University of Padova

Department of Developmental Psychology and Socialization

PhD School in Psychological Sciences

XXXIV Series

Conscious processing of facial expressions and the contribute of somesthetic signals: Evidence from binocular rivalry dynamics

Thesis written with the financial contribution of University of Padova

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1 Abstract (English)

This work aims to give a theoretical contribution to embodied cognition theory and science of consciousness. Taken together, these two fields of research raise important questions regarding each field as well as their interaction.

Regarding the contribution to the embodied cognition theory, experiments using mimicry (Experiment 1 and Experiment 2), will test the model proposed by Wood and colleagues (2016). This model proposes that sensorimotor signals may feedback to visual areas and play a role in modulating the visual processing of emotional faces. The possible role of facial mimicry in conscious perception of emotional facial expressions is almost totally neglected. My findings confirm the importance of mimicry in conscious processing of facial expressions. So far, integration of information between sensorimotor (i.e., mimicry) and visual areas modulates experience of facial expressions.

Regarding science of consciousness, this work will explore the consciousness time-course mechanisms. A particular focus is given to the mechanisms related to the content of consciousness once such content is built up. Conscious experience modulation is observed in two different ways: the stabilization effect (Experiments 1 to 3), that is the duration of a content in consciousness, and the disformation effect (Experiments 4 and 5), that is the process of fading away of a content from consciousness. I propose these two effects need to be implemented in the

consciousness time-course proposed by Aru and Backmann (2017) as they describe the possible evolution of the conscious content (i.e., remain or leave consciousness).

2 Abstract (Italiano)

Questo lavoro si prefigge di dare un contributo teorico alla teoria della cognizione incarnata ed alla scienza della coscienza. Presi insieme, entrambi gli ambiti di ricerca sollevano importanti domande riguardanti non solo ciascuno di essi, ma la loro interazione.

Riguardo al contributo dato alla teoria della cognizione incarnata, gli esperimenti svolti usando la mimica facciale (Esperimento 1 ed Esperimento 2), testeranno il modello proposto da Wood e colleghi (2016). Questo modello propone che segnali sensorimotori possano fornire un feedback alle aree visive e giocare un ruolo nel modulare l’elaborazione visiva delle espressioni emotive del volto. Il possibile ruolo della mimica facciale nella percezione consapevole di espressioni facciali emotive è quasi totalmente trascurato. I miei risultati confermano l'importanza della mimica nell'elaborazione consapevole delle espressioni facciali. Da quanto finora noto, l'integrazione delle informazioni tra le aree sensorimotorie e le aree visive modula l'esperienza delle espressioni facciali.

In relazione alla scienza della coscienza, questo lavoro esplorerà i meccanismi temporali della coscienza. Un'attenzione particolare sarà data ai meccanismi relativi al contenuto della coscienza una volta che tale contenuto sia stato costruito. La modulazione dell'esperienza cosciente è osservata in due modi diversi: l'effetto di stabilizzazione (Esperimenti da 1 a 3), ovvero la durata del contenuto in consapevolezza, e l'effetto di disformazione (Esperimenti 4 e 5), ovvero la dissoluzione di un contenuto dalla consapevolezza. Propongo che questi due effetti

debbano essere implementati nel decorso temporale della coscienza proposto da Aru e Backmann (2017) in quanto descrivono la possibile evoluzione del contenuto consapevole (rimanere consapevole o abbandonare la consapevolezza).

3 Embodied cognition and emotion recognition

3.1 Simulation theory and emotion recognition

Recognizing others' emotions and affective states is one of the most extraordinary human abilities. In a purely evolutionary perspective, detecting and understanding − quickly and accurately − others' emotions, desires and intentions clearly offers adaptive advantages and promotes affiliation, mating and parenting. For a long time, psychological and neuroscientific research has explored the cognitive and neural bases of this ability (Carr et al., 2003; Caruana & Borghi, 2013; Gallese & Sinigaglia, 2011; Goldman & Vignemont, 2009; Niedenthal, 2007; Pitcher et al., 2008; Wicker et al., 2003). It is now consolidated evidence that the brain networks for facial expressions processing comprise several regions, cortical and subcortical, including the fusiform face area, the occipital face area, the superior temporal sulcus (regions of the core system of Haxby's distributed model of face processing; Gobbini et al., 2011; Grill-Spector et al., 2004; Haxby et al., 2000; Ishai et al., 2005; Lee et al., 2010; Rotshtein et al., 2005; Winston et al., 2004; Yovel & Kanwisher, 2004) the insula, the amygdala, the inferior frontal gyrus (Fox et al., 2009; Furl et al., 2013, 2015; Harris et al., 2014; Johnston et al., 2013; Trautmann et al., 2009), and several other not strictly face-sensitive regions (Liang et al., 2018).

In this context, motor (or sensorimotor) simulation models propose that the observer's subthreshold motor simulation of the observed facial expression facilitates recognition and understanding of others' congruent facial expression[1] (Bastiaansen et al., 2009; Goldman & Sripada, 2005; Likowski et al., 2012). This theoretical view is supported by a substantial body of evidence. On one side it has been highlighted how brain regions supporting motor and somatosensory representations of facial expressions are involved in recognition of emotions in others (Wood, Rychlowska, et al., 2016), such that, for instance, lesions of these regions are associated with emotion recognition deficits (Adolphs et al., 2000; Sprengelmeyer et al., 1999) and, similarly, repetitive transcranial magnetic stimulation disrupting the right somatosensory (Pitcher et al., 2008; Pourtois et al., 2004) and the right primary motor (Korb et al., 2015) cortices impairs some aspect of emotional face processing; on the other side there is evidence that muscular facial feedback incongruent with the observed expression causes a decrease in emotion recognition accuracy (Borgomaneri et al., 2020; Hyniewska & Sato, 2015; Ipser & Cook, 2015; Neal & Chartrand, 2011; Oberman et al., 2007; Ponari et al., 2012; Stel & Knippenberg, 2008; Wood, Rychlowska, et al., 2016), (but also see Bourgeois & Hess, 2008; Hess, 2021; Hess & Fischer, 2013, 2014). The rationale behind this last series of studies is that, if facial mimicry − which can be measured by electromyography (Achaibou et al., 2008; Dimberg & Petterson, 2000) − is a manifestation of sensorimotor simulation triggered by the observation of others' facial expressions, then an experimental manipulation aimed at interfering with it should consequently interfere with the simulation process itself and thus affecting the processing of facial expressions. For example, Ponari and colleagues (Experiment 1; Ponari et al., 2012) required participants to identify the emotion (among the basic six categories) expressed by the faces presented one at a time while the production of their facial mimic patterns was manipulated through a Chinese chopstick (which participants had to keep horizontally between the teeth to prevent the movements of the lower portion of the face) or through two stickers near the inner portion of the eyebrows (which participants had to actively try to bring near

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[1] Facial feedback hypothesis must not be confused with simulation theory. Importantly, the feedback during the simulation process is triggered by a mirror mechanism. Such distinction, for example, should explain the failure in the Strack's replication (Wagenmakers et al., 2016) since the basic paradigm and its variations do not hinge on a simulation process.

through an active contraction of the frontal muscles). The results highlighted an impairment of the accuracy in the identification task as a function of the type of facial mimicry manipulation, i.e. that involving the muscles of the lower portion of the participants' faces was associated with an impairment in the processing of happiness, disgust and fear, while that involving the muscles of the upper portion of the face was associated with an impairment of the processing of anger and fear.

While the behavioral evidence is accumulating to support the role of sensorimotor activity and facial mimicry in facilitating the recognition of others' congruent emotional expressions, it remains unclear at what level of the visual processing of emotional faces the sensorimotor activity might exert its influence (Lomoriello et al., 2021; Sessa et al., 2018). In this regard, a recent sensorimotor simulation model has proposed that sensorimotor signals may feedback to visual areas early modulating the visual processing of emotional faces (Wood, Lupyan, et al., 2016; Wood, Rychlowska, et al., 2016; see figure 1).

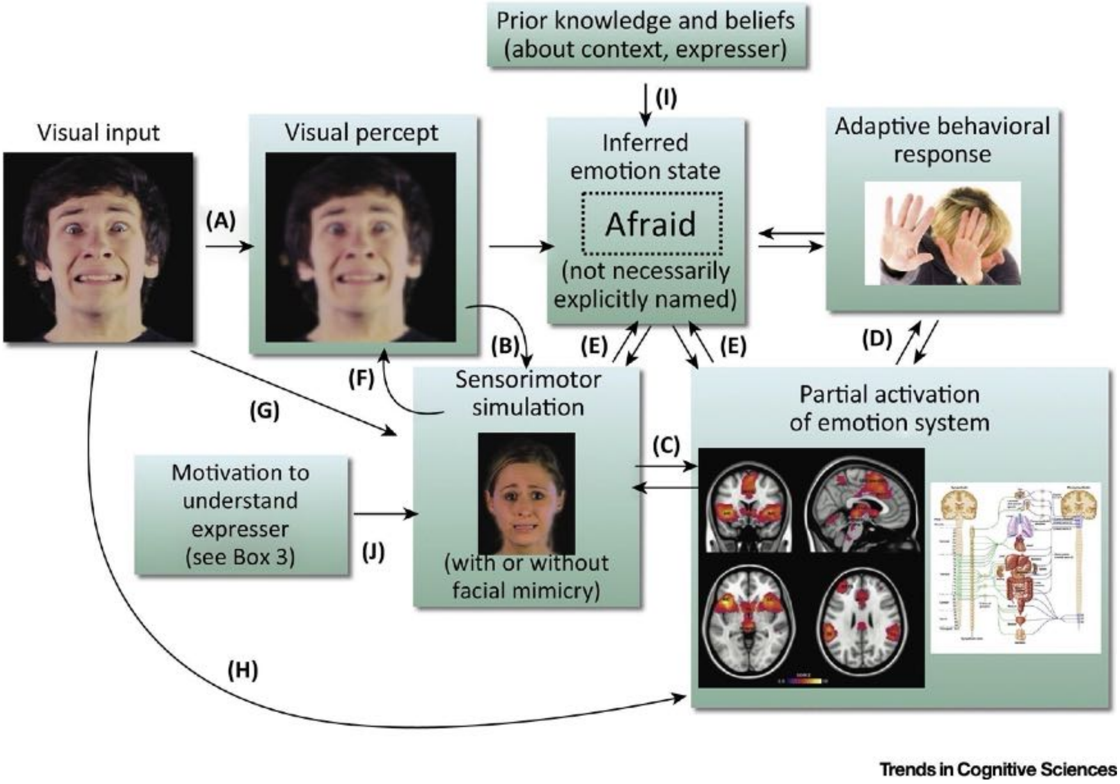

Figure 1. Reprinted from TRENDS in Cognitive Sciences, 20/3, Wood, A., Rychlowska, M., Korb, S., & Niedenthal, P., Fashioning the face: sensorimotor simulation contributes to facial expression recognition, 227-240, Copyright (2016), with permission from Elsevier: Simulation and the Recognition of Facial Expression. (A) The female perceiver observes the fearful face of a male expresser. (B) The percept activates the face region of the sensorimotor cortices, and other motor control areas, which may result in facial mimicry. (C) The somatosensory, motor, and premotor cortical activity generates activity in other regions of the brain involved in fear states [26] resulting in either overt cognitive, behavioral, and physiological changes (D) or simulation of those states. (E) This partial activation of the fear state allows the perceiver to explicitly or implicitly recognize the emotion of the expresser. (F) Recent evidence [12] suggests that sensorimotor simulation recursively modulates the clarity of the visual percept. (G) Simulation and (H) emotional responding to a perceived facial expression do not require conscious awareness [5]. (I) Conceptual emotion knowledge contributes to the inferred emotion state [121], while affiliation with and motivation to understand the expresser (J) modulate the likelihood that sensorimotor simulation and facial mimicry will occur (Box 3). While box and arrow diagrams of this sort seem to imply neural modularity and a specific sequence of events, we emphasize the distributed and recursive nature of the emotion perception process, which iteratively recruits visual, somatosensory, motor, and premotor cortices, as well as, subcortically, parts of the limbic system and brainstem (fMRI image from [122]).

3.2 Mimicry and consciousness

Notably, in these theoretical and empirical frameworks an aspect that has been almost totally neglected is that concerning the possible role of facial mimicry in conscious perception of emotional facial expressions. The present Thesis, and especially Experiment 1 and Experiment 2, aimed at investigating precisely this aspect of facial mimicry/sensorimotor simulation using binocular rivalry (BR), a paradigm widely used in the studies of visual conscious perception and its neural correlates (Alais & Blake, 2005; Blake & Logothetis, 2002; Maier et al., 2012; Tong et al., 2006).

Previous research has used the BR paradigm to study conscious perception of emotional stimuli, but rarely distinguished the three components of the BR (as I will describe later). For example, some focused on how emotional faces predominate over neutral faces in BR (Alpers & Gerdes, 2007; Anderson et al., 2011; Bannerman et al., 2008; Yoon et al., 2009). Yoon and colleagues (Yoon et al., 2009), expanding on the research by Alpers and Gerdes (Alpers & Gerdes, 2007), demonstrated that emotional faces, regardless of their valence, predominate over neutral faces, although the effect was particularly strong (89% increase in dominance) for positive facial expressions (i.e., happy) which predominated also over negative facial expressions (i.e., disgusted). Unfortunately, the authors did not report the other two measures and the data are not openly available for further research.

Crucially, it is unknown if the observer's facial mimicry can influence conscious perception of facial expressions in the BR paradigm. I propose that there can be at least two possible ways, which are not mutually exclusive, to affect the BR. First, facial mimicry can influence the initial ambiguity resolution. Second, facial mimicry may stabilize such representations once they are the current content of consciousness. I aimed at investigating precisely this aspect of facial mimicry using BR under facial mimicry manipulation with a neutral and an emotional (i.e., happy) expression of the same identity in rivalry. Firstly, I tested the impact of facial mimicry manipulation on both ambiguity resolution (i.e., initial percept and onset resolution time) and stabilization of conscious contents (i.e., cumulative time), secondly, I tested the impact of positive emotion on the time-course of consciousness (i.e., including two main phases: forming the content and disforming the content, see (Aru & Bachmann, 2017)).

With regard to mimicry manipulation, only one previous study (Korb et al., 2017) investigated the impact of the integration of proprioceptive information from the face on visual awareness of facial expression of emotions using a variant of CFS, called breaking continuous flash suppression (b-CFS; Jiang et al., 2006; Stein et al., 2011; Tsuchiya & Koch, 2005). In the b-CFS paradigm, a mask with a high contrast dynamic pattern is presented to one eye, thereby effectively suppressing a stimulus of increasing intensity presented to the other eye. After a certain interval of time, the ocular dominance is reversed, and the previous suppressed stimulus becomes visible. Thus, this paradigm measures the time for a stimulus to access consciousness. In a series of 3 experiments, Korb and colleagues manipulated participants' facial mimicry using a b-CFS paradigm by requiring them to voluntarily take facial expressions of frown vs. smile vs. relaxed (Experiments 1 and 2) or by measuring spontaneous electromyographic activity (Experiment 3). Overall, the results did not support the hypothesis of a modulation of visual consciousness on the basis of the integration of the proprioceptive activity of the face in conditions of congruence and incongruence with the observed emotion. That is, the time to break suppression did not differ between conditions. This suggests that facial mimicry does not influence the access to consciousness of emotional facial expressions. To note, b-CFS cannot inform on the potential role of facial mimicry in stabilizing conscious representations of facial expressions.

With regard to the time-course, only one previous study has investigated the relationship between electrophysiological brain activity and visual awareness when content is fading from consciousness (Pun et al., 2012). The authors recorded the neural activity (EEG) while a bilateral shape-from-motion (SFM) was displayed to the participant. Participants visually experienced a dolphin that was separated from a noisy background until SFM was in motion, otherwise, the experience of seeing the dolphin faded gradually from consciousness. A specific neural activity, namely the contralateral delay activity (CDA; also called sustained posterior contralateral negativity, SPCN; Luria et al., 2009; Meconi et al., 2014; Sessa et al., 2011, 2012; Sessa & Dalmaso, 2015; Vogel et al., 2005; Vogel & Machizawa, 2004), was associated with sustained awareness, suggesting that this activity is involved in the maintenance of conscious content.

3.3 Mimicry and facial palsy

A challenging practice to test the involvement of sensorimotor simulation in conscious perception of facial expressions in the BR paradigm is to compare patient population to healthy individuals. Facial palsy that impairs mimicry is present in multiple pathologies. Acquisition of the palsy, consequently impacts sensorimotor simulation, but not necessarily the sensorimotor representation of emotions. In Bell's palsy, which is a temporary disease, sensorimotor representations are preserved but the palsy itself has an impact on facial sensorimotor feedback. In Moebius syndrome disease, the palsy is a congenital neurological disorder in which facial sensorimotor simulation is compromised due to affection of cranial nerves VI and VII (Briegel, 2006). In other words, Moebius individuals must develop from birth an alternative system for the perception of facial expressions. Moebius syndrome remains a rare disorder (one estimate places the incidence at 1 case per 50,000 live births in the United States).

Unfortunately, Moebius syndrome is also characterized by the impairment of ocular abduction (due to the VI nerve compromission). This characteristic requires an adaptation of the binocular rivalry setting (see Appendix).

4 Consciousness

4.1 Definition of consciousness

Consciousness is a complex concept; there are many definitions of what consciousness should be. Some researchers propose it is an artificial artifact, some not, and others believe it pervades everything (Cabanac et al., 2009; Dennett & Hofstadter, 1982; Searle, 1990). Consciousness is sometimes considered as a state, sometimes as an experience and also as a content (Koch & Tsuchiya, 2007; Steven Laureys, 2005; Tononi, 2004). Up to date, there is no consensus or specialized vocabulary. That is why I need to clarify my position about the phenomena to avoid any confusion. Consciousness is not only a philosophical concept. Neuroscience also tries to give a theoretical description of the brain processes that are involved in consciousness. As we will see, such descriptions or models can be either mathematical, logical, or conceptual. The debate about consciousness is often split into two areas, the "hard problem" and the "easy problem".

The former was proposed by the philosopher David Chalmers in these terms (Chalmers, 2001):

> *. . .even when we have explained the performance of all the cognitive and behavioral functions in the vicinity of experience—perceptual discrimination, categorization, internal access, verbal report—there may still remain a further unanswered question: Why is the performance of these functions accompanied by experience?*

In this approach, the question “Why” brain processes sometimes produce experience cannot be resolved in theory. That is the reason why the problem is hard and uncomfortable. A second important aspect in Chalmers formulation is “experience”. Regarding the hard problem, the term experience is problematic for science investigation of consciousness, as it is impossible to observe the conscious experience of others. The philosopher Thomas Nagel exposed this problem using the well known "What is it like to be a bat?" question (Nagel, 1974). Nagel affirmed that we have no idea of others’ subjective experiences and even more if the neural structure is different (i.e., human vs bat), because such experience is essentially connected with a single, unique, and personal point of view.

If the hard problem is clearly problematic to overcome, the debate and the research are quite active since it is possible to tackle the “easy problem” of consciousness I mentioned before. The "easy problem" approach tends to explain the physical underpinnings that give the ability to be conscious. Here, the existence of consciousness is assumed and research by inductive process tends to find its neural correlates. If X system is conscious, X processes raised X consciousness. The question will not be “why these X processes are accompanied by X phenomenal experience” but “how X phenomenal experience is formed”, for example, how information used in emotion recognition are integrated to form “X” phenomenal consciousness.

The philosopher Ned Block (Block, 1995) draws our attention to an important distinction between phenomenal-consciousness (P-consciousness) and access-consciousness (A-consciousness). P-consciousness content is phenomenal and A-consciousness content is representational. P-consciousness is, in some way, a concept near to the “it is like " to be in that state (Nagel, 1974). For example, what it is like to see “something” differs by using the left or the right eye. According to Ned Block, a person seeing a blue square has P-consciousness of the blueness and squareness, but A-consciousness of a blue square. The conscious experience can have both P-consciousness and A-consciousness by its phenomenal feeling and by its representational properties, respectively. A-consciousness is the phenomenon where information gets into a functional position to be noticed, reasoned about, reported by a subject (Block, 1995). It is important to note that “access to another consciousness” requires that this “other” reports its own conscious experience, which is possible only if he has A-consciousness.

