics (10 hours of testing in each of 29 subjects permitting collection of a representative sample of partial awareness trials) concurred with the modeling results. Consequently, the findings from Chapter 4 suggested a resolution between the GNW and IIT, where network behaving as describe in GNW may nonetheless support graded consciousness.

In Chapter 5 I continued to leverage the process of multisensory integration to arbitrate between the GNW and IIT. According to the IIT's "consciousness-meter" (phi), within a three node network, if two nodes (i.e., unisensory nodes) amalgamate on an integrative node, this network should support about 3 times as much consciousness than the same network amalgamating on a convergent node (i.e., a node that fires in response to input from either sensory modality, but that is not further driven by the simultaneous presence of both sensory stimuli; i.e., AND gate vs. XOR gate in the language of computer science and electrical engineering). Thus, to test this conjecture we recorded single-unit spiking activity in primary somatosensory area (S1) and ventral pre-motor (vPM) area of non-human primates, as these were presented with auditory (A), tactile (T), or audio-tactile (AT) stimuli, and were progressively anesthetized via propofol administration. If the IIT was correct, I reasoned that integrative neurons, as opposed to neurons that indiscriminately fire as a consequence of input regardless of sensory modality but do not integrate, should be most readily impacted during the loss of consciousness. As depicted in Figure 2A, evoked firing rates to sensory input (AT=purple; T=blue; A=red; none=black) in both S1 (top) and vPM (bottom) were reduced when animals were anesthetized (colored vs. grayscale). Interestingly, as predicted by the GNW it was particularly later components of the evoked response that were suppressed during unconsciousness. On the other hand, the prediction derived from the IIT was not supported in empirical data, as integrative neurons retained their category more frequently than convergent neurons, as animals loss consciousness (Figure 2B). Similarly, convergent neurons and not integrative neurons exhibited noise-correlation and neural complexity patterns that most faithfully tracked the primates' state of consciousness (not shown). Overall, this chapter represents the first neurophysiological test of the IIT, and results seemingly further support the GNW than the IIT.