4.2 Content vs state of consciousness

A well-studied concept that could help understanding consciousness by analogy is the experience of emotion. Having the experience to be happy consists of an emotional state (functional aspects, including physical and mental responses) as well as a feeling (the conscious experience of being happy). The distinction between state and feeling is in some way similar to the concepts of state and content of consciousness. The state refers to the level of consciousness (e.g., coma, vegetative state, and wakefulness) and the content refers to the P or A-consciousness (what we are conscious of). Let's look more deeply into this decomposition regarding consciousness. The two main components of consciousness are well described by Laureys (Steven Laureys, 2005): the term “wakefulness” indicates the state scale from coma to wakefulness, and the term “awareness” is used to describe the level or quality of the content (see figure 2):

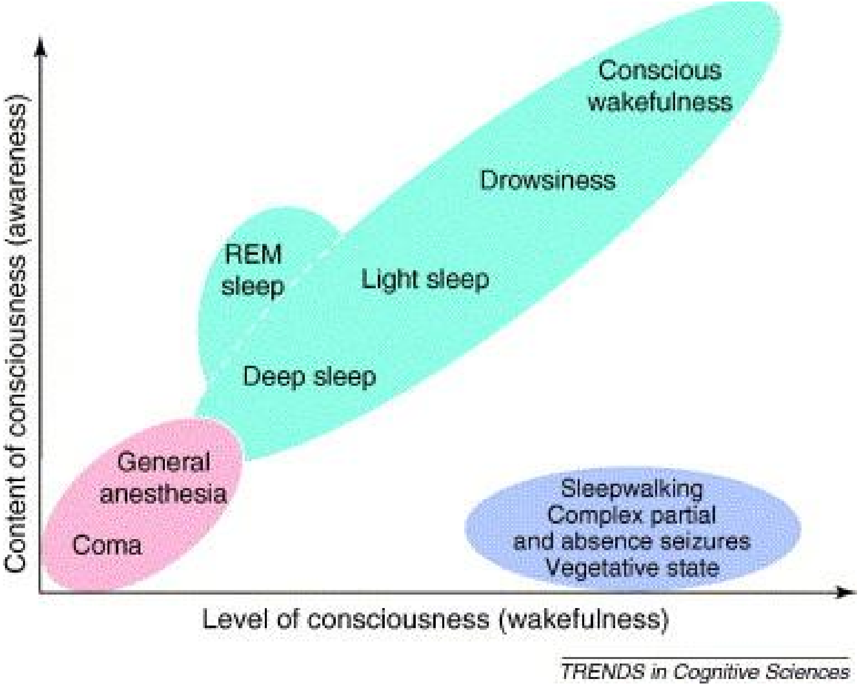

Figure 2. Reprinted from TRENDS in Cognitive Sciences, 9 /12, Laureys, S., The neural correlate of (un) awareness: lessons from the vegetative state, 556-559, Copyright (2005), with permission from Elsevier: Oversimplified illustration of the two major components of consciousness: the level of consciousness (i.e. wakefulness or arousal) and the content of consciousness (i.e. awareness or experience). In normal physiological states (bluegreen) level and content are positively correlated (with the exception of dream activity during REM-sleep). Patients in pathological or pharmacological coma (that is, general anesthesia) are unconscious because they cannot be awakened (red). Dissociated states of consciousness (i.e. patients being seemingly awake but lacking any behavioral evidence of 'voluntary' or 'willed' behavior), such as the vegetative state or much more transient equivalents such as absence and complex partial seizures and sleepwalking (purple), offer a unique opportunity to study the neural correlates of awareness.

For example, a state that is characterized by the presence of wakefulness and absence of awareness is the vegetative state. Four combinations of awareness and wakefulness are possible: aware and awake (let say "full conscious"), aware and non awake (REM sleep, some coma state), not aware but awake (vegetative state, seizures, sleepwalking; Bassetti et al., 2000; S. Laureys et al., 1999; Salek-Haddadi et al., 2003) and not aware and not awake (some coma state and death).

If consciousness can be characterized on two scales (wakefulness, awareness), it is still unclear whether the level of neural activation accounts for the level of awareness (Steven Laureys, 2005). Compared to the conscious resting state in healthy participants, metabolic dysfunction has been shown in vegetative state patients (S. Laureys et al., 1999) and identified in the frontoparietal network (left and right, lateral and medial frontal regions, parieto-temporal and posterior parietal also bilaterally, posterior cingulate, precuneal cortices and thalami; S. Laureys et al., 1999; S Laureys et al., 2000). Excluding thalami, this frontoparietal network is known to be active in resting state (Gusnard & Raichle, 2001). The importance of the network will be covered also in the “Models of consciousness” section (p. 14). In the work presented in this Thesis, I focused on awake participants and manipulated their awareness. The expressions “to be conscious” and “to be aware” are used here as synonyms.

4.3 Consciousness and Attention

In introducing the concept of consciousness, the relationship between consciousness and attention deserves a special consideration. As we will see, attention and consciousness are distinct functions (Koch & Tsuchiya, 2007) that optimize information management. Researchers based at the University of Pennsylvania in Philadelphia, US, registered the speed of sight of a guinea pig retina. Interestingly, the guinea pig optic nerve transfers data at approximately 875 kilobit per second (K. Koch et al., 2006). Considering that Human retina has 10 times more cells than the guinea pig, I can estimate a data transfer of 8.75 megabit per second (Mbps). Streaming a video from the internet requires in general 3 Mbps in order to compare to the huge human optic nerve bandwidth. Dealing with this amount of data would put the brain at risk in terms of energy requirement. It is known that the human brain accounts for only 2% of the total body mass, but that it requires 20% of the metabolism consumption. If neural pathways consume a lot of energy, and this consumption increases at high speed, the question is why the brain has to spend a lot of energy without optimizing the information selection, for example keeping relevant information and excluding useless information. To resolve the energy part of the problem, natural adjustment splitted the ganglion cells of the retina into two general categories: fast cells that fire at high frequencies, increasing energy cost (Attwell & Laughlin, 2001; Lennie, 2003), and slow cells, allowing different rates of information transfers. Slow cells are more numerous than fast cells and do not lose in encoding quality. According to Koch, the fast cells contribute only for 6% of the transferred information. In this neural architecture, slow cells save energy, with respect to a full fast cell architecture. But what about the information saliency? Does the brain have to manage with all information from sensory input and so forth?

Selecting the most salient part of the signal, in real time, may help avoid overloading the brain capacity. In this view, attention "filters" relevant information, while the non-relevant information remains neglected. By attention I am precisely speaking about the top down attention that is driven by endogenous factors in opposition to bottom-up attention where attention is transiently attracted by exogenous cues. In this view, attention, by top down processes, selects part of the possible signals. For example, spatial or focal attention will focus on a spatially restricted region (left, right), feature-based will focus on a particular feature (color, shape), then the selected information is available for further processing.

Now that pieces of information are selected, the consciousness function in this framework will be to summarize all pieces from multiple modules (i.e., sensory, memory, etc…) and make this summarized information available for further treatment, like planning, error detection, action control, and so forth. This integrative aspect is emphasized by the Integrated Information Theory of consciousness (Tononi, 2004, 2008; Tononi et al., 2016) and will be presented later.

From this point of view, I can consider attention as an analyser and consciousness as a synthesiser. Insofar as I admit that attention and consciousness have different functions, I must accept that they cannot be the same process. Importantly, for Posner attention is consciousness (Posner, 1994), but recent debate seems to focus on the kind of dissociation between the two. One position affirms a single dissociation between attention and consciousness in which attention is independent of consciousness but not the opposite (Cohen et al., 2012), while another position proposes a double dissociation (Koch & Tsuchiya, 2007; Tsuchiya & Koch, 2016).

4.4 Multiple models of consciousness

As I showed before, consciousness science is hard, even insolvable. Looking at the phenomenon of consciousness in the light of the brain functioning, the most widely accepted line of thought is that it is based on a dynamic, generalised and integrated activity between brain areas. From a theoretical point of view, models of consciousness try to relies the brain properties of consciousness (e.g., widespread brain activation, NCCs: neural correlates of consciousness, DMCs: difference markers of consciousness, connectivity) to the phenomenal properties of consciousness (e.g., P-consciousness, A-consciousness, qualia, experience). One of my principal interests, as I just covered before, is the integrative function of consciousness. In considering consciousness as a function that summarizes information for availability, the importance of the integration is currently shared by two robust theories, namely the 'Global Neuronal Workspace Theory' (GNWT; Dehaene, Kerszberg, et al., 1998; Dehaene et al., 2003; Mashour et al., 2020) and the Integrated Information Theory (IIT; Oizumi et al., 2014; Tononi, 2004; Tononi et al., 2016). A third useful theory, the "Recurrent Processing Theory" (RPT; Lamme, 2010) is focused on feedback activity and brain connectivity. In RPT, the kind of connectivity is used to explain the difference between the P and A-consciousness.

4.4.1 Global neuronal workspace theory

According to Stanislas Dehaene, consciousness arises when the selected information accesses a “global workspace” (i.e., brain network), where it can be transmitted to task-specific modules (Dehaene et al., 2003; Dehaene & Changeux, 2011). This workspace imposes a kind of information processing based on a distributed network in the fronto-parietal cortex. In this view, consciousness is created by the workspace itself in selecting information based on its saliency. A particular focus is given to the working memory mechanisms during stimulus processing. According to the authors, incoming sensory information is processed non-consciously[2] by a large number of competitive peripheral and parallel processors. Access to the conscious dimension is determined by a shift from processing by single nodes (independent from each other) to processing involving a global workspace (dependent on each other). When a non-linear and ‘all-or-none’ transition occurs (i.e. ignition), one of the stimuli gains access to a group of distributed neurons of the global workspace. This results in perceptual information globally broadcasted ensuing in its consciousness. Within the global workspace only one representation can be analysed and made conscious at a time, so, for instance, only part of a scene becomes conscious (see figure 3).

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[2] According to Tsuchiya and Adolphs’s nomenclature (box 2; Tsuchiya & Adolphs, 2007). The term non-conscious will be used as a synonym of unaware. The term “Unconscious” will never be used in Freudian acceptance. Except for the original didascalies, the term “Unconscious” will be used to describe the absence of the state of consciousness.

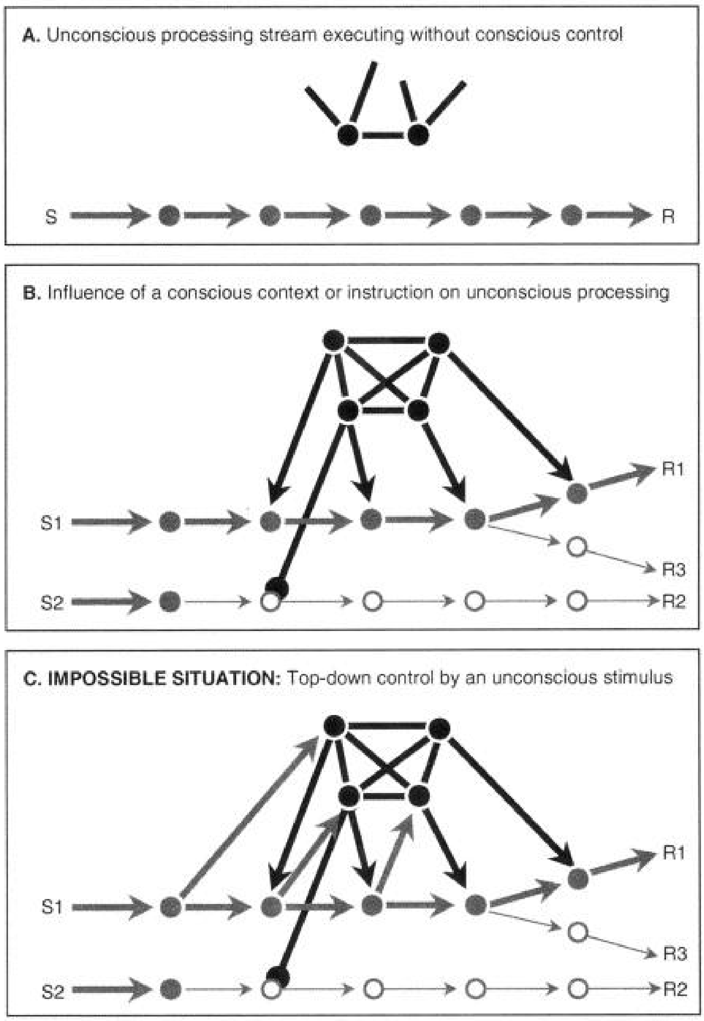

Figure 3. Reprinted from Cognition, 79/1-2, Dehaene, S., & Naccache, L. , Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework, 1-37, Copyright (2001), with permission from Elsevier: Which tasks may or may not proceed unconsciously? In these schemas, the gray lines represent the propagation of neural activation associated with the unconscious processing of some information, and the black lines the activation elicited by the presently active conscious workspace neurons. The workspace model predicts that one or several automated stimulus±response chains can be executed unconsciously while the workspace is occupied elsewhere (A). Even tasks that require stimulus and processor selection may be executed unconsciously once the appropriate circuit has been set up by a conscious instruction or context (B). However, it should be impossible for an unconscious stimulus to modify processing on a trial-by-trial basis through top-down control (C). A stimulus that contacts the workspace for a duration sufficient to alter top-down control should always be globally reportable.

It is important to note that in the GNWT there is no P-consciousness. Authors assume three levels of accessibility. Level 1: some information encoded is permanently inaccessible; Level 2: some information communicates with the workspace; Level 3: at any given time, only a subset of information in Level 2 is mobilized into the workspace (Dehaene & Naccache, 2001). In order to access consciousness the workspace needs multiple categories of neural systems, such as: perceptual modules that provide information about the environment; motor circuits that interface with the environment; long-term memory systems that track all previous workspace states; attentional systems that select information, and so forth. According to the authors, the subjective feeling that consciousness is unitary is a consequence of the general connection of such systems.

In GNWT, consciousness is required for specific mental operations that provide benefits to the subject that is conscious. Essentially, having consciousness allows; 1) to keep information on-stream even if the stimulus is not anymore physically present. This task that requires working memory is coherent with the global workspace network and also associated with dorsolateral prefrontal regions (Goldman, Rakic, 2013); 2) to unify and coordinate multiple operations in order to create appropriate tasks. In general, automated or non-conscious processing are not associated with the feeling of mental effort, that is why the authors propose to use this experience of "effort" as a marker of conscious processing (Dehaene, Kerszberg, et al., 1998); 3) to initiate intentional behavior. Examples are given by Blindsight patients. These patients are clinically blind due to occipital brain lesions, but are able to extract visual information from their environment without any conscious experience (Gelder et al., 2008; Humphrey, 1974; Pöppel et al., 1973). However, they never spontaneously initiate action based on the visual information they extracted (Block, 1995). It is important to conclude that all these specific mental operations require a system that summarizes information for availability, i.e. consciousness.

4.4.2 Integrated information theory

Tononi argues that we should understand consciousness as the integration of information (Tononi, 2004, 2008; Tononi et al., 2016). IIT begins with the postulate that consciousness exists: “To be conscious is to have an experience” and translates the essential phenomenological properties of experience to identify a physical substrate of consciousness (PSC). PSC will be the state of the brain in terms of anatomical and functional networks from which a specific conscious experience arises. Consciousness is evaluated from a qualitative and quantitative point of view within a mathematical framework (Oizumi et al., 2014; Tononi, 2004). IIT is based on Phi (Φ), which measures the amount of information that is integrated. Φ is associated with a PSC, consequently both Φ and PSC change each time the conscious experience changes. The main step of the process is the selection of information, that is the structured extraction of experience features. At this point, pieces of information are not summarized, and require a next step that is the integration. For example seeing a red triangle is the integration of a triangle and red color, and it is impossible to see a triangle but not a red color or a red patch but no triangle. A direct consequence of the integration is the segregation or exclusion of part of the information, each experience excludes all others. The experience or content of consciousness has a border and is unique also in terms of PSC (see figure 4). Tononi used the metaphor of a digital camera. Such an example is often reused as it explains the theory clearly. Each pixel of the photo camera carries a bit of information, and so the camera can enter different states proportional to the number of the pixels. As the camera is divided into individual pixels that work independently it is considered non conscious. The thalamocortical system, just like the camera, runs different modules, but these elements are highly interconnected. According to the authors, integrated information and consciousness are based on this interconnection. Either, too low connectivity or too high connectivity will produce lower Φ because of the lack of shared information or because the elements that constitute the network lose specificity, respectively. Consequently, measures of Φ based on connectivity can explain why the thalamocortical network has the capacity to generate high levels of Φ, while other brain structures, such as the cerebellum or basal ganglia, do not (Tononi, 2004). It also explains why the high and unspecific connectivity in sleep or epileptic seizures can be associated with non-consciousness (Alkire et al., 2008; Tononi & Massimini, 2008).

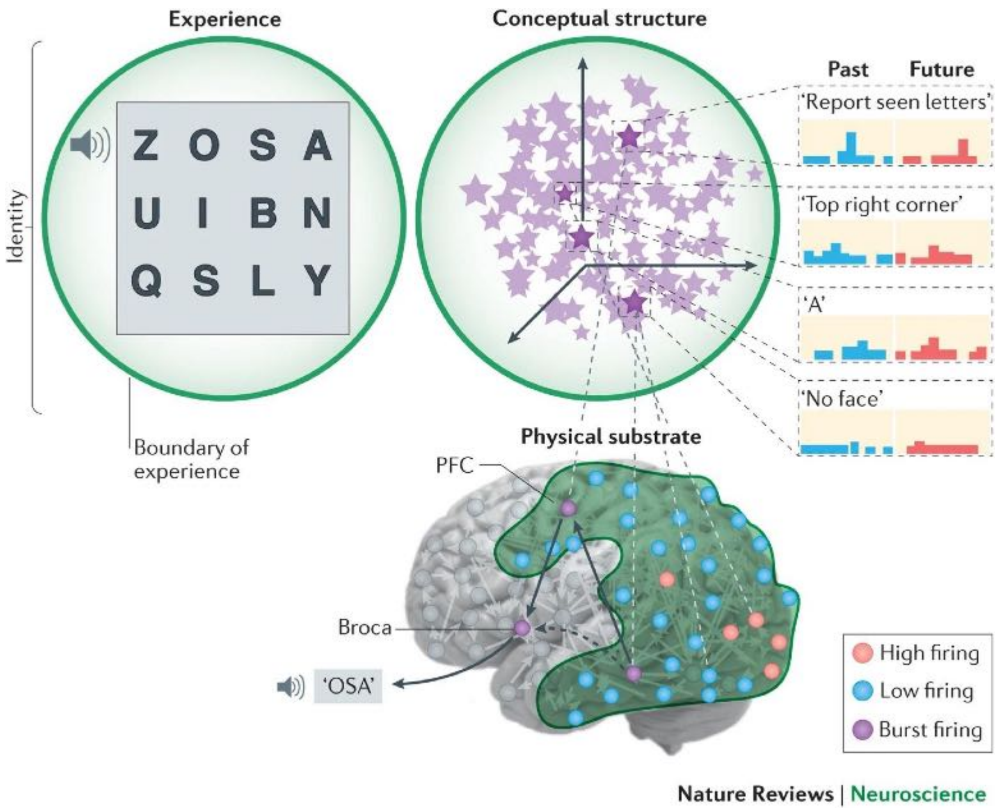

Figure 4. Reprinted from Nature Reviews Neuroscience, 17/7, Tononi, G., Boly, M., Massimini, M., & Koch, C., Integrated information theory: from consciousness to its physical substrate, 450-461, Copyright (2016), with permission from Nature Publishing Group: The content of an experience is much larger than what can be reported by a subject at any point in time. The left-hand panel illustrates the Sperling task, which involves the brief presentation of a three by four array of letters on a screen, and a particular row being cued by a tone. Out of the 12 letters shown on the display, participants correctly report only three or four letters — the letters cued by the tone — reflecting limited access. The top middle panel illustrates a highly simplified conceptual structure that corresponds to seeing the Sperling display, using the same conventions as outlined in Fig. 1. The myriad of positive and negative, first- and high-order, low- and high invariance concepts (represented by stars) that specify the content of this particular experience (seeing the Sperling display and having to report which letters were seen) make it what it is and different from countless other experiences (rich phenomenal content). The bottom panel schematically illustrates the physical substrate of consciousness (PSC) that might correspond to this particular conceptual structure (its boundary is represented by a green line). The PSC consists of neuronal groups that can be in a low firing state, a high firing state or a bursting state. Alone and in combination, these neuronal groups specify all the concepts that compose the conceptual structure. Stars that are linked to the PSC by grey dashed lines represent a small subset of these concepts. The PSC is synaptically connected to neurons in Broca's area by means of a limited capacity channel (dashed black arrow) that is dynamically gated by top-down connections (shown as solid black arrows) originating in the prefrontal cortex to carry out the instruction (that is, to report the observed letters 'OSA').

One of the principal advantages of the IIT, is the quantification of consciousness related to a PSC. Measuring the quantity of information in a signal is possible since information theory was founded by the mathematician Claude Shannon in 1948. Information theory measure is based on an entropy function that quantifies the amount of uncertainty involved in the signal of a random variable. As information entropy measure is exclusively sensitive to the uncertainty of the signal, it should be impossible for such a measure to discriminate if the information is integrated or not. Here, IIT differs from information entropy as the Φ measure considers the integration of the information. Nevertheless, implementation of the Φ measure in ecological context remains a challenge.

4.4.3 Recurrent processing theory

Lamme's theory focuses on the visual areas and consequently visual awareness (Lamme & Roelfsema, 2000). In RPT, Lamme proposes a distinction between non-conscious and conscious functions. Non-conscious functions are supported by feedforward processes while conscious functions are mediated by recurrent cortico-cortical connections (Lamme, 2010). Examples of non-conscious functions are information selection, feature extraction and categorizations.

Such neural processing is distinguished in four different but gradual stages characterized by feedforward or recurrent processing (see figure 6). Processing remains at the feedforward level or becomes recurrent on the basis of two variables, that are 1) the level of attention to the stimulus (attended vs unattended) and 2) the visibility of the stimulus (masked vs unmasked see figure 5).

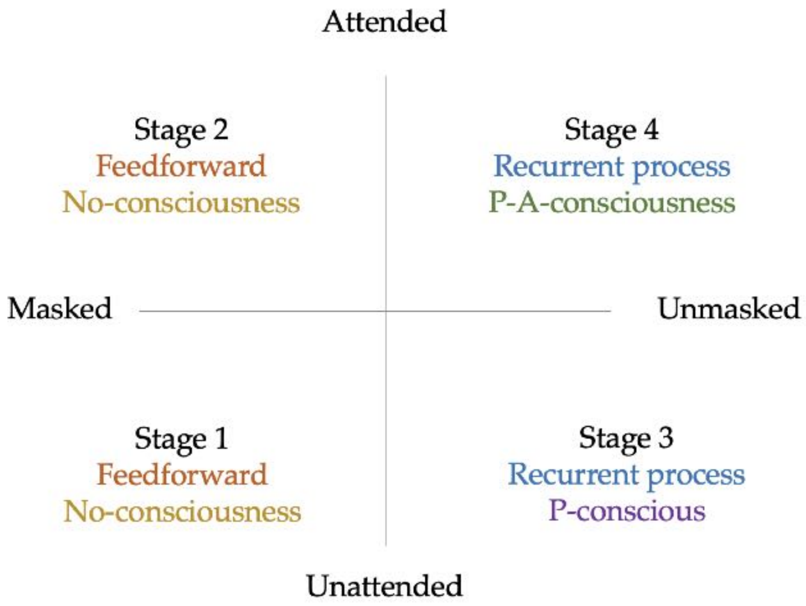

Figure 5. Summary of Lamme neural 4 stages, x axis account for stimuli visibility, y axis account for attention to stimuli.

Stage one (unattended and masked stimuli) is the most superficial form of non-conscious processing. Lamme and colleagues explain this stage as a fast feedforward sweep (FFS) in which early visual areas extract features of the image such as orientation, shape, color, or motion (Bullier, 2001; Lamme & Roelfsema, 2000). Importantly, a FFS of an unattended or masked stimulus cannot propagate enough to reach higher-level areas and, according to Lamme, this is the reason why this stage of processing remains non-conscious (Lamme, 2010).

Stage two (attended and masked stimuli) consists of a deeper FFS processing. For example, the process is similar to the precedent but in this case the stimuli is attended and masked. The information extracted from the stimulus travels through the whole hierarchy of sensory to motor and prefrontal areas, and may influence behavior. This non-conscious processing is also known as non-conscious priming (Dehaene, Naccache, et al., 1998; Eimer & Schlaghecken, 2003; Thompson & Schall, 1999).

Stage three (unattended and unmasked stimuli) is the most superficial and local form of a recurrent/re-entrant process (RP, see figure 6); The example here, is a visual stimulus that is not attended or is neglected, as in multiple visual paradigms, neglect (Driver & Mattingley, 1998), inattentional blindness (Scholte et al., 2006), change blindness (Landman et al., 2003; Schankin & Wascher, 2007), and attentional blink (Marois et al., 2004), see Table I). Possibly stage 3 could be associated with P-consciousness.

Stage four (attended and not masked stimuli) consists of the deepest RP. The information extracted from the stimulus travels through the whole hierarchy of sensory from low level to high level executive areas. This stage of processing occurs when a stimulus is attended and when the system has enough time to process information. A similar situation is given by the GNWT, when the stimulus has entered the global workspace.

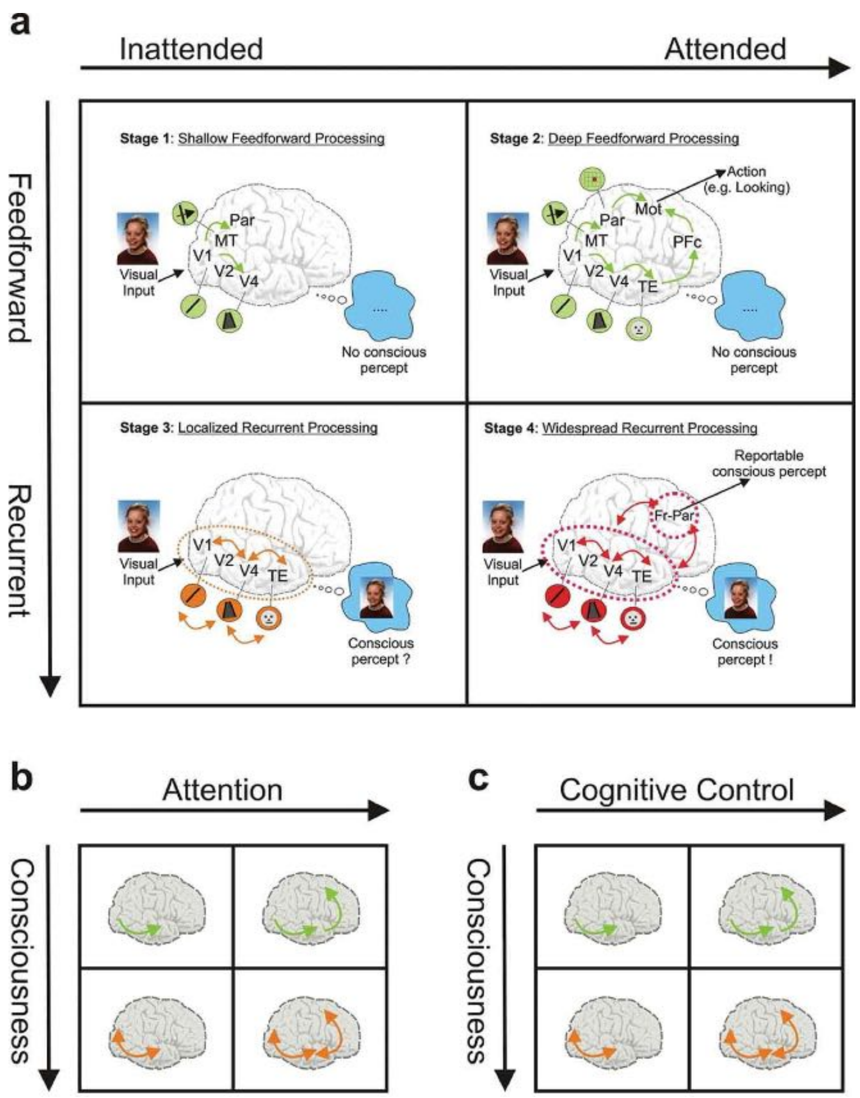

Figure 6. Reprinted from Cognitive Neuroscience, 1/4, Victor A. F. Lamme, How neuroscience will change our view on consciousness, 204-220, Copyright (2010), with permission from Taylor & Francis: (a) Four stages of cortical processing (see text for explanation). (b, c) When the difference between feedforward and recurrent processing (vertical axis, panel a) is identified to the difference between unconscious and conscious processing (vertical axis, panels b and c), how consciousness is orthogonal and independent of attention (b) and cognitive control (c) is readily explained.

Since the FFS alone is insufficient to produce experience, stage 1 and 2 can be excluded from what is sufficient for producing P and A-consciousness. Stage 3 is characterized by RP but does not reach frontal areas and lacks report. This stage corresponds probably to what should be P-consciousness. Stage 4 is characterized by RP which spans the whole brain and it is the underpinning of A-consciousness. As in

GNWT, RP involves frontal areas, but according to Lamme it is the RP that accounts for conscious phenomenology, not the frontal area involvement per se. If stage 3 actually is equivalent to P-consciousness, humans, and seemingly animals, can be visually conscious of stimuli without being able to report about them, that is they could be P-conscious of the visual stimuli in the absence of A-consciousness. This is problematic for the consciousness debate and consciousness assessment, which mainly employ introspection as the main way to collect conscious experience. According to Lamme (Lamme, 2010), RP should be a privileged index with respect to subjects' reports based on introspection in establishing whether there is consciousness or not.

Given a facial visual stimulus, we know that its categorization as a face (or not) will depend on the activation (or not) of face selective areas, but the extraction of the context (i.e. colour, motion,...) will depend on V1 and the integration of information processed in low-level areas (Lamme, 2010). RP satisfies multiple criteria that I covered in presenting the IIT model, by producing enough information integration, but not too high to become a non-specific information, thus impairing consciousness. A complementary argument regards FFS, which generates low integrated information which further supports the IIT viewpoint, being insufficient in generating consciousness (Lamme, 2010). In addition, there is another crucial difference between the RP and FFS, that presynaptic and postsynaptic neurons are active at the same time during RP. Such synaptic plasticity is a prerequisite for the Hebb’s rule which is a key neural process in learning and memory (Lamme, 2006, 2010). These neural arguments are valid for stage 3 and 4 which are both based on RP. Lamme concluded that “We could even define consciousness as recurrent processing” (Lamme, 2006, p. 499). A key aspect is that report and consciousness are different things and I will return to this point later. According to Lamme, Stage 4 and Stage 3 are linked to consciousness, but in Stage 3 (without report) consciousness will be restricted to P-consciousness.

4.5 Models of consciousness convergences

According to the GNWT perspective, it seems that consciousness is something that emerges, following the all-or-nothing rule, only if information is available and processed in a global working space (Baars & J., 1988). IIT proposes an alternative for which consciousness is an intrinsic property of a system that emerges gradually in relation to the level of information integration (Tononi, 2004). Another difference between GNWT and IIT should be defined considering centralized and decentralized processes. GNWT requires the involvement of a central module for access consciousness, where the ITT does not. In GNWT, the system is governed by a specific network. Whereas in IIT, the process is decentralized, it is PSC-dependent, it is the conscious phenomenon itself that shapes, but also is shaped by, cortical activation. In other words, While Baars and Dehaene speak in favor of a global neural involvement system, Tononi, through the calculation of Φ, attempts to formalize and to provide a metric of how integrated the system is, and these approximations reflect different degrees of awareness.

GNWT and IIT are based on two different conceptions of the spatial architecture of the network that raise consciousness.

Beyond these differences, GNWT and IIT share a fundamental key concept, which is specifically addressed in Lamme's RPT. As I covered before, in Lamme’s formulation, it is the quality (i.e., FFS, RP) of the connectivity and attention to determine the presence of consciousness. All presented theories hypothesize that at the basis of consciousness there is a dynamic and functional change of the neural activity and/or connectivity, which operates as an information synthesizer. Returning to the comparison of theories, another common concept is the existence of a superior system (i.e., superior network, superior amount of connectivity, superior quality of the connectivity) that is responsible for being conscious. This system coordinates different processes, all of which are involved in high-level processing, deals with the distribution of attentional resources, and flexibly process perceptual input.

Finally, the idea that the brain is activated in a coherent manner, promoting loops that move in a recursive manner in order to create a unified and integrated conscious content was in part already described by Crick and Koch (1990). The authors have spoken of a form of consciousness characterized by a kind of neural coalition corresponding to a stable global situation. This view was supported by neural activity measures, such as a synchronized 35-75 Hertz neural oscillation in the sensory areas of the cortex. The authors no longer consider these oscillations as sufficient for being a neural correlate of consciousness (NCC; Crick & Koch, 2003).

4.6 Timing of consciousness

GNWT, IIT and RPT attempt to model the consciousness network not only in terms of function but also in terms of time. To know how consciousness arises over time, Electroencephalography (EEG) and Magnetoencephalography (MEG) are the most appropriate techniques. EEG and MEG share a high temporal resolution and the ability to simultaneously record the entire neural activity of the brain. Consciousness timing is a challenging question. However, the time-course of the conscious processing differs depending on the theory under consideration. All of the theories consider a processing window that goes from approximately 100 to 500 ms after the stimulus onset, but with a different focus on P-consciousness, A-consciousness, report. Consequently, the temporal characterization can be early or late, depending if the focus was on the early process of sensory integration or on the higher level of processing, in other words if the focus was at the beginning or at the end of the process that raises consciousness.

According to GNWT, it is the neural component P3 that originates at around 300 ms and typically recorded at parietal electrodes that reflects the sudden and global activation of workspace neurons (Dehaene et al., 2003). More precisely, the subcomponent P3b is related to conscious processing (A-consciousness), as it is modulated by the subjective report and independent of the nature of the stimulus. The P3 component can be recorded in a simultaneous manner in multiple areas, being generated by a distributed and diffuse neural set that includes the hippocampus and the temporal, parietal and frontal associative cortices; these areas constitute the conscious processing network according to the theory (Dehaene & Changeux, 2011).

With regard to the IIT, there is no explicit mention of the time-related characterization of conscious onset. The conscious experience follows the phenomenal manifestation of the stimulus characteristics. The theory predicts that the time requirements for the generation of a conscious experience in the brain depend directly on the time requirements for the PSA to be activated. According to Tononi, 100 ms will be sufficient to obtain a considerable Φ. It is important to note that particular importance is given to neural firing rate that ERPs analysis neglect.

Lamme's theory focuses on the visual areas and consequently visual awareness (Lamme & Roelfsema, 2000). The FFS connection timing is dependent on the stimulus saliency and visibility. A high-contrast stimulus, for example, is processed by the ventral system and reaches the higher visual areas in 100 ms (i.e., P1) while processing at each successive level in the hierarchy will be approximately 10 ms slower than the previous one. Immediately after the early P1 component, there is another amplification in the visual cortex with an onset between 110 and 140 ms (Fahrenfort et al., 2007). According to RPT, RP and the EEG correlates of visual awareness should not occur before 200 ms.

Independently of the precedent models, electrophysiological recordings during visual tasks would allow the identification of correlates of visual awareness operationalized as the difference between ERPs in response to stimuli that enter awareness and stimuli that do not (A-consciousness - P-consciousness). There are three candidates for such neural correlates: P1 (~100 ms), early posterior negativity (~200 ms, also named visual awareness negativity, VAN), late positivity (LP, ~ 400 ms in the P3 time window). EEG research on visual evoked potentials has suggested two possible neural correlates of visual awareness: VAN and LP (Eklund & Wiens, 2018). Sensory events around 100 ms reflect indistinguishable sensory-evoked activity for visible versus non-visible stimuli (Dehaene & Changeux, 2011; Gaillard et al., 2009). VAN and LP may represent different moments in the process of consciousness, an earlier stage reflecting the sensory experience of perception (P-consciousness?) and a later stage denoting the conscious experience (A-consciousness?). However, a time window between 150 and 350 ms seems to be coherent with the emergence of consciousness.

I deserve a final consideration about the timing of consciousness. Notably, research so far almost exclusively focused on the phase in which the content is built up and becomes conscious. In contrast and complementary to consciousness genesis, from 2012 a few researchers drew attention to the anti-genesis of consciousness, the moment in which the content fades out from consciousness (Aru & Bachmann, 2017; Pun et al., 2012; see figure 7). As I will present later, paradigms that allow such investigation are limited, but significant contributions to consciousness science would be provided by investigating the whole cycle of consciousness.

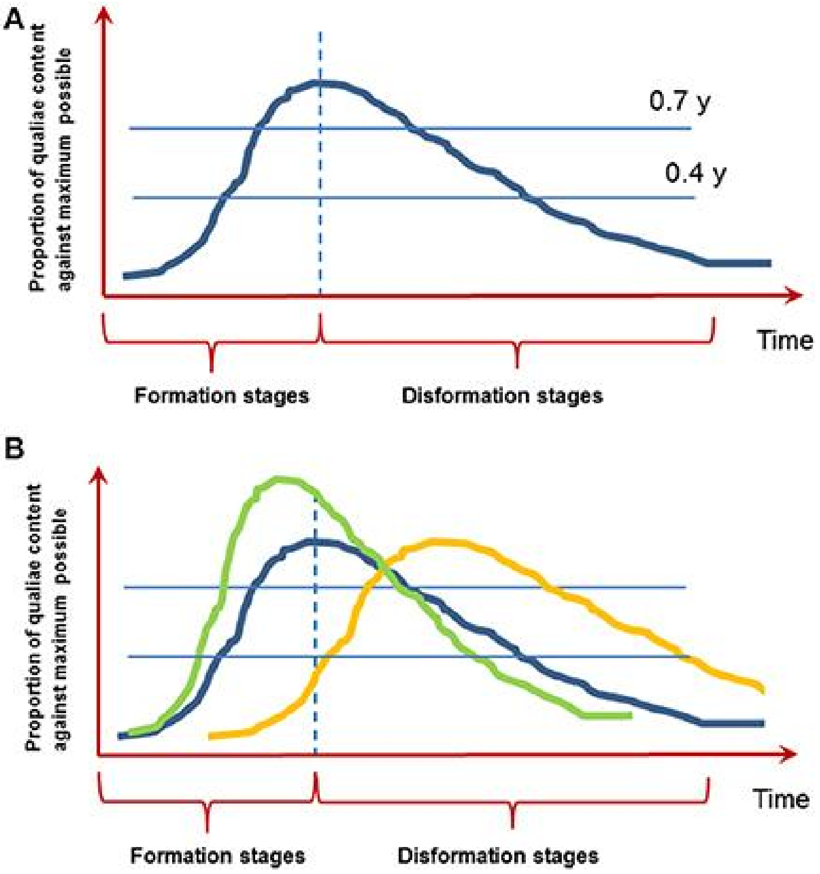

Figure 7. Reprinted from frontiers in Psychology, 8, Aru, J., & Bachmann, T., In and out of consciousness: How does conscious processing (d) evolve over time?, 128, Copyright (2017), with permission given by the Creative Commons Attribution License (CC BY): Figure 1. The function of conscious experience evolving over time. (A) Microgenesis of perception with its formative and disformative stages. The image is based on empirical research reviewed in Bachmann (2000). Note the proposed asymmetric inertia of formation and disformation. (B) It is conceivable that the functions over time are different for two types of conscious experience: immediate iconic perception (blue line) and slower memory-based experience (yellow line; see point 7 below). How is this shape influenced by top-down factors like attention, prior knowledge or working memory? Do these factors lead to a quicker build up and higher clarity of conscious content (green line; see point 6 below)? The units on the Y-axis are arbitrary units to be worked out.

4.7 Methods to study consciousness

Almost all paradigms for the study of consciousness rely on the visual system. This methodological choice is justified by the fact that visual input is highly structured and easy to manipulate, and the visual system is also deeply studied in animal research (F Crick & Koch, 1998). Paradigms explanations are reported in table 1. In general "masking" paradigms try to disrupt the visual process for rendering a stimulus inaccessible to visual awareness or conscious report, such as backward masking (Haynes et al., 2005; Lamme et al., 2002; Macknik & Livingstone, 1998; Rolls et al., 1999; Thompson & Schall, 1999) and dichoptic masking (Moutoussis & Zeki, 2002). Other paradigms are based on brain lesions, such as blindsight (Azzopardi et al., 2003; Goebel et al., 2001; Stoerig & Cowey, 1997), visual agnosia (James et al., 2003) where participants have no access to visual awareness but process information from the visual input, and brain functioning altered by stimulation (Boyer et al., 2005; Jolij & Lamme, 2005; Pascual-Leone & Walsh, 2001; Sarasso et al., 2014; Silvanto et al., 2005). An important recent paradigm that is not presented in table 1 is the continuous flash suppression (CFS), that is specifically designed for the investigation of the visual process until awareness access. In CFS, one eye is continuously rapidly flashed by different images while the input to the corresponding location in the other eye remains the same; the non flashed eye input remains sometimes invisible for several minutes (Tsuchiya & Koch, 2005). CFS is based on a binocular rivalry that is also a paradigm that I will present deeply in the next paragraph as I have used this particular paradigm for my research. Other paradigms from section b of table 1 are just informative as they may not measure exclusively consciousness: split brain (Gazzaniga, 2005; Sperry, 1986), neglect or extinction (Driver & Mattingley, 1998; Rees, Kreiman, et al., 2002; Rees, Wojciulik, et al., 2002), change blindness (Beck et al., 2001; Landman et al., 2004; Simons & Rensink, 2005), inattentional blindness (Mack, 2003) and attentional blink (Marois et al., 2004).

Table 1: Reprinted from TRENDS in Cognitive Sciences, 10/11, Victor A.F. Lamme, Towards a true neural stance on consciousness, 494-501, Copyright (2006), with permission from Elsevier: Table 1. Conflating conscious experience with other cognitive functions[a]

Phenomenon	**Brief description of phenomenon, and conscious (C) versus unconscious (U) behavior**	**Lesion and other relevant neural data**	**Conclusion with respect to the NCC**
(a) True manipulations or impairments of conscious experience			
Blindsight 37, 38, 39	Subjects report no conscious experience for the visual field contralateral to the lesion but can guess stimulus properties, localize stimuli, show vegetative or emotional responses, etc. C: Detection U: Localization, guessing, pupil dilation and priming	Lesion to V1. In monkeys, ventral stream areas no longer respond to stimuli whereas parietal cortex (e.g. area MT) still responds. In human subjects, ventral stream areas also respond to stimuli.	NCC sits in the ventral stream, in V1 itself, or is the interaction between V1 and higher visual areas.
Visual agnosia [40]	Failure to recognize objects or their shape, while still seeing basic features. Yet these objects can be localized, picked up or manipulated according to shape. C: Object recognition U: Localization, handling and acting	Results from a lesion to extrastriate and/or ventral stream cortex.	Dorsal stream performs unconscious action towards objects and is not part of the NCC. The NCC sits in the ventral stream cortex.
Backward masking 14, 27, 36, 41, 42	Presenting a stimulus, shortly followed by another stimulus, the mask, that renders the first stimulus less (or in-) visible. Other varieties exist that might	Invisible stimuli (d′ = 0) still activate neurons throughout the brain, such as in V1, IT cortex, frontal eye fields or motor cortex, albeit briefly (about as long as the stimulus is physically	The NCC sits nowhere (i.e. is not localizable). The NCC is neural activity passing a certain threshold. The NCC is

	all have different effects. Masked stimuli might cause priming of subsequent choices. C: Detection U: Priming and galvanic skin response (GSR)	present). Interrupts delayed signals, probably reflecting feedback or recurrent/re-entrant processing.	re-entrant processing.
Dichotic masking [28]	Presenting stimuli with opposite features (e.g. colors) to the two eyes, so that it becomes invisible in the fused binocular percept. C: Detection U: Localization	Activates the same areas as visible versions of the stimulus, only weaker. Even highly selective areas, such as those responding to faces, are activated.	The NCC is not localizable. Neural activity has to pass a threshold for becoming the NCC.
Transcranial magnetic stimulation (TMS) 11, 43, 44, 45	Brief (ms) disruption of neural activity with a magnetic field pulse over the scalp. TMS over the occipital cortex at ~100 ms after stimulus onset disrupts visual awareness. TMS over V1 might still allow unconscious (blindsight) behaviour. C: Detection, discrimination and localization U: Forced choice guessing of stimulus attribute	Shows that activity at ~100ms in V1 (and adjacent early visual areas) is necessary for visual awareness. In higher areas, disruption by TMS is effective at earlier latencies, suggesting that the effect of TMS is mainly due to the disruption of feedback signals to V1.	The NCC is feedback or re-entrant processing.
Binocular rivalry 46, 47, 48	Different stimuli to the two eyes results in suppression of one or the other. Spontaneous alternations of which stimulus is seen, each dominant percept lasting a few seconds.	In monkeys, cells in low-level areas (e.g. V1) respond to the suppressed stimulus, whereas in higher areas (e.g. IT) cells only respond to the conscious percept. In human fMRI studies, there is a strong correlation between neural activity in V1 and perceptual dominance. Switches are accompanied by activation of the frontoparietal network.	Unclear: at first it was thought that high-level areas in the ventral stream are the NCC, but recent fMRI data (and a reanalysis of the early monkey data [48]) cast doubt on this conclusion.
	Additional manipulations have shown that the phenomenon is about switching between percepts rather than eye of		

	input. C: Reported dominance of one or the other percept U: Priming by subdominant percept		
(b) Failures of reportability instead of conscious experience?			
Split brain 4, 5	Failure to verbally report objects that are presented contralateral to the non-language hemisphere (usually the left). But these objects can be drawn, associated with other objects or words, selected from a row of alternative choices or cognitively manipulated. C: Speech U: Drawing, selecting, recognition, pointing out and other simple cognitive manipulations **Manipulation of language instead of consciousness?**	Results from a trans-section of the corpus callosum and commisures that connect the two hemispheres. As a result, what 'happens' to the right hemisphere cannot be verbally reported.	NCC sits in the left hemisphere, the right hemisphere is unconscious.
Neglect or extinction 49, 50, 51	Failure to report or attend to contralateral objects when presented alone (neglect) or in combination with ipsilateral objects (extinction). Yet the unattended objects can induce various forms of priming. C: Selecting, localizing, drawing, recognizing, manipulation U: Priming	Results from a lesion to (occipito- or temporo-) parietal cortex (arteria cerebralis media region). Ventral stream areas still process visual information.	NCC sits in the frontoparietal network that is necessary for attention. V1 and ventral stream are not the NCC.