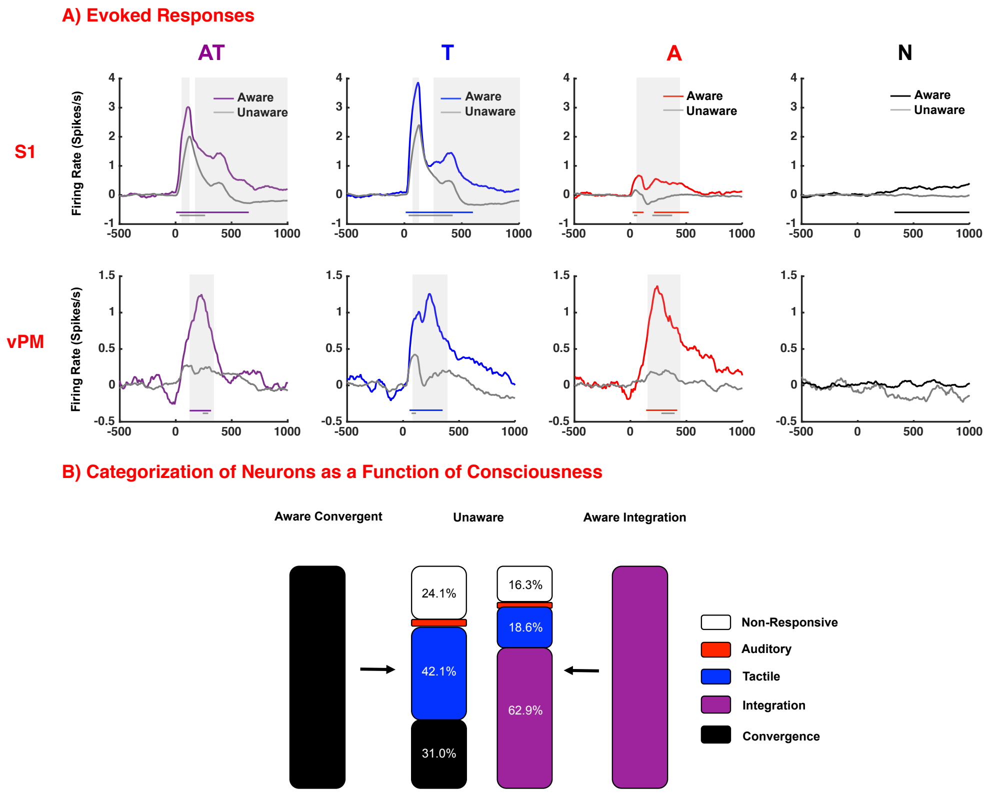

Figure 2. Testing the GNW and IIT in neurophysiology recordings in S1 and vPM. A) Firing Rates of S1 and vPM single-units as a function of sensory stimulation and consciousness state. S1 neurons respond to audio-tactile (purple) and tactile (blue) stimulation, but not during auditory stimulation (red) or during no stimulation (top). Contrarily, vPM neurons did respond to auditory stimulation. Overall firing rates are abated when monkeys are anesthetized, a finding that is particularly true for late responses. **B) Categorization of neurons as either integrative or convergent as a function of consciousness.** Contrarily to predictions that may be derived from IIT, convergent and not integrative neurons, seemed to be most readily impacted – loss their category - during the loss of consciousness.

SECTION II: CONSCIOUNESS FROM THE INSIDE-OUT

The second section of the dissertation was more hypotheses-driven than the first, and specifically aimed at testing Blanke's (Blanke, 2012; Blanke et al., 2015) prediction that body-related multisensory integration occurs within the peri-personal space (PPS) and that this integrative process scaffolds a sense of bodily self-consciousness. A first step in testing this hypothesis is to confirm that PPS responses are instances of true multisensory integration.

Chapter 6: Peri-personal space encoding is not only cross-modal, but truly multisensory

(Adapted from Bernasconi, Noel, et al., 2018, Cerebral Cortex)

While it is widely taken that bodily self-consciousness – the sense of owning one's body and being self located within it – is rooted in our long developmental history of spatio-temporally congruent tactile, visual, auditory, vestibular, and proprioceptive signals (e.g., Makin et al., 2008), surprisingly few studies have queried whether the nature of this cross-modal congruency is truly multisensory. Neurons encoding the PPS respond to tactile stimuli on the body and visual or auditory stimuli when these are presented near and not far from the body (Graziano et al., 1997). However, it is unclear whether this is a bimodal response, or truly a multisensory (integrative) one. The best indication that PPS neurons integrate sensory information is from Avillac et al., 2007, whom demonstrated that neurons in the ventral intra-parietal sulcus, an area known to possess PPS neurons, responded non-linearly to the co-presentation of visual and tactile signals. Nonetheless, it is unknown whether these authors were recording from PPS neurons. In Chapter 6, therefore, we recorded electrocorticography (i.e., intracranial EEG; ECOG) from 6 pharmacoresistant epileptic patients (~500 electrodes in total) as audio-tactile stimuli were administered. The auditory signals could be presented either near, at an intermediate position, or far from the participants. In a first step we labeled sensors that demonstrated multisensory integration (A+T ≠ AT; Figure 3; top row shows multisensory electrodes location and responses to audio, tactile, and audio-tactile stimulation; left panel on bottom row shows the contrast between the AT pair and A+T sum). Then, in a second step we asked whether PPS processing – the modulation of AT responses as a function of auditory distance – was most commonly observed in multisensory or non-multisensory sensors. Results demonstrated that the majority of multisensory sensors encoded for the PPS, while this was not true of sensors that were not multisensory. Further, the majority of PPS sensors showed a step-like function wherein they were driven by audio-tactile stimulation when the auditory component was presented either near or an intermediate distance, but not when it was presented far (see Figure 3 bottom right). That is, these sensors truly indexed a boundary between the peri- and extra-personal space.