	Manipulation of attention instead of consciousness?		
Change blindness 19, 52, 53	Changes between two views of the same scene are not detected, even when as dramatic as changing persons or whole objects. C: Change detection U: Having a hunch that a change occurred **Manipulation of attention instead of consciousness?**	Unseen changes evoke activity in the ventral stream and early visual areas. Seen changes activate the frontoparietal network.	The NCC sits in the frontoparietal network.
Inattentional blindness 17, 54	Subjects cannot report afterwards on objects that were unexpectedly presented outside of the focus of attention. C: Detection, memorization and familiarity upon recall U: Priming and grouping effects **Manipulation of memory instead of consciousness?**	Not remembered stimuli have activated selective areas in the ventral stream, and have evoked re-entrant processing in early visual cortex.	The NCC sits in the frontoparietal network.
Attentional blink [55]	Detection of a target from a stream of stimuli prevents detection of a second target for about half a second (the ‘blink’ period). C: Detection and identification U: Priming **Manipulation of attention instead of consciousness?**	Early visual cortex (V1) and ventral stream areas are still activated by non-detected targets. Frontoparietal activation is absent.	The NCC sits in the frontoparietal network.

[a] In blindsight, resulting from a lesion to V1, subjects can point at visual stimuli, or guess their shape, color or motion direction. However, subjects verbally deny any conscious experience, nor can they detect the stimuli (i.e. discriminate presence or absence). Detection and talk carry more weight for the presence of conscious experience than localization or guessing (Figure 1), and therefore blindsight is considered the classical example of visually guided behavior in the absence of conscious experience, even in monkeys [37].

Under the ecological circumstances, slightly discordant visual inputs to the two eyes result in a stable stereo experience (see Gallagher & Tsuchiya, 2020). When the dissimilarity exceeds a certain threshold, periods of perceptual dominance of one stimulus over the other stochastically alternate, such that one monocular image is dominantly consciously experienced while the other is suppressed and invisible (Alais & Blake, 2005; Brascamp et al., 2015). This condition is called binocular rivalry (BR; Wheatstone, 1843), and as far as I know, it is the only paradigm to cover the complex process from access consciousness to fading from consciousness.

In the BR paradigm, participants are often required to report their content of consciousness in a continuous manner among several alternatives (see figure 8). The time series data of the BR report is quite rich and has been dissected into at least 3 components, each of which can characterize the underlying neural and psychological processes from different perspectives. First, initial percept measures which of the rivaling stimuli dominates first in consciousness, potentially characterizing any bias or advantage of one stimulus over the other. Second, onset resolution time measures the time of the first initial percept button press, characterizing how long it takes the visual system to resolve perceptual ambiguity, or, in other words, it is an estimate of the time cost necessary for the brain to select (or inhibit) one percept[3] over the other. These two BR components are then indicative of the “winner” percept (i.e., initial percept) of this initial phase of unresolved competition (i.e., onset resolution time). A third component, which is called predominance or cumulative time, measures instead the proportion or total time of dominance in awareness of one percept over the other, i.e. the periods of relatively stable resolution following the initial competition.

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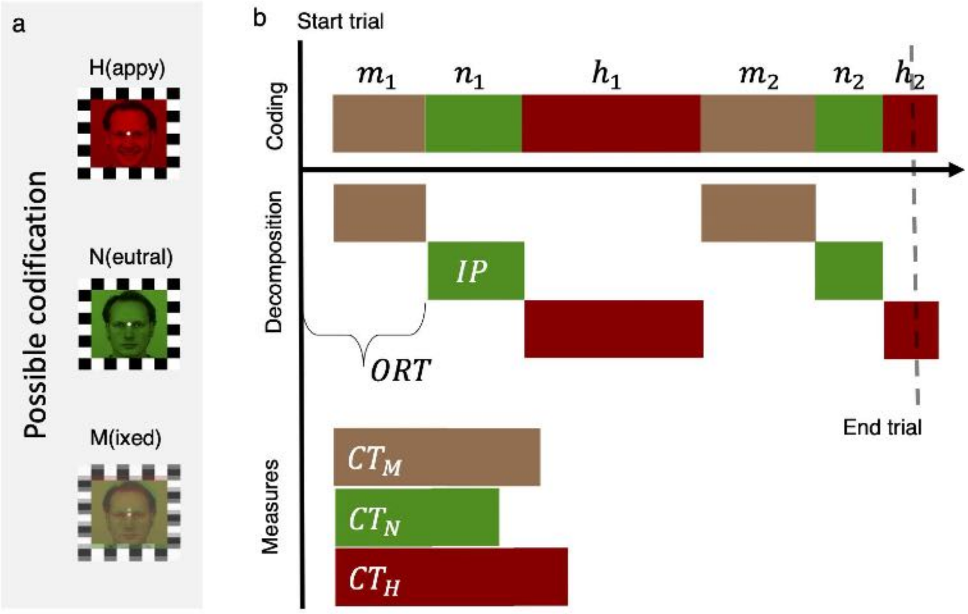
[3] The term “percept”is not strictly related to consciousness experience, for this reason, it will be specified when necessary.



c

$$CT_H = \sum_{i=1}^{n} h_i$$

Figure 8. Rivalry during trials and BR measures. panel a: possible coding of the rival stimuli. panel b: an example of a subject rivalry trials and coded percepts (e.g., h1: first happy face coded in a trial, n1: first neutral face coded in a trial, m1: first mixed percept coded in a trial…). The three behavioral measures extractable from this time course are 1) initial percept (IP) (either Happy, Neutral), 2) onset resolution time (ORT in [sec]), and 3) cumulative time (CT for percept in [sec]), formula in panel c.

4.8 Limits in investigating consciousness

A final consideration about consciousness science is the potential limitation that consciousness carries by itself. As I covered before, investigation of consciousness requires the participants to report their experience. Such a report, often verbal, does not allow the dissociation from other cognitive functions that are required for reporting the conscious content (Lamme, 2006). An interesting point of view on this potential problem is provided by comparative research that assumes the presence of consciousness in animals. The fact that animals cannot communicate clearly their internal states, prompted researchers to state in “The Cambridge Declaration on Consciousness” [4] the following:

> *“The absence of a neocortex does not appear to preclude an organism from experiencing affective states. Convergent evidence indicates that non-human animals have the neuroanatomical, neurochemical, and neurophysiological substrates of conscious states along with the capacity to exhibit intentional behaviors. Consequently, the weight of evidence indicates that humans are not unique in possessing the neurological substrates that generate consciousness. Non-human animals, including all mammals and birds, and many other creatures, including octopuses, also possess these neurological substrates.”*

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[4] The Cambridge Declaration on Consciousness was written by Philip Low and edited by Jaak Panksepp, Diana Reiss, David Edelman, Bruno Van Swinderen, Philip Low and Christof Koch. The Declaration was publicly proclaimed in Cambridge, UK, on July 7, 2012, at the Crick Memorial Conference on Consciousness in Human and non-Human Animals, at Churchill College, University of Cambridge, by Low, Edelman and Koch. The Declaration was signed by the conference participants that very evening, in the presence of Stephen Hawking, in the Balfour Room at the Hotel du Vin in Cambridge, UK. The signing ceremony was memorialized by CBS 60 Minutes.

4.9 General introduction to the experiments

In this Thesis, five experiments using binocular rivalry (BR)[5] are reported. Two experiments investigated the impact of facial mimicry on visual awareness of faces characterized by an expression. One experiment investigated the impact of facial tactile stimulation on visual awareness of these faces with an expression. Two experiments investigated the impact of facial emotional expression on visual awareness time-course.

Experiments 1 & 2 aimed at testing whether facial sensorimotor feedback during facial expression perception has a role in the conscious processing of such expressions. Facial mimicry manipulation implemented in Experiment 1 was congruent with a neutral facial expression, while in Experiment 2 was congruent with a happy facial expression. Taken together, these two complementary experiments will test the role of congruency between mimicry and observed facial expression predicting that a sensorimotor signal will favor the conscious processing of the congruent expression (i.e., neutral faces in Experiment 1 and happy faces in Experiment 2).

Experiment 3 (which is to be considered as a pilot experiment), aimed at testing whether somatosensory facial feedback during facial expression perception has an independent role (with respect to facial mimicry/sensorimotor information) in the

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[5] All acronyms are reported at p. 151 in section 11: Acronyms table.

conscious processing of such expressions, an issue that has been totally ignored by the previous research. Kragel and colleagues (Kragel & LaBar, 2016) suggested that the subjective experience from facial expression perception is linked with responses in the somatosensory cortex (SC) but not with responses in the motor cortex. With respect to Experiments 1 and 2 that are focused on sensorimotor mechanisms, Experiment 3 aimed to investigate this privileged role of somatosensory activity in conscious experience of others' facial expressions as raised by Kragel and LaBar. In order to do so, in this experiment I implemented a manipulation aimed at manipulating facial somatosensory information during visual exposition to facial emotional expressions.

Experiments 4 & 5, aimed at testing whether the time-course of the switches of conscious content that occur during BR are dependent on the content properties. In Experiments 4 I investigated consciousness time-course of happy and neutral facial expressions (under conditions of free facial mimicry), while in Experiment 5 I investigated the same issue testing participants with congenital facial palsy (i.e., Moebius syndrome).

Finally, on an exploratory basis, in the present investigation I also tested the hypothesis of a relationship between alexithymic traits and empathy with awareness of emotional expressions[6]. Alexithymia is defined as a difficulty in experiencing emotions and Empathy is defined as the ability to share and understand others' emotions and affective states (Nemiah, 1976; Zaki et al., 2012). I hypothesized that the different binocular rivalry metrics I analyzed could show a relationship with the levels of alexithymic traits, in the direction of the decreasing in conscious perception

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[6] Correlation tables are available in the appendix.

for emotional expressions with increasing levels of alexithymia and could show a relationship with the levels of empathy, in the direction of the increasing in conscious perception for emotional expressions with increasing levels of empathy.

5 Experiments sensorimotor-visual integration

5.1 Experiments 1 and 2: Introduction

The present studies investigated the role of the observer's facial mimicry when manipulated congruently with neutral (Experiment 1) and happy (Experiment 2) facial expressions. I manipulated participants' facial mimicry by means of a chopstick for half the experiment, while in the other half the facial mimicry was free (the order of the two mimicry conditions was counterbalanced between participants; for similar manipulations see Baumeister et al., 2015; Kraft & Pressman, 2012; Lomoriello et al., 2018; Niedenthal et al., 2001; Oberman et al., 2007; Stel & Knippenberg, 2008; Wood, Lupyan, et al., 2016). In Experiment 1, the chopstick manipulation had the objective to inhibit the activation of the zygomatic major, associated with mimicry of facial expression of happiness (Oberman et al., 2007; Strack et al., 1988), while it is not incongruent with a neutral facial expression. For instance, Tan (2012) demonstrated that the zygomaticus EMG pattern can discriminate between a positive emotion and a neutral and/or negative emotion, but does not discriminate between a neutral and a negative emotion. Absence of zygomatic muscle activity is also confirmed in healthy participants during a pouting task (Cui et al., 2021).

In Experiment 2, the chopstick manipulation had the aim to activate the zygomatic major, associated with mimicry of facial expression of happiness (see figure 11, right panel).

I expected that blocking/altering facial mimicry could interfere with the alternation in BR. In Experiment 1, I expected that interfering with the sensorimotor signal (i.e., by means of the active inhibition of facial mimicry) would have favored the neutral facial expressions and interfered with happy expressions with respect to the condition of free mimicry by either biasing competition and ambiguity resolution at the early stage and/or stabilizing representations following initial resolution at the late stage. In Experiment 2, I expected that manipulating the sensorimotor signal (i.e., by means of the activation of facial mimicry) would have favored the happy facial expressions and interfered with neutral expressions with respect to the condition of free mimicry by either biasing competition and ambiguity resolution at the early stage and/or stabilizing representations following initial resolution at the late stage.

This last scenario (stabilizing representations) seems more plausible in the light of the results reported by Korb and colleagues. To test the early account (i.e., ambiguity resolution), I analyzed the frequency and time of the first rivalry report, i.e. initial percept and onset resolution time, respectively (Carter & Cavanagh, 2007). To test the late account (i.e., stabilization), I analyzed the cumulative time. As an auxiliary although interesting aim, I wanted to replicate the few interesting results previously reported in the literature about an advantage in terms of predominance of emotional stimuli, and in particular of facial expressions of happiness when in rivalry with neutral facial expressions (Alpers & Gerdes, 2007; Bannerman et al., 2008; Yoon et al., 2009).

Since previous studies have suggested that facial mimicry manipulations have a greater impact on female than male participants (Stel & Knippenberg, 2008; Wood, Lupyan, et al., 2016) (for compatible results see also Korb et al., 2015), I decided to recruit exclusively female participants in order to maximize power. Therefore, on the basis of the hypotheses introduced in the previous paragraph, from a statistical point of view, the effect that I expected, both for the tests of the early and the late accounts, was an interaction between facial expression and mimicry manipulation, with opposite directions for Experiment 1 and Experiment 2. In Experiment 1 I expected to observe an advantage for neutral expressions under the condition of blocked mimicry when compared to free mimicry, and a disadvantage for happy expressions under the condition of blocked mimicry when compared to free mimicry. In Experiment 2, I expected to observe an advantage for happy expressions under the condition of forced mimicry when compared to free mimicry, and a disadvantage for neutral expressions under the condition of forced mimicry when compared to free mimicry.

5.2 Experiment 1

5.2.1 Method

Participants. Thirty-two female healthy participants were recruited among students at the University of Padua (average age in years = 24.7, SD = 4.8, 2 left-handed). The sample size is considered appropriate on the basis of a meta-analysis on facial feedback and emotional experience (Coles et al., 2019). Given the methodological heterogeneity, I selected a subsample of the originally included studies with these characteristics: a) facial mimicry manipulated as a within-subjects factor and b) happiness as the main emotion. Using Coles and colleagues' (2019) approach, the estimated effect in terms of Cohen's d (Jacob, 1988) is 0.478 (SE = 0.162, 95% CI [0.117 0.839]). Power was estimated using the pwr package (Champely et al., 2020). Since I have hypothesized a specific direction of the effect due to mimicry, in this case we could consider a one-sided paired t-test, which would need a sample size of 28 participants to reach an 80% power level.

All volunteers gave written informed consents in accordance with the Declaration of Helsinki, and all experimental procedures were approved by the local research ethics committee (Comitato Etico della Ricerca Psicologica Area 17, University of Padua) and performed in accordance with its guidelines. Participants had normal or corrected-to-normal vision. Color blindness was assessed using the Ishihara color blindness test (Shinobu, 1918). A total of 4 participants were excluded from analysis (one did not follow the coding instruction, two failed in holding the chopstick correctly and one did not complete the experiment). At the end of the experiment, participants completed the Toronto Alexithymia Scale (Bagby et al., 1994) (TAS-20) and the Interpersonal Reactivity Index (Davis, 1983) (IRI) questionnaires. Scores on both questionnaires were in the normal range (TAS-20: M = 43.6, SD = 11.5 IRI: M = 98,75, SD= 8).

Material and apparatus. Visual stimuli were displayed using E-Prime 2.0 Software (version 2.0.10.242; Psychology Software Tools, Pittsburgh, PA) on a LG flatron F700B (Brightness: 85; Contrast: 90) 85 Hz monitor. Original stimuli were selected from the Karolinska Directed Emotional Faces (Lundqvist et al., 1998) and included one male (AM10) and one female (AF01) face, each displaying a neutral and happy expression[7]. Visual stimuli were presented covering 8 degrees of visual angle in height and width. Images were cropped with the software GIMP (version 2.8.10; see figure 9) 562 x 562 pixels centering the face in the middle of the square. Images of the same individual expressing the two emotions (happy and neutral) were superimposed and shifted by 4 pixels in order to facilitate the rivalry between two percepts. Happy and neutral faces of the same identity were analyzed and matched (in terms of contrast and luminance histograms) by using Fiji (Schindelin et al., 2012) and MATLAB (version R2019; see figure 9).

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[7] The use of anaglyph google requires adding two levels (red, green) in counterbalancing conditions. This exponential implementation restricted the use to two different identities.

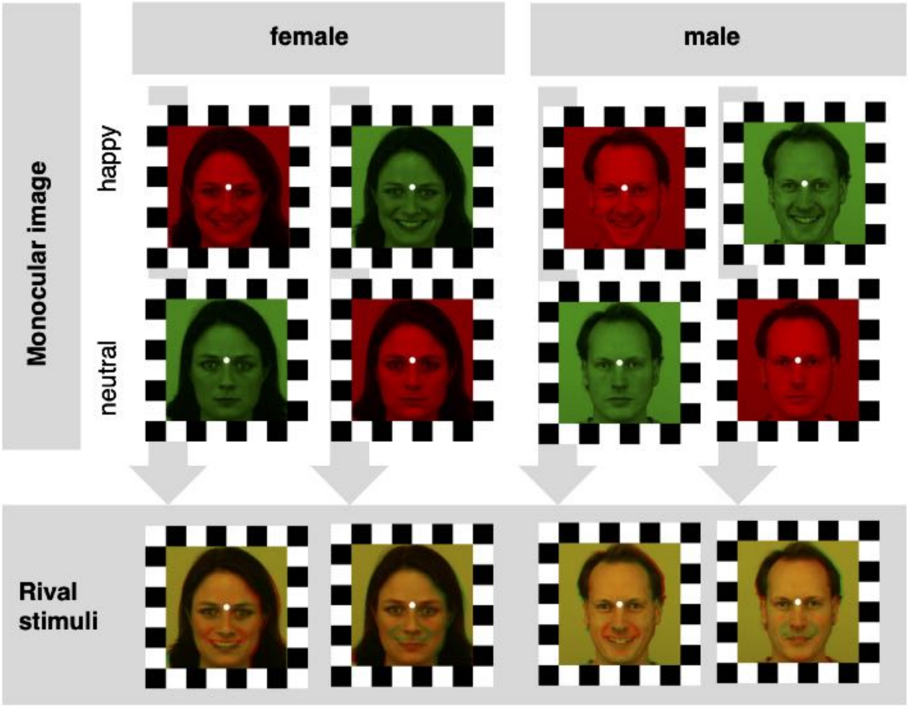

Figure 9. Monocular images and rival stimuli. Arrows indicate the resulting rival stimuli. Following the binocular rivalry experiment, the monocular stimuli in isolation were evaluated with regard to valence and arousal. A white 12-pixel fixation point and 40-pixel black and white squares frame were applied to the images to facilitate binocular fusion using GIMP (version 2.8.10, https:// www. gimp.org). Monocular images contrast and luminance histograms were matched by using Fiji (ImageJ 1.52c, https://fiji.sc). Original pictures (AM10NES, AM10HAS, AF01NES, AF01HAS) of facial expressions have been selected from the Karolinska Directed Emotional Faces set (KDEF; https://www.kdef.se/).

Procedure. Participants seated on a comfortable chair in a silent, temperature-controlled room. They were asked to place their head on a chin rest, with a distance of 70 cm from the screen. Before starting the experiment, the anaglyph filters (red/green) were set, and participants were trained (see figure 10). The side of the color filters was counterbalanced across participants. During the experiment, participants were asked to focus on a fixation point located in the middle of the screen. The experiment consisted of one session of four blocks. Each participant performed two blocks where they could freely use their facial mimicry ("free mimicry condition") and in other two blocks they were asked to hold a chopstick between their lips without using their teeth ("blocked mimicry condition"; see Figure 11 left panel). The order of the two mimicry conditions was counterbalanced across participants. In each block, four rivalry stimuli were presented in a random order for a total of eight trials (twice per stimulus) in each block. Rivalry stimuli were presented for 15-s preceded by a 2-s fixation point and followed by a 3-s black screen. Participants were asked to code what they saw in real time by pressing one of three keys of the keyboard ("b", "n", "m", these keys are adjacent to each other on the standard keyboard in this order from the left to the right). Participants were asked to use the keyboard with their writing hand. Participants were informed that on each trial they could see one of two faces, and that the appearance might change from one to the other during the trial. Coding instructions were presented before the beginning of the block; the order of the "b" and "m" keys, corresponding to the coding of the "happy" and "neutral" facial expression, was counterbalanced across blocks, while the "n" key always corresponded to the coding of a "mixed" percept. In the middle and at the end of each block a short break was recommended to the participant to reduce any fatigue. At the end of each mimicry conditions (i.e., two blocks) valence and arousal of each stimulus were measured respectively on a − 3/+ 3 and + 1/+ 7 scales.

Figure 10. Experimental setting of Experiment 1.

Figure 11. Reprinted from Psychological Science, 23/11, Kraft, T. L., & Pressman, S. D., Grin and bear it: The influence of manipulated facial expression on the stress response, 1372-1378, Copyright (2012), with permission from SAGE Publications: Examples of photographs shown to participants in the neutral group (left), standard-smile group (middle), and Duchenne-smile group (right) to help them form the appropriate expressions. In experiment 1, the chopstick is held without using teeth.

Data reduction. Firstly, for each trial I extracted the initial percept (IP), namely the first reported percept during the ongoing trial (neutral and happy facial expressions), in order to analyze whether initial percept frequencies changed as a function of the emotionality of the face and/or as a function of the mimicry manipulation. I further computed onset resolution time (ORT), namely the time to code each IP as a mean value per emotion per subject. ORT log transformation was used for the analysis. I also computed cumulative times (CTs), as a measure of perceptual predominance, for mixed percept, neutral and happy facial expressions separately. That is, CTs were computed by summing the perceptual duration for each of mixed, neutral and happy percept segments during a trial. Two participants did not code a total of three trials (Subject 9, one trial in the blocked mimicry condition; Subject 18, two trials in the free mimicry condition).

Data analysis. Differences in stimuli rating for valence and arousal were assessed in separate analyses of variance (ANOVAs) and post hoc comparisons. Differences in mimicry (blocked and free) were assessed for ORT (ORT are related to IPs) in analyses of variance (ANOVA) and post hoc comparisons. All post hoc comparisons are Bonferroni corrected for multiple comparisons. Differences in mimicry (blocked and free) and facial expression percept (happy, neutral and mixed) were assessed for CTs in analyses of variance (ANOVA) and post hoc comparisons. All post hoc comparisons are Bonferroni corrected for multiple comparisons. In order to estimate the probability of the IP as a function of facial mimicry manipulation, I applied a mixed-effects logistic regression model with IP (happy or neutral) explained by mimicry condition (blocked vs. free). Subjects were inserted as random effect with a varying intercept. The mimicry effect was evaluated as the odds ratio between free and blocked conditions.

5.2.2 Results

Ratings. Evaluation of valence and arousal were performed on individual stimuli at the end of each mimicry condition (i.e., two blocks). No effect of the session (i.e., two blocks) in terms of mimicry manipulation was observed (valence F(1, 27) = 2.28, p = 0.143 d = 0.58; arousal F(1, 27) = 0.08, d = 0.11, p = 0.775). Valence ratings differed according to a priori expectations, F(1, 27) = 330.02, p < .001, d = 6.99. Neutral facial expressions were rated close to zero (M = − 0.63; SD = 0.98; range = − 3 to 3), which was more negative than happy (M = 2.15; SD = 1.12; range = − 3 to 3). Happy expressions were rated more positively than neutral expressions, t(27) = 18.16 p < .001, d= 3.49. Arousal ratings also differed according to a priori expectations, F(1, 27) = 56.54, p < .001, d = 2.89. They were lower for neutral expressions (M = 2.74; SD = 1.54; range = 1–7) than for happy expressions (M = 4.97, SD = 1.63; range = 1–7). Neutral facial expressions were rated as significantly less arousing than happy facial expressions, t(27) = 7.52, p < .001, d = 1.45.

Testing the early effects of blocked mimicry (i.e., resolution of ambiguity). For both initial percept (IP) and onset resolution time (ORT), the statistical models included the factors mimicry (free vs. blocked).

Initial percept (IP). In terms of IPs, happy expressions were reported more frequently in both mimicry conditions (blocked: 304 trials; free: 317 trials) than neutral expressions (blocked: 128; free: 113). The odds ratio is not statistically significant, and the estimated value is 0.83 ($\beta = -0.184$, $SE = 0.159$, 95% CI [-0.50, 0.13], $t - 1.15$, $p = 0.248$).

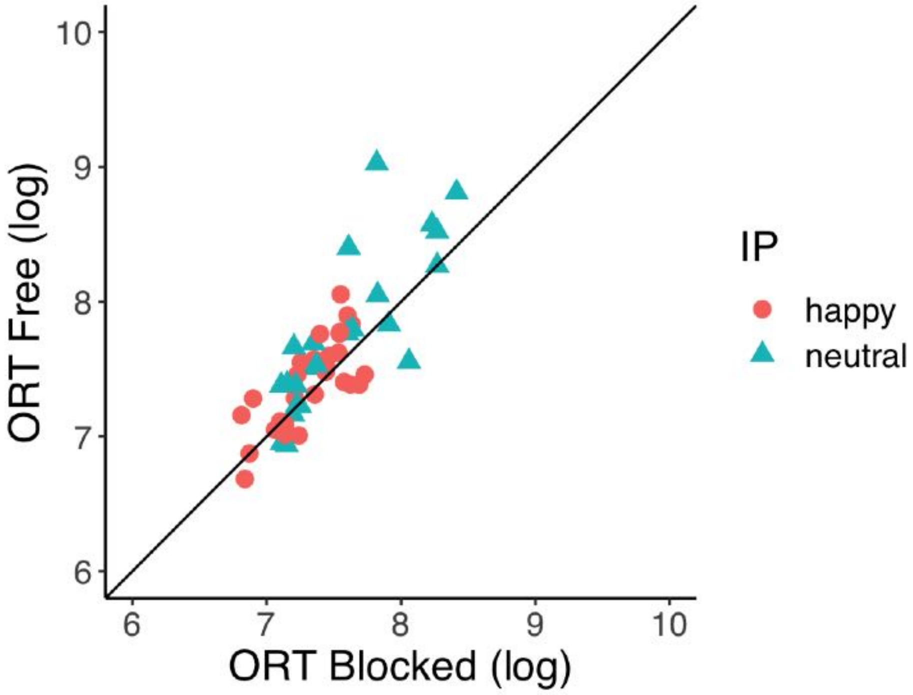

Figure 12. Each point represents a participant’s onset resolution time (ORT) for a specific IP. Mimicry condition is projected on the x and y axes, the black line represents the axes equidistance. The ORT is expressed in milliseconds.

Onset resolution time (ORT). Due to the IP distribution, five participants were removed from analysis (i.e., they did not have all possible IPs). Significant differences were found for the mimicry condition independently of the first clear facial expression reported (i.e., IPs), $F(1,22) = 6.38$, $p = 0.019$, $d = 1.08$, and for the IPs independently of mimicry condition, $F(1,22) = 13.90$, $p < .001$, $d = 1.59$. See figure 12. In general, the findings related to the IP and ORT metrics seem not to support an impact of mimicry on the early stage, that is, the inhibition of the zygomatic muscle did not influence the resolution of ambiguity in favor of neutral faces and/or at the expense of happy facial expressions. These results seem to be in line with the previous evidence provided by Korb et al. (2017). To note, in terms of IP frequency and ORT, emotional faces showed an advantage when compared to neutral faces irrespective of the mimicry conditions[8].

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[8] It is important to note the difference between CFS and BR paradigms which could account for differences in results using one or the other method. One main difference between the two blinding techniques regards the functional hierarchy of unconscious visual processing they would allow; in particular, BR ranks to the deepest level of ‘blinding” methods (see Breitmayer, 2015) .

Testing the late effects of blocked mimicry (i.e., stabilization of conscious contents). For the cumulative time (CT) metric, the statistical model included the factors mimicry (free vs. blocked) and the reported content (happy vs. neutral vs. mixed). A significant difference was observed for reported content independently of the mimicry condition, F(1.79, 48.26) = 69.18, $p < .001$, d = 3.55. CT for happy facial expressions was longer than CT for neutral faces, t(54) = 9.78, $p < .001$, d = 1.33, and than CT for mixed percepts, t(54) = 10.54, $p < .001$, d = 1.43. This result is in line with previous findings (Alpers & Gerdes, 2007; Yoon et al., 2009). The main effect of mimicry did not yield to significant differences, F(1, 27) = 1.2, p = 0.283, d = 0.42. In accordance with the hypothesis, CT for reported content showed an opposite trend as a function of the mimicry conditions, that is CT for neutral faces was expected to increase when mimicry was blocked (blocked mimicry condition: M = 3.39 s; SD = 4 s; free mimicry condition: M = 2.69 s; SD = 3.28 s), conversely CT for happy facial expressions was expected to decrease when mimicry was blocked (blocked mimicry condition: M = 7.51 s; SD = 4.96 s; free mimicry condition: M = 7.75 s; SD = 4.87 s). This observation was substantiated by the significant interaction between mimicry manipulation and the reported content, F(1.85,49.86) = 3.53, p = 0.04, $\eta^2 = 0.12$. However, the hypothesis was only partially supported by the post-hoc comparisons. In particular, the observed interaction was statistically conveyed entirely by a modulation of CTs for neutral expressions as a function of the mimicry manipulation, such that for neutral faces CT in the blocked mimicry condition was longer than CT in free mimicry condition, t(56.6) = 2.78, p = 0.007, d = 0.37. The evidence in favor of the alternative hypothesis H1 may be classified, in terms of Bayes factor, as moderate, BF10 = 5.84. In order to substantiate the conclusions I further report the post-hoc comparisons for happy and mixed percepts (t(56.6) = − 0.928, p = 0.357, d = 0.12, BF10 = 0.28; t(56.6) = − 1.348, p = 0.18, d = 0.18, BF10 = 0.60, respectively). To note, the evidence in favor of the null hypothesis H0 for happy faces, can be classified as moderate, overall suggesting that the pattern of the observed findings is robust. See Figure 13.

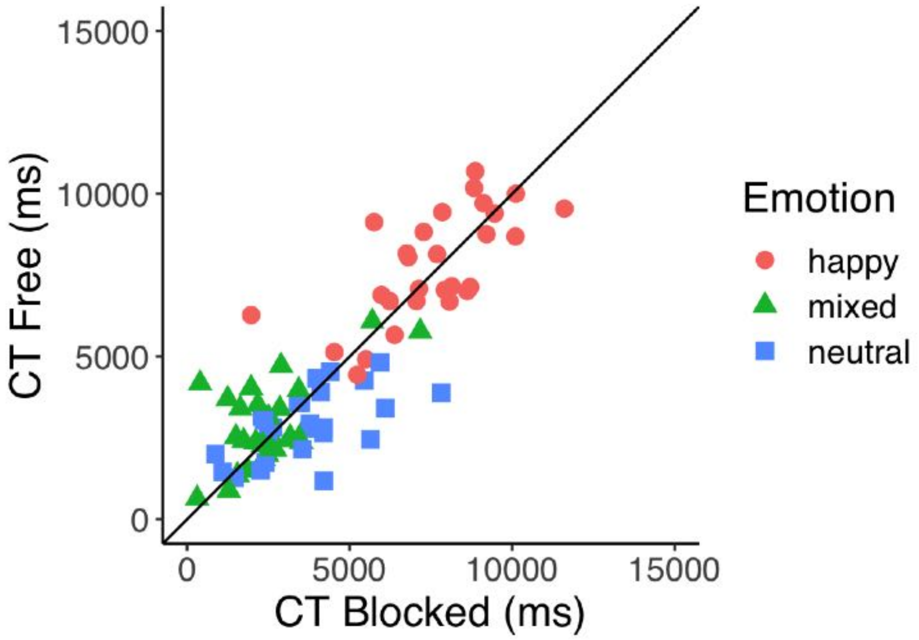

Figure 13. Each point represents a participant's cumulative time (CT) for a specific emotion. Mimicry condition is projected on the x and y axes, the black line represents the axes equidistance. The CT is expressed in milliseconds.

Questionnaires. In exploratory analyses, I tested if ORT and CT were correlated (Pearson, two-sided correlations) with the TAS-20 and the IRI. No correlations were significant with the IRI scores. TAS-20 is one of the most commonly used measures of alexithymia traits, with a higher TAS-20 score indicating a higher inability to experience their own bodily emotions. Given that these tests were exploratory and since the study was not designed in terms of statistical power to directly answer this question on the relationship between alexithymic traits and BR metrics for facial expressions, I report the results without strict corrections for multiple comparisons, so that future studies can look into the promising correlations in a planned confirmatory testing. TAS-20 score was negatively correlated with the cumulative time for the happy expressions in the free mimicry condition (i.e., CTfree_happy; $r(26) = -0.42$, $p = 0.02$), and positively correlated with onset resolution times for the happy expressions in the free mimicry condition (i.e., ORTfree_happy; $r(26) = 0.49$, $p = 0.007$). The correlation with the cumulative time (i.e., CTfree_happy) indicates that individuals with difficulty in experiencing their own emotion (as indicated by the high traits of alexithymia), tend to maintain emotional (here happy) faces as the content of their consciousness for a shorter time than individuals with lower levels of alexithymia. Furthermore, as indicated by the correlation with ORT (i.e., ORTfree_happy), the initial time for perceptual disambiguation and conscious selection of an emotional face is greater in individuals with higher levels of alexithymia than in individuals with lower levels of alexithymia. This can be interpreted that alexithymic individuals tend to have difficulty and take longer time in resolving ambiguity in the direction of a more emotional face. It is interesting to note that these effects emerged in the condition in which participants could freely use their facial mimicry and these correlations are reduced in the blocked condition (CTblocked_happy: $r(26) = -0.23$, $p = 0.24$ ORTblocked_happy: $r(26) = 0.35$, $p = 0.06$), which is along the direction that sensorimotor simulation theory would predict (see “Discussion”).

5.3 Experiment 2

5.3.1 Method

Participants. Twenty-two healthy female participants were recruited among students at the University of Padua (average age in years = 24.01, SD = 4.16, 2 left-handed). The sample size is considered under powered on the basis of Experiment 1 effect size. For the estimated effect size, a sample size of 22 participants reaches a 70% power level[9].

All volunteers gave written informed consent in accordance with the Declaration of Helsinki, and all experimental procedures were approved by the local research ethics committee (Comitato Etico della Ricerca Psicologica Area 17, University of Padua) and performed in accordance with its guidelines. Participants had normal or corrected-to-normal vision. Color blindness was assessed using the Ishihara color blindness test (Shinobu, 1918). One participant was excluded from analysis due to an experimenter's error in following the procedure for the application of the lens. At the end of the experiment, participants completed the TAS-20 and the IRI questionnaires. Scores on both questionnaires were in the normal range (TAS-20: M = 42.62, SD = 9.76 IRI: M = 105.04, SD= 10.17).

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[9] Data collection stopped prematurely because of COVID 19 protocols and guidelines.

Procedure. The same material and apparatus as in Experiment 1 was used, and also the same measures and analyses. Only the specific chopstick manipulation and anaglyph google setting differed from Experiment 1. Here the participant was asked to hold the chopstick between her/his teeth (see figure 11, right panel), which induce a modification of facial mimicry that engages the zygomaticus major muscles and is congruent with a "standard" smile. As in Korb's et al. (2017) procedure, participants wore the red lens of the glasses over the non-dominant eye. Eye dominance was assessed using a hole-in-the-card test[10].

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[10] The participants were instructed to hold a card with both hands and to view a 3 m distant target through a hole in the middle of the card, keeping both eyes open. The eye that was able to see the target through the hole was considered to be the dominant eye.

5.3.2 Results

Ratings. Evaluation of valence and arousal were performed on individual stimuli at the end of each mimicry condition (i.e., two blocks). No effect of the session in terms of mimicry manipulation was observed (valence F(1, 20) = 0.38, p = 0.544, d = ; arousal F(1, 20) = 0.0002, p = 0.946, d = 0.006). Valence ratings differed according to a priori expectations, F(1, 20) = 364.84, p < .001, d = 8.54. Neutral facial expressions were rated close to zero (M = − 1.12; SD = 0.87; range = − 3 to 3), which was more negative than happy (M = 2.49; SD = 0.49; range = − 3 to 3). Happy expressions were rated more positively than neutral expressions, t(20) = 19.1 p < .001, d = 4.27. Arousal ratings also differed according to a priori expectations, F(1, 20) = 68.46, p < .001, d = 3.7. They were lower for neutral expressions (M = 2.47; SD = 1.18; range = 1–7) than for happy expressions (M = 5.48, SD = 1.17; range = 1–7). Neutral facial expressions were rated as significantly less arousing than happy facial expressions, t(20) = 8.27, p < .001, d = 1.85.

Testing the early effects of forced mimicry (i.e., resolution of ambiguity). For both initial percept (IP) and onset resolution time (ORT), the statistical models included the factors mimicry (free vs. forced).

Initial percept (IP). In terms of IPs, happy expressions were reported more frequently in both mimicry conditions (blocked: 225 trials; free: 211 trials) than neutral expressions (blocked: 108; free: 120). The odds ratio is not statistically significant, and the estimated value is 0.386 ($\beta = \ 0.173$, $SE = 0.166$, 95% CI $[-0.15, 0.50]$, $t \ 1.04$, $p = 0.298$).

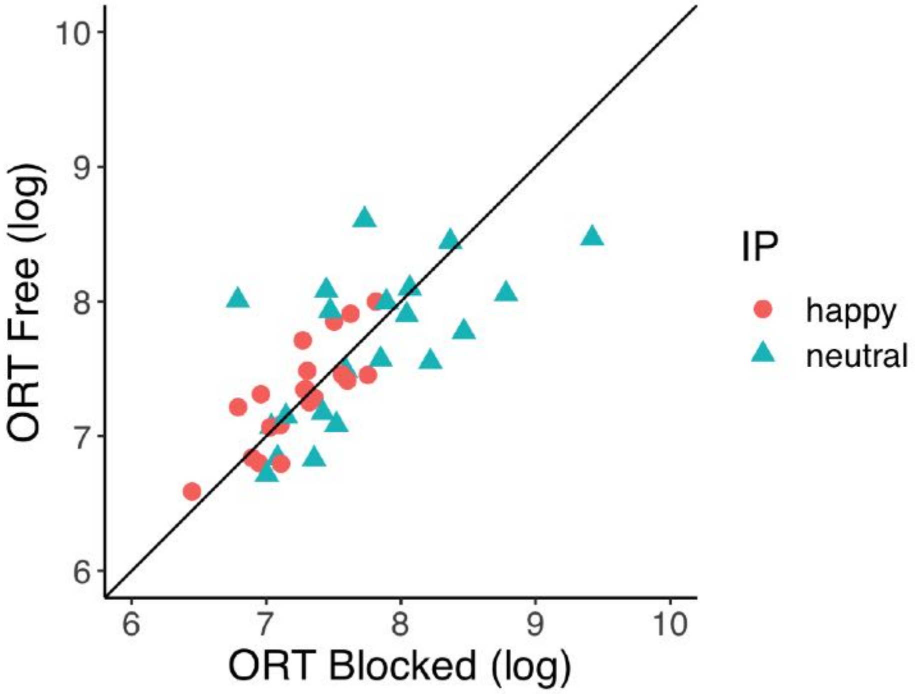

Figure 14. Each point represents a participant's onset resolution time (ORT) for a specific IP. Mimicry condition is projected on the x and y axes, the black line represents the axes equidistance. The ORT is expressed in milliseconds.

Onset resolution time (ORT). Significant difference was found for the IPs independently of mimicry condition, F(1,20) = 35.92, p < .001, d = 2.68. See figure 14. In general, the findings related to the IP and ORT metrics seem not to support the early account, that is, the contraction of the zygomatic muscle did not influence the resolution of ambiguity in favor of happy faces and/or at the expense of neutral facial expressions. These results seem to be in line with Experiment 1. To note, in terms of IP frequency and ORT, emotional faces showed an advantage when compared to neutral faces irrespective of the mimicry conditions t(20) = -5.99, p < .001, d = 1.34.

Testing the late effects of forced mimicry (i.e., stabilization of conscious contents). For the cumulative time (CT) metric, the statistical model included the factors mimicry (free vs. blocked) and the reported content (happy vs. neutral vs. mixed). A significant difference was observed for reported content independently of the mimicry condition, F(1.86, 37.25) = 40.08, $p < .001$, $\eta^2 = 0.67$. CT for happy facial expressions was longer than CT for neutral faces, t(40) = 6.56, $p < .001$, d = 1.04, and longer than CT for mixed percepts, t(40) = 8.56, $p < 0.001$, d = 1.04. This result is in line with Experiment 1. The main effect of mimicry did not yield to significant differences, F(1, 20) = 0.12, p = 0.735, d = 0.15. In accordance with the hypothesis, CT for reported content showed an opposite trend as a function of the mimicry conditions, that is CT for happy facial expressions was expected to increase when mimicry was manipulated congruently with the happy expression (forced mimicry condition: M = 7.05 s; SD = 4.65 s; free mimicry condition: M = 6.94 s; SD = 4.88 s), conversely CT for neutral faces was expected to decrease when mimicry was forced (forced mimicry condition: M = 3.72 s; SD = 3.7 s; free mimicry condition: M = 3.68 s; SD = 3.9 s). This observation was substantiated by the significant interaction between mimicry manipulation and the reported content, F(1.65, 32.99) = 3.67, p = 0.04, $\eta^2 = 0.16$. However, the observed interaction was statistically conveyed entirely by a modulation of CTs for happy expressions as a function of the mimicry manipulation, such that for happy faces CT in the forced mimicry condition was longer than CT in free mimicry condition, t(41.7) = 2.6, p = 0.013, d = 0.4. The evidence in favor of the alternative hypothesis H1 may be classified, in terms of Bayes factor, as strong, BF10 = 18.18. In order to substantiate the conclusions we further report the post-hoc comparisons for neutral and mixed percepts, t(41.7) = − 0.502, p = 0.618, d = 0.08, BF10 = 0.25; t(41.7) = − 1.947, p = 0.058, d = 0.3, BF10 = 0.80, respectively. To note, the evidence in favor of the null hypothesis H0 for neutral faces, can be classified as weak, overall suggesting that the pattern of the observed findings is robust. See Figure 15.