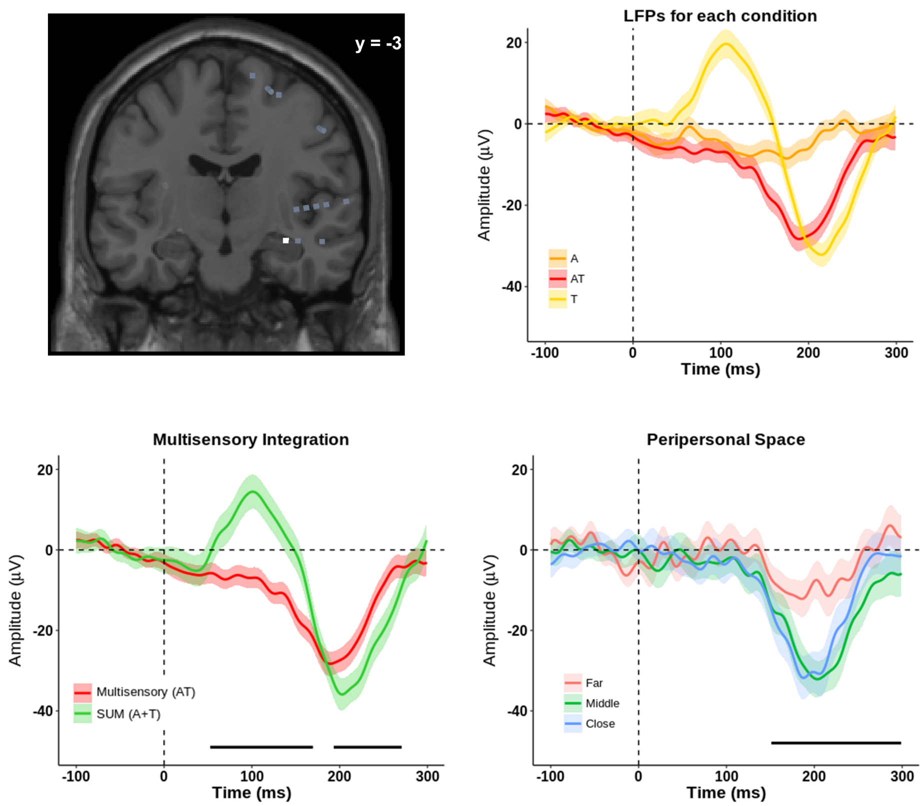

Figure 3. Multisensory Integration within the Peri-Personal Space. Top left; Location of sensors demonstrating multisensory integration. **Top right;** Temporal profile of sensory responses in electrode highlighted in white on top left panel (x-axis = 0 is stimuli onset). **Bottom left;** Comparison of paired multisensory response and audio + tactile sum at electrode highlighted in top panels. **Bottom right;** Multisensory responses as a function of auditory distance in the electrode highlighted in the rest of panels. Responses demonstrate a step-function where responses are strong to close and middle distances, but not far.

<u>Chapter 7 & 8: Peri-personal space pre-reflectively encodes the location of the bodily self</u>
(Respectively adapted from Noel et al., 2015, Cognition, & Salomon, Noel, et al., 2017, Cognition)

Having confirmed that PPS encoding was at least partially scaffolded on an integrative process, in Chapters 7 & 8 I employed virtual-reality aided psychophysics to test whether PPS maps the location of the physical body or the self. Indeed, Botvinick & Cohen (1998) demonstrated via the Rubber-Hand Illusion that while we may think that our sense of body ownership is immutable, via a simple visuo-tactile manipulation wherein touch is concurrently applied to one's hand and visual stroking is given to a fake hand, participants report the eerie sensation that the fake hand is their hand. Lenggenhager and colleagues (2007) and Ehrsson (2007) extended on this finding by demonstrating that it is not only hand ownership that may be manipulated via cleverly designed multisensory stimulation paradigms, but in fact whole body ownership and self-location may also be subject to experimental manipulation. In Chapter 7, therefore, we replicated Lenggenhager et al., 2007, full-body illusion by showing participants a virtual avatar of themselves as if placed 2 meters in front of where they were standing (Figure 4, top panel). During synchronous visuo-tactile stimulation participants reported felling ownership over the virtual body, and mapping of their PPS via an audio-tactile interaction task suggested that their PPS shifted as to delineate the location of the virtual avatar and not of their physical body (see Figure 4, bottom panel).