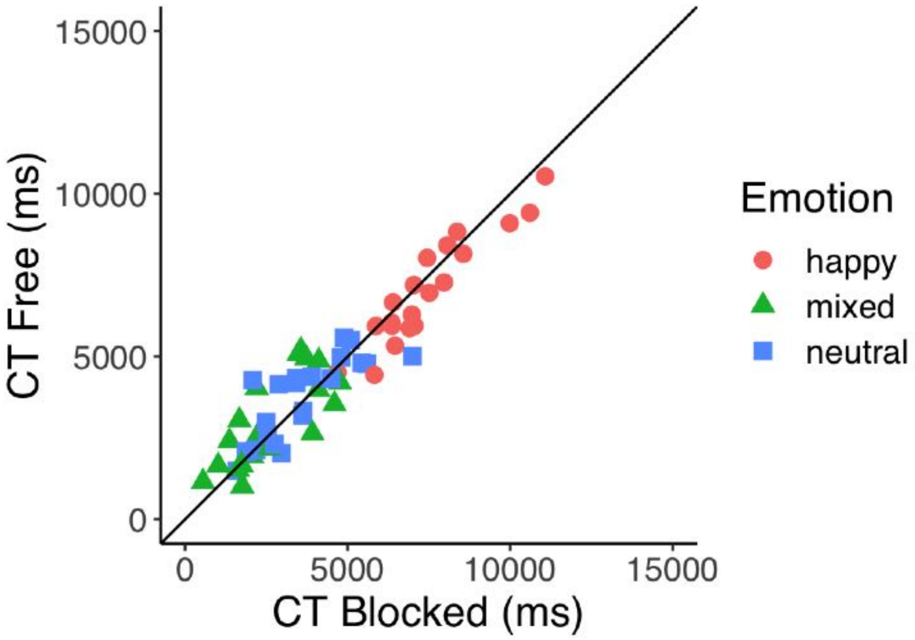

Figure 15. Each point represents a participant's cumulative time (CT) for a specific emotion. Mimicry condition is projected on the x and y axes, the black line represents the axes equidistance. The CT is expressed in milliseconds.

Questionnaires. In exploratory analyses, I tested if ORT and CT were correlated (Pearson, two-sided correlations) with the TAS-20 and the IRI. No correlations were significant with the TAS-20 scores. IRI is one of the most commonly used statements to measure individual differences in empathy. IRI subscales measure empathy as various types of both cognitive processes (perspective taking and fantasy subscales) and affective processes (empathic concern and personal distress subscales). Given that these tests were exploratory and since the study was not designed in terms of statistical power to directly answer this question on the relationship between empathy and BR metrics for facial expressions, I reported the results without strict corrections for multiple comparisons, so that future studies can look into the promising correlations in a planned confirmatory testing. IRI score was positively correlated with the cumulative time for the neutral expressions in the free mimicry condition (i.e., CTfree_neutral; r(19) = 0.44, p = 0.04), and positively correlated with IP for the neutral expressions in the free mimicry condition (i.e., IPfree_neutral; r(19) = 0.54, p = 0.012) and negatively correlated with IP for the happy expressions in the free mimicry condition (i.e., IPfree_happy; r(19) = - 0.5, p = 0.021). The correlation with the cumulative time (i.e., CTfree_neutral) indicates that individuals with higher IRI score, tend to maintain emotional (here neutral) faces as the content of their consciousness for a longer time than individuals with lower levels of empathy. This correlation seems incoherent with the previous finding. An explanation could rely on the notion that the simulation mechanism is especially triggered in those conditions in which facial expressions are particularly subtle or ambiguous (see, e.g., Wood, Rychlowska, et al., 2016). Along this line of reasoning, neutral expressions may be conceived as more ambiguous than full expressions of happiness. Indeed, it is known that neutral expressions can be more easily misinterpreted than full emotional expressions, in both healthy (Bell et al., 2017) and clinical populations (Bourke et al., 2010; Daros et al., 2013; Eack et al., 2015; Kohler et al., 2003). In this case, participants were free to use their mimicry, therefore the ambiguity of the neutral stimuli may have triggered the activation of the mimicry. In particular, the subscale perspective taking (i.e., cognitive processes) is positively correlated with the CT neutral (i.e., CTfree_neutral; r(19) = 0.5, p = 0.02, CTblocked_neutral; r(19) = 0.48, p = 0.02,) and negatively correlated with the CTblocked_happy (r(19) = - 0.44, p = 0.047). The subscale empathic concern (i.e., affective processes) is negatively correlated with the CT free_mixed (r(19) = - 0.47, p = 0.03). Furthermore, as indicated by the correlation with IP (i.e., IPfree_happy), the initial content of the perceptual disambiguation is greater in individuals with higher levels of empathy than in individuals with lower levels of empathy. In particular, the subscale perspective taking (i.e., cognitive processes) is positively correlated with the IPfree_neutral (r(19) = 0.5, p = 0.02), and negatively correlated with the IPfree_happy (r(19) = - 0.5, p = 0.02). This can be interpreted in the fact that cognitive processes involved in empathy tend to take a longer time when the facial expression is ambiguous. It is interesting to note that these effects emerged in the condition in which participants could freely use their facial mimicry and these correlations are reduced in the blocked condition (CTblocked_happy: r(19) = - 0.44, p = 0.047), which is along the direction that sensorimotor simulation theory would predict (see "Discussion").

5.4 Experiments 1 and 2: Discussion

In the present investigations, I wanted to test the hypothesis of a functional role of the observer's facial mimicry in ambiguity resolution and/or stabilization within awareness of faces with happy and neutral facial expressions during a binocular rivalry task. In particular, in the light of the sensorimotor simulation model by Wood and colleagues (Wood, Lupyan, et al., 2016), I hypothesized that the communication between sensorimotor and visual systems could either modulate the (initial) resolution of ambiguity under conditions of binocular rivalry or that signals from sensorimotor system could stabilize conscious representations of face stimuli in a later stage once the ambiguity is resolved. In order to test my hypothesis, I asked participants to perform a standard binocular rivalry task by presenting a happy and a neutral face (from the same identity) in rivalry. Crucially, I manipulated participants' facial mimicry such that in one condition of the experiment they performed the task with their facial mimicry restricted by a chopstick to be held between the lips (i.e., Experiment 1) or between the teeth (i.e., Experiment 2) in order to inhibit or activate the contraction of the zygomatic major, that is the muscle mainly involved when smiling; in the other half of each experiments participants could freely use their facial mimicry.

I reasoned that if the signal from the sensorimotor cortices is involved in the early conscious processing of facial expressions, manipulating (i.e., inhibition vs excitation) the zygomaticus major should have biased the initial competition between the two rivalry stimuli, such that initial resolution of the ambiguity would have been in favor of neutral faces when the chopstick was held between the lips and in favor of happy faces when the chopstick was held between the teeth when compared to the free mimicry condition. My primary outcome measures were the frequency of the initial percept (*IP*) and the onset resolution time (*ORT*) until the first rivalry as a function of the facial mimicry manipulation. A different but equally interesting scenario foresees that if the sensorimotor signal is integrated with the visual percept only at later stages of processing when the ‘winning’ stimulus is the content of consciousness, then blocking of facial mimicry would have modulated the stabilization of conscious perception of facial expressions. I tested this scenario through the analysis of the cumulative time (*CT*) as a function of the mimicry manipulation. I reasoned that, under an iterative model scenario (i.e., sensorimotor and visual systems that iteratively share information from very early stages of processing), an impact of mimicry manipulation could have been expected either on the initial percept and/or on the cumulative time.

First, and importantly, I replicated previous findings (Alpers & Gerdes, 2007; Yoon et al., 2009) (see also Bannerman et al., 2008) for similar findings) such that cumulative time for happy facial expressions was longer than cumulative time for neutral faces, regardless of the mimicry manipulation condition in both experiments. Furthermore, with regard to the initial percept analysis, in both experiments I found that happy expressions were more frequently perceived as first stimuli compared to neutral faces. These results corroborate the adequacy of the present paradigm and the quality of the present data. It is to be understood whether these CT results can depend on differences in the low-level visual features, such as the greater power in high-spatial frequencies of the happy face due to the presence of the teeth. Notably, these low-level differences cannot account for the impact of the mimicry manipulation on CTs.

Notably, in Experiment 1 & 2 the interaction between reported content (i.e., happy, neutral, and mixed percepts) and mimicry manipulation did yield significant differences for the cumulative time, such that cumulative time for neutral and emotional expressions showed opposite trends as a function of the mimicry conditions. Further, analyses of data from Experiment 1 provided evidence that cumulative time for neutral faces increased when mimicry was blocked (i.e., lips) compared to when participants could freely use their facial mimicry, thus providing only partial support to my hypothesis. In fact, although I observed a modulation of the cumulative time for neutral faces as a function of the mimicry manipulation, I did not observe any effect of the mimicry manipulation on the cumulative time for happy faces.

In Experiment 2, analyses provided evidence that cumulative time for happy faces increased when mimicry was forced (i.e., teeth) compared to when participants could freely use their facial mimicry. As for Experiment 1, thus results provided only partial support to my hypothesis. Again, although I observed a modulation of the cumulative time for happy faces as a function of the mimicry manipulation, I did not observe any effect of the mimicry manipulation on the cumulative time for neutral faces. All these results (i.e., Experiments 1 and 2) are corroborated by the Bayes factor, which suggests that both provide robust evidence, the first in favor of the alternative hypothesis and the other in favor of the null hypothesis.

How to reconcile these results in the light of my initial hypothesis and the (sensorimotor) simulation models? A possible explanation could lie in the type of experimental manipulation of facial mimicry I have adopted here. In the condition of active alteration of mimicry (through the chopstick), it is possible that it was the *congruent cross-modal match* between the sensorimotor feedback and the visual representation of faces with neutral expression (in Experiment 1) and happy expression (in Experiment 2) that has facilitated their stabilization in awareness. This will also explain the coherence of results between experiments. Future studies should clarify – possibly also including electromyographic monitoring – whether it is this cross-modal congruence (sensorimotor-visual) that may facilitate stabilization in awareness for faces with different facial expressions, both neutral and emotional.

As a limitation, I admit that the present results are only generalizable to neutral and happy facial expressions and to the role that facial mimicry can play in their stabilization in awareness. Regarding the CT distribution during BR, the increase in CT for neutral faces in the blocked mimicry condition could be the result of an overall loss of CTs for mixed and happy facial expression, as the results plotted in Figure 13 seem to suggest. This CT redistribution requires further investigations to understand more precisely the role/content of mixed components.

An open debate regards the possibility to trigger a simulation process when looking at a neutral face. One may argue that neutral faces lack visible muscle contractions, and therefore cannot elicit muscle contractions in the perceiver. Unfortunately, EMG measures are absent in the present experiments, but evidence in favor of simulation during observation of neutral facial expression is given by Sessa (2018).

Another aspect of the present work that will require future studies to provide a complete picture of the generalizability of these results concerns the female samples of the present studies. In the light of the novelty of this field of investigation, I deemed it appropriate to include a sample of only women in order to maximize the probability of observing an effect because of the large body of previous evidence showing that women are more expressive than men (Kring & Gordon, 1998), more accurate in processing emotional expressions (Hoffmann et al., 2010), and selectively impaired in their ability to process expressions of happiness following the disruption of M1 by repetitive transcranial magnetic stimulation (Korb et al., 2015). My results are currently generalizable to women and future experimental designs should include the participants' gender as a factor.

Although a similar trend to that observed for the cumulative time was observed for the initial percept metric (i.e., a higher frequency for faces with neutral expression in the condition of manipulated mimicry compared to the condition of free mimicry and an opposite trend for faces with expression of happiness), the effect was not statistically significant (when corrected for multiple comparisons). These findings indicate that the signal of the sensorimotor system tends not to play a role before the resolution of the ambiguity in favor of one of the two stimuli in rivalry, but rather that the signal from the sensorimotor system mainly acts as a 'stabilizer' of the conscious representation of the face once the congruent stimulus is the current content of consciousness (to note, the concept of 'stabilization' used here is not to be intended as for Leopold (2002) and for Pearson and Brascamp (2008)).

At the present, this whole pattern of findings is almost entirely in line with the results previously reported by Korb and colleagues (Korb et al., 2017) using a breaking continuous flash suppression (b-CFS) task, especially with regard to the early account I tested. However, and importantly, I observed an effect of the mimicry manipulation on the conscious stabilization of the neutral expressions in Experiment 1 and of the happy expressions in Experiment 2, suggesting indeed a role of the sensorimotor system during a later stage of conscious processing which deserves to be investigated further, exploring the possibility that it can be generalized to other emotional expressions.

Taking into account the line of studies on the neural correlates of consciousness and the debate on the temporal onset of consciousness (see, e.g., Förster et al., 2020), it is interesting to remember that two different temporal *loci* have been proposed, one "early" (associated in terms of event-related potentials, ERPs, with the visual awareness negativity in the range of the N2 ERP component; Koivisto & Revonsuo, 2003; Ojanen et al., 2003; Wilenius-Emet et al., 2004), and one "late" (associated with P3b/LP ERP component; e.g., Dehaene & Changeux, 2011). Instead, as regards the effects of the blocking of facial mimicry on the construction of a visual percept, a previous study (Sessa et al., 2018) has shown an impact of the facial mimicry manipulation on visual working memory representations of neutral and emotional faces in terms of a modulation of the sustained posterior contralateral negativity ERP component detected at occipito-temporo-parietal sites (SPCN; e.g., Sessa et al., 2011, 2012; Vogel & Machizawa, 2004). To note a) this ERP component has an onset of about 300 ms post-stimulus, thus supporting the view that visual and sensorimotor information may interact/combine within 300-400 ms following the exposure to a facial expression, and b) the onset of this ERP component is later than the visual awareness negativity (i.e., early temporal locus of the onset of consciousness) and earlier than the P3b/LP (i.e., late temporal locus of the onset of consciousness). Intriguingly, in another study designed to investigate the lower edge of this interaction between sensorimotor and visual systems, it was found that the ERP components P1 and N170 are not modulated as a function of facial mimicry manipulation, except in relation to alexithymic traits, in the direction of a modulation which tends to manifest itself only for individuals with low alexithymic traits (Lomoriello et al., 2021). An attempt to interpret this whole pattern of results could indicate that facial mimicry manipulations may affect high-level visual processing of facial expressions (approximately) after 170 ms and before 300-400 ms. The results of the present studies, on the other hand, indicate that manipulation of facial mimicry does not have an effect on the early resolution of perceptual ambiguity but rather on later stabilization of representations within awareness. Taken together, these results may suggest that the integration of somatosensory information with visual information occurs after the onset of awareness for facial expressions, thus suggesting an early onset of visual awareness. Considering the different time scales of the investigative phenomena (i.e., binocular rivalry and ERP findings), I propose this interpretation with great caution as a possible starting point for future studies.

Finally, although exploratory, I observed noteworthy correlations between the TAS-20 scores with metrics of binocular rivalry as a function of the mimicry manipulation in Experiment 1, and between the IRI scores with metrics of binocular rivalry in Experiment 2. Correlation between TAS-20 scores and onset resolution time suggests that highly alexithymic participants tend to be slower in consciously accessing happy facial expressions when their facial mimicry is free and furthermore correlation with cumulative times indicated, instead, that individuals with higher traits of alexithymia under conditions of free mimicry tend to consciously perceive happy facial expressions for a shorter time compared to individuals with lower traits of alexithymia. These findings are perfectly in line with the very definition of alexithymia which is a subclinical condition involving a lack of emotional awareness and difficulty in identifying (and describing) feelings and facial expressions of emotions (Nemiah, 1976). Regarding IRI correlations, results suggest that participants with a high perspective taking score (that is the subscale associated with the cognitive component of empathy) are disturbed to a larger degree by mimicry manipulation. I do not expand on the subject as the correlations I have investigated are currently exploratory, however I believe that this relationship deserves future investigation.

6 A Pilot study on somatosensory-visual integration

6.1 Experiment 3: Introduction

The present study investigated the role of the observer's somatosensory facial proprioception under conditions of face stimulation. For the purposes of the present work, it is relevant to note a specialized contribution for the somatosensory cortex during emotion recognition in linking visual perception and somatosensory information in a subjective sensory experience (Adolphs et al., 2000; Kragel & LaBar, 2016). In particular, two lines of evidence provide support for the specific involvement of somatosensory cortex (SC) in simulation. The first of these lines demonstrates that failure in emotions recognition in others is linked with somatosensory impairments (Adolphs et al., 2000; Kragel & LaBar, 2016). Brain lesions analyses explicitly reveal that primary SC (S1) and secondary SC (S2), anterior supramarginal gyrus, and insula lesions are associated with a decline in emotion recognition. In line with this body of evidence, virtual brain lesions by means of repetitive transcranial magnetic stimulation (rTMS) over the right somatosensory and right primary motor cortices offered further evidence that SC is crucially involved in emotion recognition (Adolphs et al., 2000; Kragel & LaBar, 2016). In the study by Korb and colleagues (2015), participants were stimulated with rTMS in order to inhibit the activity of the cheek region of the right primary motor cortex (M1) or S1 while they were observing a morphing video from neutral or angry to happy facial expressions. An additional condition of stimulation over the vertex served as a control condition. Interestingly, only the rTMS applied to S1 or M1 had an effect in reducing the mimicry of smiles (S1 $d = 0.654$; M1 $d = 0.700$), and this effect was selective for female participants (Adolphs et al., 2000; Kragel & LaBar, 2016). Korb and colleagues hypothesized that smiling in response to the observation of a smile (i.e., mimicry) is part of the simulation that improves the recognition process and gender differences that are usually observable at the level of perception and production of facial expressions could just reside in a simulation mechanism preferentially activated in women. Previously, other TMS studies have supported similar conclusions, indicating a role of SC in the perception of fearful expressions (single-pulse TMS; Adolphs et al., 2000; Kragel & LaBar, 2016; Pourtois et al., 2004), and demonstrating that SC is involved in the discrimination of facial expressions but not of facial identities (double-pulse TMS; Pitcher et al., 2008). A further complementary study measured somatosensory evoked potentials elicited by tactile stimulation during an emotion recognition task providing information on the time-course of SC involvement during discrimination of facial expressions, which occurs between 40 and 80 ms after facial expression onset (Sel et al., 2014). Overall, this evidence suggests that S1 causally contributes to visual emotion recognition from faces.

Building on this body of evidence, the recent model of sensorimotor simulation by Wood and colleagues (Wood, Rychlowska, et al., 2016) (see figure 1) proposes a key role for the somatosensory cortex in emotion recognition. The model specifies that simulation could or could not include facial mimicry (which is considered by the authors as a spillover of the simulation). In this vein, somatosensory body representations in the SC could be activated from proprioceptive afferent signals (i.e., from mimicry when present) and/or copies of motor commands (i.e., from motor cortex) (Longo et al., 2010). Nevertheless, models of sensorimotor simulation converge on the idea that somatosensory representations and visual representations are integrated (Gallese & Goldman, 1998; Goldman, 1992; Rizzolatti et al., 1996). Accordingly, emotion recognition, as the output of a complex process, could be accomplished from the combined sources of processing, including somatosensory and visual.

Here, I want to test whether the somatosensory activity may influence conscious visual processing of emotional facial expressions. To this aim, I presented facial expressions in binocular rivalry (BR). As in the previous experiments, I have considered three measures. First, the initial percept (IP). Second, onset resolution time (ORT). Third, cumulative time (CT).

I specifically hypothesized that recruiting somatosensory representations will facilitate conscious experiencing of happy facial expressions, in terms of conscious stabilization (i.e., dominance, CT) over neutral facial expressions. I also expect a replication of experiment 1 and 2 regarding the IPs and ORTs measures. In order to test this hypothesis, I implemented a BR paradigm with a neutral and an emotional (i.e., happy) expression of the same identity in rivalry under a manipulation of facial tactile stimulation. Participants' facial somatosensory feedback was manipulated by means of solenoid tappers fixed on the face, bilaterally, and activated for half of the trials. Solenoid tappers were applied on the labial commissure of the mouth[11]. To my knowledge, despite several BR studies using emotional stimuli (Alpers & Pauli, 2006; Alpers et al., 2005; Alpers & Gerdes, 2007; E. C. Anderson et al., 2013; Hernández-Lorca et al., 2019), this is the first attempt to investigate such somatosensory influence on conscious visual perception of emotional expressions.

I expected that congruent somatosensory signal (i.e., due to the tactile stimulation on the labial commissure in half of the trials) with the somatosensory representations of happy expressions could favor the conscious content of happy facial expressions and interfere with the conscious processing of neutral expressions with respect to the absence of tactile stimulation in the other half of the trials.

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[11] Deep EMG tests in peri-oral muscles were conducted in the neurology service of San Bortolo Hospital in Vicenza thanks to Dr Minicucci. We found no peripheral reflexes due to facial stimulation.

Therefore, to test the effect of the tactile stimulation, I analyzed the dominance time in terms of CT. In the present pilot investigation, I opted for a straightforward 2 (facial expression: neutral vs. happy) x 2 (tactile stimulation: stimulation vs. no-stimulation) experimental design. As for experiments 1 and 2, I recruited female participants.

6.1.1 Method

Participants. Eight healthy female participants were recruited (average age in years = 30.12, SD = 5.38, 3 left-handed). At the end of the experiment, participants completed the TAS-20 and the IRI questionnaires. Scores on both questionnaires were in the normal range (TAS-20: M = 44, SD = 5.07 IRI: M = 102.375, SD= 8.08). This is to be considered as a pilot experiment since it is severely underpowered[12] (a sample size of 34 is indeed necessary to reach a power of 80%).

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[12] Data collection was interrupted (March 2020-September 2021) due to COVID 19.

Material and apparatus. Visual stimuli have been displayed using E-Prime2 Software (version 2.0.10.242; Psychology Software Tools, Pittsburgh, PA) on a Bestview S5 (luminosity: 50; contrast: 50) 60 Hz monitor mounted on a VR headset. Original stimuli have been selected from the Karolinska Directed Emotional Faces (Lundqvist et al., 1998) and included one male and one female face each displaying a neutral and a happy expression (AM10NES, AM10HAS, AF01NES, AF01HAS). Visual stimuli were presented covering 16.5 ± .5 degrees of visual angle in height and width. Images have been cropped with the software GIMP (version 2.8.10, https:// www. gimp. Org) 320 x 320 pixels centering the face in the middle of the square (e.g. figure 16). Happy and neutral faces of the same identity have been analyzed and matched (in terms of contrast and luminance histograms) by using Fiji (Schindelin et al., 2012).

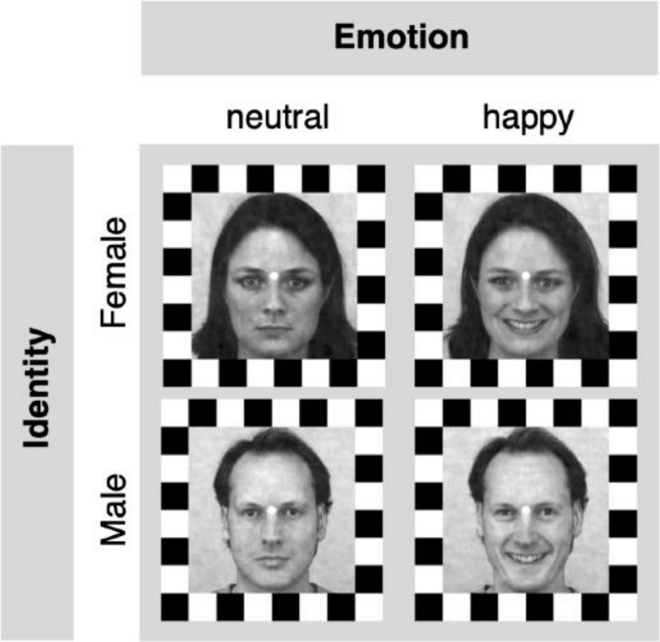

Figure 16: Visual stimuli. A white 12-pixel fixation point and 40-pixel black and white squares frame were applied to the images to facilitate binocular fusion using GIMP (version 2.8.10, https://www.gimp.org).

Procedure. Participants seated on a comfortable chair in a silent, temperature-controlled room. Solenoid tappers (Dancer Design, St. Helens, UK) were fixed on the two-labial commissures of the mouth (see figure 17). The amplitude of the solenoid tappers was set in two steps. First, stimulation (10 sec low amplitudes) was presented to the participants in order to let them familiarize with the tactile sensation. Then, the participant was asked to match the sensation in order to be neutral (i.e., not comfortable and not uncomfortable) by adjusting the amplitude. Before starting the experiment, the visual apparatus was set, and participants were trained. During the experiment, participants were asked to focus on a fixation point placed in the middle of the visual field. The experiment consisted of two blocks. In each block, all combinations of rivalry stimuli (i.e., 4 pairs) were randomly presented twice, with and without the tactile stimulation, for a total of 16 trials in each block. Each rivalrous stimulus was presented for 30 seconds (that is optimal to avoid the solenoid to be warm) preceded by a 2-second fixation point and followed by a black screen lasting 3 sec. Participants were asked to report the predominant percept in real time by means of a keyboard (keys: j, k, l; these keys are adjacent to each other on the standard keyboard in a left to right order). Participants were asked to use the keyboard with their writing hand. Coding instructions were presented before the beginning of the block; the order of the “j” and “l” keys for the coding of “happy” and “neutral” facial expressions was counterbalanced between blocks; “k” key was always corresponding to “mixed” percept. At the end of the first block (16 trials), a short break was recommended to the participants in order to avoid any kind of visual tiredness. At the end of the second block, valence and arousal of each stimulus were measured respectively on a -3/+3 and 1/7 scales. The order of the two block conditions (coding instructions) was counterbalanced between subjects.

Figure 17. Photograph of experiment 2 apparatus.

Data reduction & data analysis. As a further extension to Experiment 1 & 2, the same measures and analysis are used in this experiment.

6.1.2 Results

Ratings. Evaluation of valence and arousal were performed on individual stimuli at the end of the second block. Valence ratings differed according to a priori expectations, $F(1, 7) = 147.56$, $p < .001$, $d = 9.18$. Neutral facial expressions were rated close to zero ($M = -0.6$; $SD = 1.03$; range $= -3$ to 3), which was more negative than happy ($M = 2.87$; $SD = 0.33$; range $= -3$ to 3). Happy expressions were rated more positively than neutral expressions, $t(7) = 12.148$ $p < .001$, $d = 4.59$. Arousal ratings also differed according to a priori expectations, $F(1, 7) = 33.17$, $p < .001$, $d = 4.35$. They were lower for neutral expressions ($M = 2.14$; $SD = 1.3$; range = 1–7) than for happy expressions ($M = 4.62$, $SD = 1.3$; range = 1–7). Neutral facial expressions were rated as significantly less arousing than happy facial expressions, $t(7) = 5.76$, $p < .001$, $d = 2.18$.

Testing the early effects of blocked mimicry (i.e., resolution of ambiguity). For both initial percept (IP) and onset resolution time (ORT), the statistical models included the factors mimicry (tactile stimulation vs. no stimulation).

Initial percept (IP). In terms of IPs, happy expressions were reported more frequently in both stimulation conditions (tactile stimulation: 94 trials; no stimulation: 90 trials) than neutral expressions (tactile stimulation: 25 trials; no stimulation: 20 trials). The odds ratio is not statistically significant, and the estimated value is 1.6 ($\beta = 0.256$, $SE = 0.354$, 95% CI [-0.45, 0.97], $t\ \ 0.721$, $p = 0.471$).

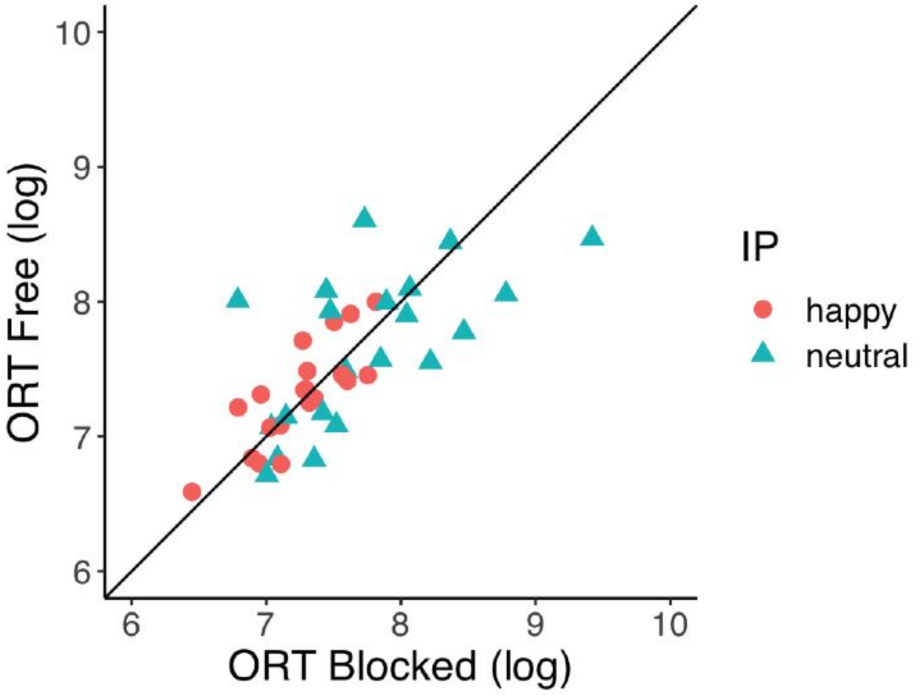

Figure 18. Each point represents a participant's onset resolution time (ORT) for a specific IP. Tactile stimulation condition is projected on the x and y axes, the black line represents the axes equidistance. The ORT is expressed in milliseconds.

Onset resolution time (ORT). No significant differences were found (stimulation F(1,5) = 0.11, p = 0.755, d = 0.3; IP F(1,5) = 5.96, p = 0.059, d = 2.18; interaction between stimulation condition and IP F(1,5) = 0.05, p = 0.84, d = 0.2). In general, the findings related to the IP and ORT metrics seem not to support the early account, that is, the tactile stimulation did not influence the resolution of ambiguity in favor of happy faces and/or at the expense of neutral facial expressions. These results seem to be in line with the previous experiments (1 and 2). See figure 18.

Testing the late effects of blocked mimicry (i.e., stabilization of conscious contents). For the cumulative time (CT) metric, the statistical model included the factors stimulation (tactile stimulation vs no stimulation) and the reported content (happy vs. neutral vs. mixed). A significant difference was observed for reported content independently of the stimulation condition, F(1.51, 10.55) = 5.66, p = 0.027, η^2 = 0.45. CT for happy facial expressions was longer than CT for neutral faces, t(14) = 3.194, p = 0.0195, d = 3.194. This result is in line with previous findings (Alpers & Gerdes, 2007; Yoon et al., 2009) and the previous experiments presented in this Thesis. The main effect of stimulation did not yield to significant differences, F(1, 7) = 2.83, p = 0.137, d = 1.27. In accordance with the hypothesis, CT_happy showed a trend as a function of the mimicry conditions, that is CT for happy faces was expected to increase when the face was stimulated (tactile stimulation condition: M = 18.766 s; SD = 12.12 s; no stimulation condition: M = 17.39 s; SD = 11.6 s; See Figure 19). This observation was not substantiated by the significance of the interaction between stimulation conditions and the reported content, F(1.30,9.08) = 0.48, p = 0.553, η^2 = 0.06. It is important to note that the evidence in favor of the alternative hypothesis H1 is taken with a 30% power level.

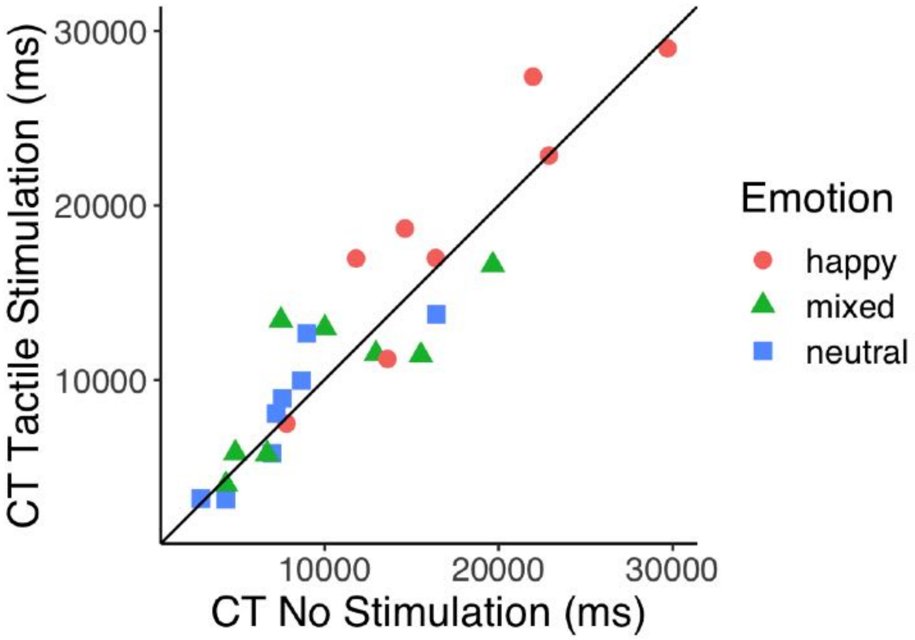

Figure 19. Each point represents a participant's cumulative time (CT) for a specific emotion. Tactile stimulation condition is projected on the x and y axes, the black line represents the axes equidistance. The CT is expressed in milliseconds.

Questionnaires. In exploratory analyses, I tested if ORT and CT were correlated (Pearson, two-sided correlations) with the TAS-20 and the IRI. No correlations were significant with the IRI scores. TAS-20 is one of the most commonly used measures of alexithymia traits, with a higher TAS-20 score indicating a higher inability to experience their own bodily emotions. As explained in Experiment 1, I reported the results without strict corrections for multiple comparisons, so that future studies can look into the promising correlations in a planned confirmatory testing. TAS-20 score was negatively correlated with the IP for the happy expressions in the tactile stimulation condition (i.e., IPstimulation_happy; $r(6) = -0.75$, $p = 0.032$), and in the no stimulation condition (i.e., IPno_happy; $r(6) = -0.8$, $p = 0.016$). The correlation with the initial percept (i.e., IP<>_happy) indicates that individuals with difficulty in experiencing their own emotion (as indicated by the high traits of alexithymia), tend to resolve the initial perceptual disambiguation selecting the neutral percept, irrespective of the stimulation condition.

6.2 Discussion

In the current pilot study, I investigated the role of somatosensory representations in facilitating the conscious experiencing of happy facial expressions. I manipulated tactile stimulation fixed on the observer face (stimulation vs no stimulation) under BR. Participants reported the changes in percept dominance (happy face vs neutral face) by means of a keyboard. I hypothesized that the communication between somatosensory and visual systems could either modulate the (initial) resolution of ambiguity under conditions of BR or that signals from somatosensory representations could stabilize conscious representations of face stimuli in a later stage once the ambiguity is resolved.

Similarly to experiments 1 and 2, I reasoned that if the signal from the somatosensory cortices is involved in the early conscious processing of facial expressions, tactile stimulation of the face should have biased the initial competition between the two rivalry stimuli, such that the initial resolution of the ambiguity would have been in favor of happy faces when stimulated when compared to the no stimulation condition. My primary outcome measures were the frequency of the initial percept (*IP*) and the onset resolution time (*ORT*) until the first rivalry as a function of the facial tactile stimulation. A different but equally interesting scenario foresees that if the somatosensory signal is integrated with the visual percept only at later stages of processing when the ‘winning’ stimulus is the content of consciousness, then facial tactile stimulation would have modulated the stabilization of conscious perception of facial expressions. I tested this last scenario through the analysis of the cumulative time (*CT*) as a function of the tactile stimulation. Again, under an iterative model scenario (i.e., somatosensory and visual systems that iteratively share information from very early stages of processing), an impact of tactile stimulation could have been expected either on the initial percept and/or on the cumulative time.

First, and importantly as in experiments 1 and 2, I replicated previous findings (Alpers & Gerdes, 2007; Bannerman et al., 2008; Yoon et al., 2009) such that cumulative time for happy facial expressions was longer than cumulative time for neutral faces, regardless of the tactile stimulation manipulation condition. Furthermore, in the initial percept analysis, I found a trend such that happy expressions seem more frequently perceived as first stimuli compared to neutral faces, but the effect was not statistically significant when corrected for multiple comparisons.

Notably, the pilot results did not yield significant interaction between reported content (i.e., happy, neutral, and mixed percepts) and tactile stimulation manipulation in terms of cumulative time, but cumulative time for happy showed expected trends as a function of the tactile stimulation, such that CT for happy percept seems to be longer when the face is stimulated (see figure 19).

Finally, although exploratory, I observed noteworthy correlations between the TAS-20 scores with metrics of binocular rivalry as a function of the tactile stimulation manipulation.

At the present, the pattern of figure 19 seems in line with the results previously reported in experiments 1 and 2 even if it is not supported by statistics with the actual pilot sample. The trend is also in line with Kragel and colleagues' results (Kragel & LaBar, 2016), where the subjective experience from facial expression perception is linked with responses in the SC activity. In figure 19 when stimulated participants seem to experience happy faces for a longer time with respect to the condition with no facial stimulation. In summary, although I did not observe any effect of the tactile stimulation manipulation on the CT for happy faces, the sample size does not allow me to take any statistical decision and interpretation must be done with great caution.

7 Experiments consciousness time course

7.1 Experiments 4 and 5: Introduction

As well as the world changes, also the conscious content (usually) does (Aru & Bachmann, 2017; Pun et al., 2012). Research has largely neglected the study of these transitions from one conscious content to different content, specifically whether the temporal dynamics of these transitions may depend on the nature of the stimuli.

In Experiment 4 and Experiment 5 I want to test whether the time-course of the switches of conscious content that occur during BR depend on the content properties, particularly regarding the emotional information of the stimuli.

According to the theories of consciousness, the shift from unconscious to conscious perception arises as a process of formation; as such, the *formation phase* consists in updating the current version of the phenomenal content (Aru & Bachmann, 2017; Bachmann, 2000; Tononi, 2008), i.e. conscious content arises and replaces previous content. Conscious content is also often the result of the integration of processing from multiple systems (e.g., visual and proprioceptive), as I showed in the previous experiments. As such, during the formation phase, processing from multiple channels is integrated to generate that particular conscious content and no other content.

We can assume that there are two options for the information that is the current conscious content: either 1) it is still maintained as the content of consciousness, or 2) it is excluded from consciousness. In this second scenario, the disformation of the conscious content is conceived as an important phase of the "later" scenario discussed in the context of Experiment 1 and Experiment 2. When using a simple two-choice response to monitor participants' experiences of alternances in BR, the researcher can only analyze data about the onset of consciousness (the "early" scenario I have explored in experiments 1 & 2) and data about the stabilization/maintenance of the conscious content (the "late" scenario I have explored in experiments 1 and 2). However, this "late" scenario embraces not only the phase in which the conscious content stabilizes but also its fading from consciousness, namely the *disformation phase*.

Intuitively, the time to build up a conscious content (i.e., formation phase) will depend on the level and complexity of processing, while the content in itself will depend on the features that the observer is able to extract from the physical world and that are integrated (Anzulewicz et al., 2015). For example, the consciousness of a noisy car will depend on the extraction of visual and auditory information and their integration.

A similar logic can be taken into consideration with regard to faces, which are characterized by several sources of information, such as visual information (their configuration, their features), and higher-level information, such as familiarity, ethnicity, and above all, emotions conveyed by facial expressions. The most accredited neural models of face processing consider multiple areas as responsible for the visual analysis of faces. In the case of faces with a facial expression, additional brain areas would be recruited to assign emotional meaning to the facial expression processed at the level of the visual system. These models are in line with sensorimotor simulation models. They assign an essential role to the premotor areas, the inferior frontal gyrus, and also to the limbic system (Carr et al., 2003; Fox et al., 2009; Furl et al., 2013, 2015; Harris et al., 2014; Haxby & Gobbini, 2011; Johnston et al., 2013; Trautmann et al., 2009). From this point of view, it is legitimate to believe the attribution of the meaning to emotional facial expressions requires the combination of multiple sources of processing by visual, limbic, and sensorimotor areas.

Based on the well-known effect that the conscious content of emotional faces predominates over neutral faces (Alpers & Gerdes, 2007) during BR, I assume a difference in terms of ‘richness’ between emotional faces and neutral faces. I propose that such a difference will modulate the consciousness time-course. This work is innovative; it is unknown if the information integration can influence the time-course of conscious perception of facial expressions in the BR paradigm.

To better characterize the consciousness time-course, here, differently from previous experiments, participants were required to report their BR content of consciousness using a joystick. The time-course of joystick response can be considered a good proxy of the time-course of the conscious experience (Naber et al., 2011).

By using the joystick, the time-series data of BR (sampled at 100 Hz) require new ad-hoc measures. Here I will compute the *predominance mean* (PM), i.e. a measure of the proportion of total time of dominance in awareness of one percept over the other (see Alpers & Gerdes, 2007 for similar measure), and furthermore, I will compute kinematic speed parameters able to capture the BR alternances as measured by the joystick movements, i.e. *movement transitions* (MT) that could be considered as proxies of the time-courses of the formation and disformation phases of conscious contents (see Methods for details).

In Experiments 4 & 5, I expect the time-course of consciousness (in terms of speed) to be different as a function of the type of facial expression (happy vs neutral). More specifically, I hypothesize that conscious contents of happy facial expressions are characterized by a slower disformation phase (slower speed) when compared to conscious contents of neutral facial expressions (higher speed), i.e. conscious happy expressions are more resistant to fading from consciousness. Regarding the formation phase it is important to consider that the mechanism involved during transitions is different from the mechanism involved during the first binocular resolution (i.e., ORT, IP) in which the two visual inputs compete equally for accessing the conscious content. During transition, one input is already part of the content, and only the suppressed percept competes for accessing the content. In this regard, I do not have a specific hypothesis about the formation phase. Finally, I wanted to test whether the time-course of consciousness (in terms of speed) differs as a function of the phase (formation vs disformation).

In Experiment 4, I also consider participants' gender as a factor, and I expect to observe interactions with this factor, since in previous studies female participants have been found to be more sensitive to emotional expressions when compared to male participants.

In Experiment 5, I hypothesize that effect of consciousness time-course dynamics of facial expressions is less evident in participants with Moebius syndrome, because of the absence of proprioceptive signals coming from facial muscles that cannot contribute to conscious representations of happy facial expressions.

Therefore, to test the hypothesis, I analyzed the movement transition (MT) in terms of speed. The advantage of happy over neutral expressions is controlled by testing the predominance (PM).