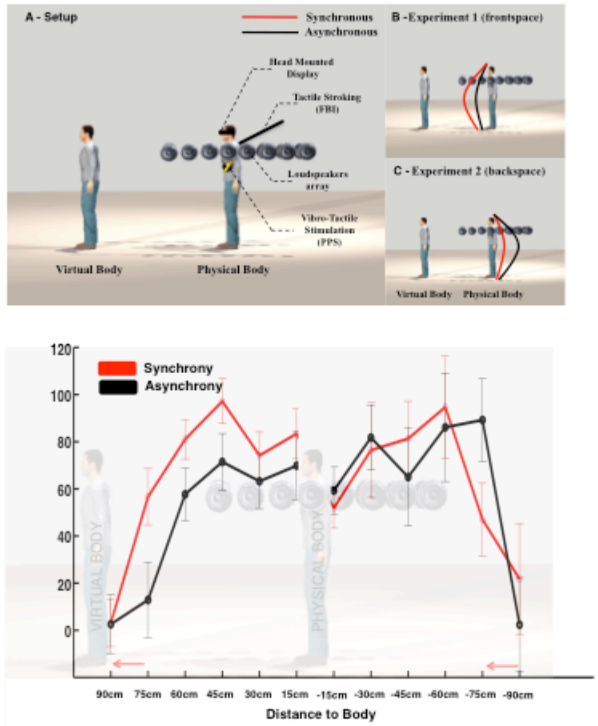

Figure 4. Audio-tactile mapping of PPS during the Full-Body Illusion. Top; Experimental setup and predictions. **Bottom;** Results demonstrating a shift in PPS during synchronous stroking toward the virtual avatar.

While Chapters 6 & 7 suggests that the PPS encoding relies on multisensory integration and maps the location of the self, and not necessarily the physical body, the philosophical argument behind the MPS approach to consciousness is that this bodily self-encoding must be pre-reflective (Legrand, 2006). Hence, in Chapter 8 we replicated the findings from Chapter 7, while novelty using a master-slave robot for visuo-tactile stroking, and masking either the stimuli used for PPS delineation or for induction of the full-body illusion (Lenggenhager et al., 2007). The usage of the robotic device allowed us to know precisely where tactile stimulation was applied onto participants and replicate this touch visually on a virtual avatar of the participant. The use of visual masking assured that in certain conditions participants could no see the location of visual stimulation on the body (which was nonetheless always presented and on occasions in synchrony with robotic touch, and on occasions out of synchrony with robotic touch). Findings suggested that even though participants could not determine whether visuo-tactile stroking was synchronous or asynchronous, under the former conditions they reported more ownership over the virtual body and their PPS enlarged as to include the virtual avatar. Therefore, seemingly unconscious multisensory interactions can shape bodily self-consciousness.

<u>Chapter 9: Using peri-personal space mapping in a clinical setting</u>

In the last experimental chapter of the dissertation I applied the basic-science findings form the rest of this section in the clinical domain. Unfortunately misdiagnoses in disorders of consciousness are prevalent, and it is believed that large portions of these errors are due to cognitive motor dissociations (Schiff, 2015). That is, clinical assessments of consciousness rely on overt behavior, and thus if patients have a motor impairment, they may nonetheless be diagnosed with a disorder of consciousness (DOC; e.g., vegetative state). In turn, researchers and clinicians have turned to neuro-technologies to assess consciousness. In Chapter 9 I follow this recent trend, by delineating PPS in DOC patients via EEG. The interest in delineating PPS is that this system straddles sensory and motor networks, and as argued above, may scaffold a primitive sense of self-awareness. Thus, if DOC patients map their PPS, it is likely they have a minimal form of consciousness and could potentially have residual access to their motor systems. In a first step I developed a "normative" EEG signal of PPS in healthy participants. Then, this PPS measure, as well as a clinical assessment and a secondary EEG measure of consciousness were probed in DOC patients. Results confirmed that according to quantitative EEG metric of consciousness (Casali et al., 2013), DOC patients were indeed impaired (Figure 5A). Further, and most importantly, the PPS measure correlated with quantitative assessments of consciousness (Figure 5B), suggesting that PPS mapping and consciousness-level co-vary.

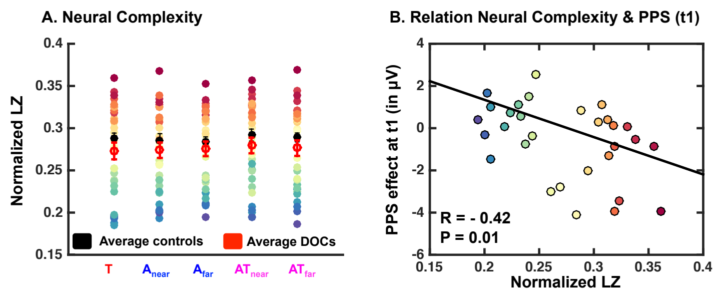

Figure 5. EEG marker of PPS processing in patients with disorders of consciousness (DOC). A; Normalized Lempel-Ziv Complexity (a quantitative measure of consciousness) is on average lower in DOC patients (red) than typical controls (black). However, the patient group shows a large inter-individual variance (colored dots). **B;** The more patients were considered to be conscious (larger values on x-axis), the clearer was their differentiation between extra- and peri-personal space (smaller values on y-axis).

Chapter 10: Discussion and conclusions

The study of perceptual awareness is one of the ultimate frontiers in contemporary neuroscience and a perennial topic within philosophy of mind. A host of neurobiological theories of consciousness exist, the vast majority of these originating from visual neurosciences/psychology and lying on a spectrum; from those posing the burden of explanation on the "outside-in" process of assembling sensory signals up the neuroaxis and ultimately leading to perception, to those arguing that perception is imposed from the "inside-out" onto the world given prior experience, bodily representations, and affordances. Interestingly, the majority of these theories speculate that information integration is central in engendering perception. In turn, in my dissertation I attempted to re-align the study of perceptual awareness with our subjective experience of the world as inherently multisensory, and to leverage the process of multisensory integration – where integration is a *de facto* process – in the study of consciousness. Further, the dissertation attempted to provide insights regarding perceptual awareness from a wide array of theoretical and philosophical stances, and by employing a panoply of cognitive science techniques – from neural network modeling and comprehensive psychophysics, to human (EEG/ECOG) and non-human primate electrophysiology (recordings from neurons), and finally virtual reality and clinical assessments. Results suggest that insights derived from visual neuroscience may not be straightforwardly applied to the multisensory case, and instead suggest that contrarily to hypotheses from prominent theories of consciousness, perceptual awareness is graded and most faithfully tracked in the firing pattern of convergent rather than integrative neurons. On the other hand, findings do support the claim that peri-personal space is (at least partially) scaffolded on the process of multisensory integration, and that this space pre-reflectively encodes the location of the self as opposed to that of the body. Finally, results suggest that the mapping of peri-personal space may be utilized in diagnosing disorders of consciousness. Taken together, this dissertation suggests that the process of multisensory integration may inform already existent, and potentially give rise to new theories of perceptual awareness. Further, it highlight that perceptual awareness is a dynamic process – both within the brain being supported by a reentrant circuit motif, and in the external milieu, with the world impacting neural processing and this latter one biasing environmental representations.

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