7.2 Experiment 4

7.2.1 Method

Participants. For a medium effect size, a sample size of 34 participants is required to reach an 80% power level. Power has been estimated using the pwr package (Champely et al., 2020). Forty healthy participants were recruited among students at the University of Padua (average age in years = 22.35, SD = 2.6, 20 males, 3 left-handed). All of them were volunteers and gave written informed consent in accordance with the Declaration of Helsinki. All experimental procedures were previously approved by the local research ethics committee (Comitato Etico della Ricerca Psicologica Area 17, University of Padua) and performed in accordance with its guidelines. Participants had normal or corrected-to-normal vision. At the end of the experiment, participants completed the TAS-20 and the IRI questionnaires. Scores on both questionnaires were in the normal range (TAS-20: M = 46.05, SD = 12.12 IRI: M = 100.2, SD= 10.45).

Material and apparatus. Visual stimuli were displayed using E-Prime2 Software (Psychology Software Tools, Pittsburgh, PA) on a Bestview S5 (luminosity: 50; contrast: 50) 60 Hz monitor mounted on a VR headset. The same stimuli as in Experiment 3 were used (see figure 20). Visual stimuli were presented covering 16.5 ± .5 degrees of visual angle in height and width.

Figure 20. Photograph of experiment 4 and 5 apparatus.

Procedure. Participants seated on a comfortable chair in a silent, temperature-controlled room. Before starting the experiment, the visual apparatus was set, and participants were trained. During the experiment, participants were asked to focus on a fixation point placed in the middle of the visual field. The experiment consisted of one session of four blocks. Each participant performed two “emotion rivalry” (happy vs neutral facial expression rivalry) and two “gender rivalry” (male vs female face gender rivalry) blocks. The order of the rivalry conditions was counterbalanced between subjects. In each block, combinations of rivalry stimuli (i.e., 4 pairs) were randomly presented, for a total of 8 trials in each block. See figure 21, which shows all the possible combinations of rivalry stimuli shown in the experiment. Each stimulus was presented for 15 seconds preceded by a 2-second fixation point and followed by a black screen lasting 3 sec. Participants were informed that on each trial they could see one of two faces, and that the appearance might change from one to the other during the trial. Participants were asked to report the predominant percept in real time by means of a joystick over the left-right axis range. Trial started with a central position of the joystick, with the leftmost and rightmost positions corresponding to the stimulus “clearly” (consciously) seen according to the coding instruction. Coding instructions were presented before the beginning of the block; the order of the “left” and “right” joystick position corresponding to the coding of the “happy or male” and “neutral or female” face was counterbalanced across blocks. Joystick responses were recorded at 100 Hz sampling frequency. At the end of each block, a short break was recommended to the participants in order to avoid any kind of visual tiredness. At the end of the last block, valence and arousal of each stimulus were measured respectively on a -3/+3 and 1/7 scales.

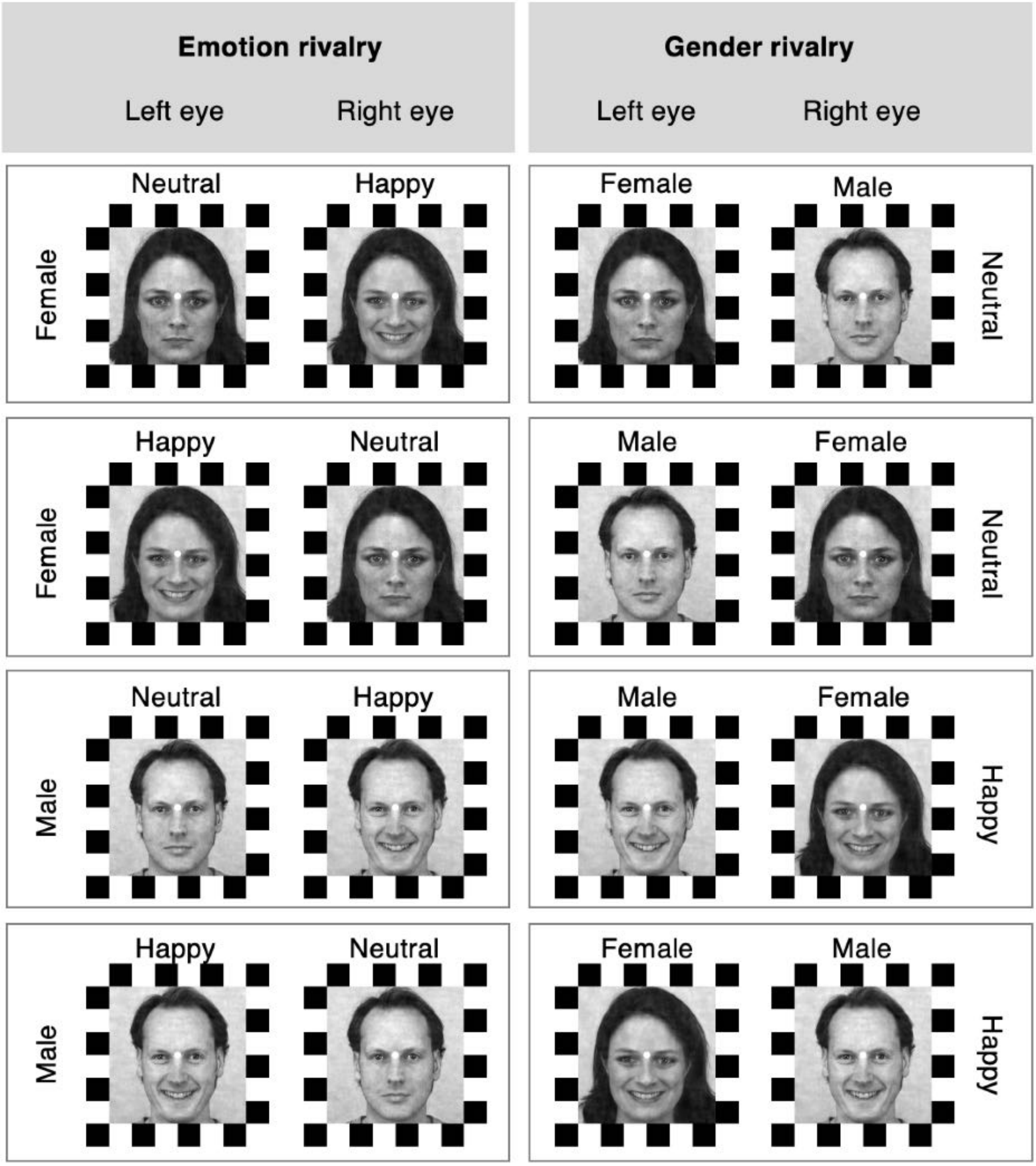

Figure 21. Rival condition for emotion and gender rivalry. Each row represents a couple of stimuli presented in rivalry, four possibilities are presented in each condition. In emotion rivalry (left column) the same identity is presented during a trial and the emotion is in competition. In gender rivalry (right column) the same emotion is presented during a trial and the identity is in competition.

Data reduction. I computed the predominance mean (PM) as a measure of perceptual dominance over trials. Joystick positions were a continuous signal ranging from -1 (i.e. leftmost position), to 1 (i.e., rightmost position). Counterbalanced trial signals could range from -1 to 1 for half and from 1 to -1 for the other half. First, all trials were aligned, multiplying by -1 those of which the range was from 1 to -1 and by inverting the labels of the joystick position. Second, to avoid confusion with the original signal, all signals now with the range -1 to 1 were transformed to have a range from 0 (leaving position) to 1 (reached position) by applying the following formula: (signal+1)/2. In Experiment 4, I opted for a 2 (emotion rivalry: neutral vs. happy, or gender rivalry: female vs. male) x 2 (MT: formation vs. disformation) x 2 (gender participants; female vs. male) experimental design. In Experiment 5, I opted for a 2 (emotion rivalry: neutral vs. happy or gender rivalry: female vs. male) x 2 (MT: formation vs. disformation) x 2 (groups; IMS: Individuals with Moebius syndrome vs. IHC: Individuals Healthy control) experimental design.

PMs were computed by averaging the joystick position values for each trial and separately for the two rivalry conditions (happy/neutral expressions and male/female). We also computed movement transition (MT) as a measure of transition from a conscious content to the other of the rivalry condition. MTs were obtained by computing the average joystick position–related speed over trials. Joystick positions were reduced into two components: 1) MT_disformation of the conscious percept (i.e., joystick values from positions 0 to .5) and 2) MT_formation the new conscious percept (i.e., joystick values from positions 0.5 to 1).

In the previous experiment I have included only female participants because of the potential greater impact of facial mimicry manipulations on female than male participants (Stel & Knippenberg, 2008; Wood, Lupyan, et al., 2016): here, I want to monitor the impact of participants' gender and, to this aim, I will test both male and female participants and will add participants' gender as a factor for statistical analyses.

Data analysis. Differences in stimuli rating for valence and arousal were assessed in separate analyses of variance (ANOVAs) and post hoc comparisons. Differences in rivalry conditions (emotion rivalry and gender rivalry) for PM were assessed in an analysis of variance (ANOVA) and post hoc comparisons. Differences for emotion and gender rivalry conditions for PM (formation and disformation) were assessed in separate analysis of variance (ANOVA) and post hoc comparisons. All post hoc comparisons are corrected for multiple comparisons.

7.2.2 Results

Ratings. Evaluation of valence and arousal were performed individually on each stimulus at the end of the second block. No group effect was observed for arousal (F(1, 38) = 3.68, p = 0.063, d = 0.62) but a difference was found in valence (F(1, 38) = 5.8, p = 0.021, d = 0.78). Female participants rated more positively than male participants, t(38) = 2.407, p = 0.021, d = 0.39. Independently of groups, valence ratings differed according to a priori expectations, F(1, 38) = 323.92, p < .001, d = 5.84. Neutral facial expressions were rated under zero (M = -2.11; SD = 0.86; range = -3 to 3), which is more negative than happy (M = 1.51; SD = 1.29; range = -3 to 3). An interaction between group and emotion was found for valence rating (F(1, 38) = 10.09, p < .001, d = 1.03). Female rated happy facial expressions more positively than male participants, t(74.8) = 3.97, p =0.003, d = 0.46. Arousal ratings also differed according to a priori expectations, F(1, 39) = 80.45, p < .001, d = 2.91. They were lower for neutral expressions (M = 2.49; SD = 1.66; range = 1 to 7) than for happy expressions (M = 4.64, SD = 1.36; range = 1 to 7). Neutral facial expressions were rated as significantly less arousing than happy facial expressions, t(38) = 17.99, p < .001, d = 2.92. An interaction between stimuli gender and emotion was found for arousal rating (F(1, 38) = 19.13, p < .001, d = 1.42). Neutral female facial expressions were rated more positively than neutral male facial expressions, t(75.7) = 4.443, p < .001, d = 0.51. Some participants reported spontaneously that the female happy facial expression seems to be not genuine.

Predominance mean (PM). No gender effect was observed for PM (F(1,38) = 2.09 p = 0.157), meaning that there is no difference in stimuli predominance as a function of participant's gender. A significant effect was observed for PM as a function of rivalry condition (F(1,38) = 100.03 p < .001); interestingly all participants in emotion rivalry showed an advantage for the happy expression. PM for happy faces (M = -0.38; SD = 0.19 s) was significantly different from zero, t(39) = -12.76 , p < .001. PM for gender rivalry (M = -0.028; SD = 0.17 s) was not significantly different from zero, t(39) = 0.967 , p = 0.339. See figure 22.

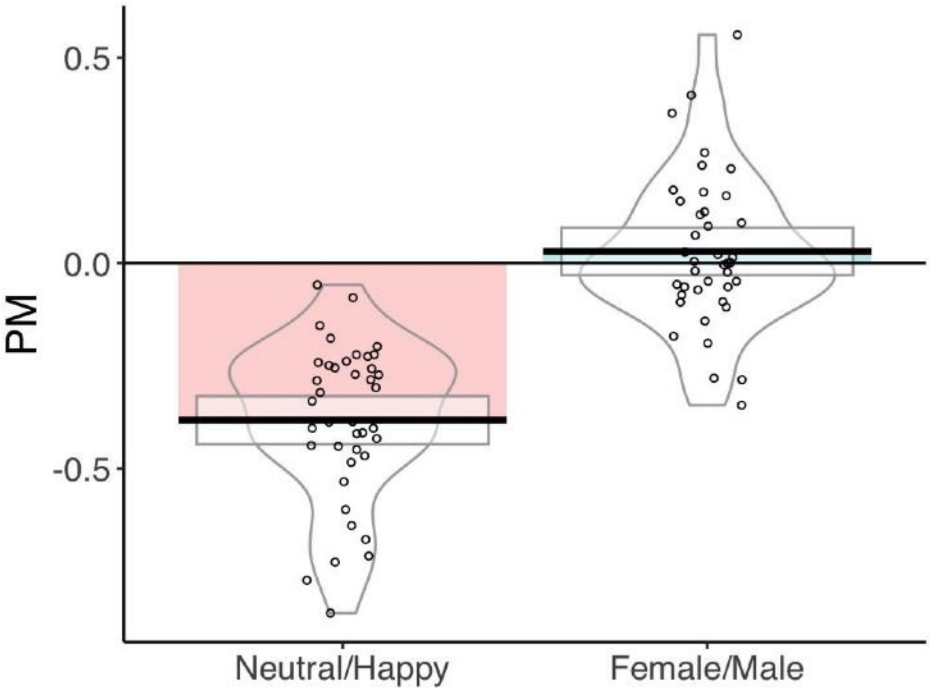

Figure 22. Colored bars show central tendencies. Rectangles, beans and points represent confidence intervals, smoothed densities and raw data respectively. PM = 0 indicates no preference between the two percepts in rivalry during the trial. Neutral/Happy PM indicates a predominance mean in favor of the happy percept. Negative values on the y axis reflect a bias for happy faces in the emotion task (and for male faces in the gender task), and positive values reflect a bias for neutral faces in the emotion task (and for female faces in the gender task).

Movement transition (MT). In emotion rivalry, a significant effect was observed for MT as a function of the type of movement transition (MT_formation vs. MT_disformation) (F(1,38) = 27.82 p < .001, d = 1.71): MTs_disformation were faster than MTs_formation (t(38) = 5.27 p < .0001, d = 0.85). A significant interaction was found between percepts and the type of movement transition (F(1,38) = 17.59 p < .001, d = 1.36): MTs_formation for neutral were faster than MTs_formation for happy (t(70.2) = 2.41 p = .0185, d = 0.29) and MTs_disformation for happy were slower than MTs_disformation for neutral (t(70.2) = -4.318 p = .0001, d = 0.52). Finally, a significant interaction was found between gender, percepts and the type of movement transition (F(1,38) = 4.63 p = 0.038, d = 0.7). MTs_disformation from happy percepts coded by female participants were slower than MTs_disformation from neutral percept (t(70.2) = -4.62 p < 0.0001, d = 0.55) and MTs_formation of neutral percepts coded by female participants were faster than MTs_formation of happy percept (t(70.2) = 2.57 p = 0.012, d = 0.31). See figure 23.

In gender rivalry, a significant interaction was found between gender, percepts and the type of movement transition (F(1,38) = 6.98 p = 0.012, d = 0.86). MTs_formation of male percepts coded by female participants were slower than MTs_formation of female percept (t(55.3) = -2.82 p = 0.007, d = 0.38).

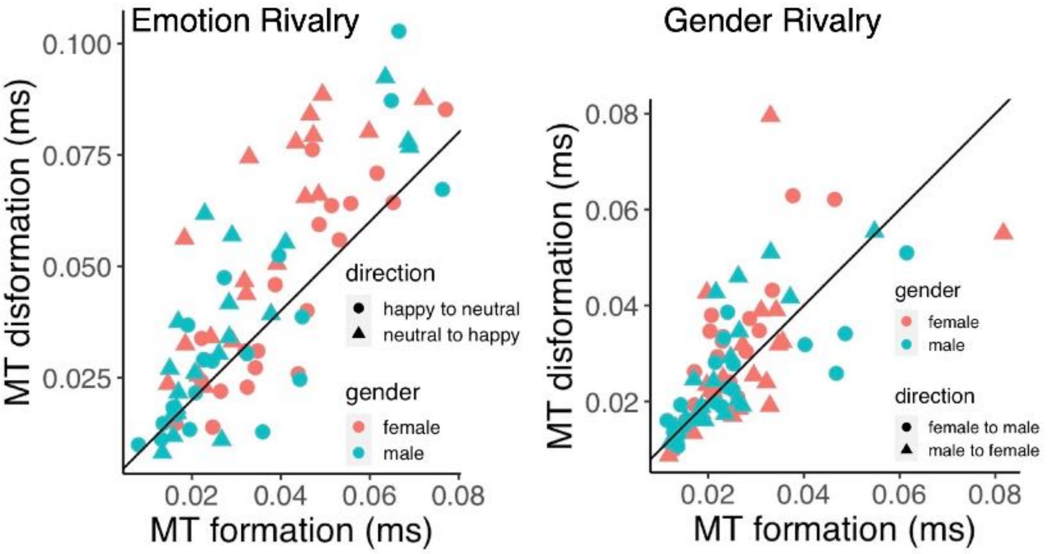

Figure 23. Each point represents a participant's MT for a specific dominant percept. Joystick position is projected on the x and y axes, the black line represents the axes equidistance. The MT is expressed in milliseconds.

Questionnaires. In exploratory analyses, I tested if PM and MT were correlated (Pearson, two-sided correlations) with the TAS-20 and the IRI. No correlations were significant with the IRI scores or TAS-20.

7.3 Experiment 5

7.3.1 Method

Participants. I tested 7 individuals with severe to complete congenital facial paralysis, i.e. with Moebius Syndrome (IMS participants; 2 females; all right-handed; various education levels; mean age ± SD: 26.3 ± 14.1 years) and compared their performance to that of 20 healthy participants recruited among students at the University of Padua (IHC participants from experiment 4; 20 males; 1 left-handed; Mean age ± SD: 23.4 ± 2.5 years). A total of 1 IMS female and 1 IMS male participants were excluded from analysis for failing in experimenting binocular rivalry or for not completing the experiment. At the end of the experiment, participants completed the TAS-20 and the IRI questionnaires. Scores on both questionnaires were in the normal range (IMS; TAS-20: M = 43.2, SD = 4.5 IRI: M = 96.5, SD= 13, IHC TAS-20: M = 45.8, SD = 12.2 IRI: M = 96.9, SD= 12.2).

Procedure. As a further extension to Experiment 4, the same material and apparatus was used and along with the same measures. IMS participants were tested in the clinical center at the University of Parma, which is specialized in the diagnosis of Moebius syndrome and therapeutic intervention. None of the participants received a smile surgery. The surgical objective is to restore muscle function through various techniques: the lengthening myoplasty of the temporal muscle, muscle transfers, cross-facial grafting, neurorrhaphy and nerve transposition.

Data analysis. Because of the potential gender influence over the gender rivalry and the mismatch between IMS participants (4 males, 1 female) it should be an error to consider the merging results as representative of such a population. In order to compare atypically (IMS) to typically (IHC) developed participants, we compared males IMS with males IHC from Experiment 4. Such manipulation implicated the exclusion of the only IMS female participant for a total of 4 IMS and 20 IHC male participants included in this experiment[13]. Differences in stimuli rating for valence and arousal were assessed in separate analyses of variance (ANOVAs) and post hoc comparisons. Differences between rivalry conditions (emotion, gender) for PM were assessed in an analysis of variance (ANOVAs) and post hoc comparisons. Differences for emotion and gender rivalry conditions for PM (formation and disformation) were assessed in separate analysis of variance (ANOVA) and post hoc comparisons. All post hoc comparisons are corrected for multiple comparisons.

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[13] The loss in power in comparing 4 IMS vs 20 IHC is due to the statistical approach that is not inferring on each IMS but considers IMS as representative of the population.

7.3.2 Results

Ratings. Evaluation of valence and arousal were performed on individual stimuli at the end of the second block. No group effect was observed for arousal (F(1, 22) = 1.7, p = 0.205, d = 0.56) but a difference was found in valence (F(1, 22) = 7.25, p = 0.013, d = 1.15). IMS participants rated stimuli more positively than IHC participants, t(22) = 2.692, p = 0.013, d = 0.57. Independently of groups, valence ratings differed according to a priori expectations, F(1, 22) = 70.71, p < .001, d = 3.59. Neutral facial expressions were rated under zero (M = -1.89 ; SD = 1.15; range = -3 to 3), which is more negative than happy (M = 1.2 ; SD = 1.39; range = -3 to 3). Happy facial expressions were rated as significantly more positive than neutral facial expressions, t(22) = 8.409, p < .001, d = 1.79. Arousal ratings also differed according to a priori expectations, F(1, 22) = 42.63, p < .001, d = 2.78. They were lower for neutral expressions (M = 2.17; SD = 1.25; range = 1 to 7) than for happy expressions (M = 4.49, SD = 1.33; range = 1 to 7). Neutral facial expressions were rated as significantly less arousing than happy facial expressions, t(22) = 6.529, p < .001, d = 1.39. Some participants reported spontaneously that the female happy facial expression seems to be not genuine.

Predominance mean (PM). No group effect was observed for PM (F(1,22) = 0.07 p = 0.797, d = 0.11), meaning that there is no difference in stimuli predominance as a function of participant group (IMS vs. IHC). A significant effect was observed for PM as a function of rivalry condition (F(1,22) = 21.72 p < .001, 1.99): interestingly, none of the participants had a PM in favor of the neutral faces, meaning that for all participants in emotion rivalry the happy expression showed an advantage. PM for happy faces (M = -0.353; SD = 0.2 s) was significantly different from zero, t(23) = -8.744 , p < .001, d = 1.82. See figure 24.

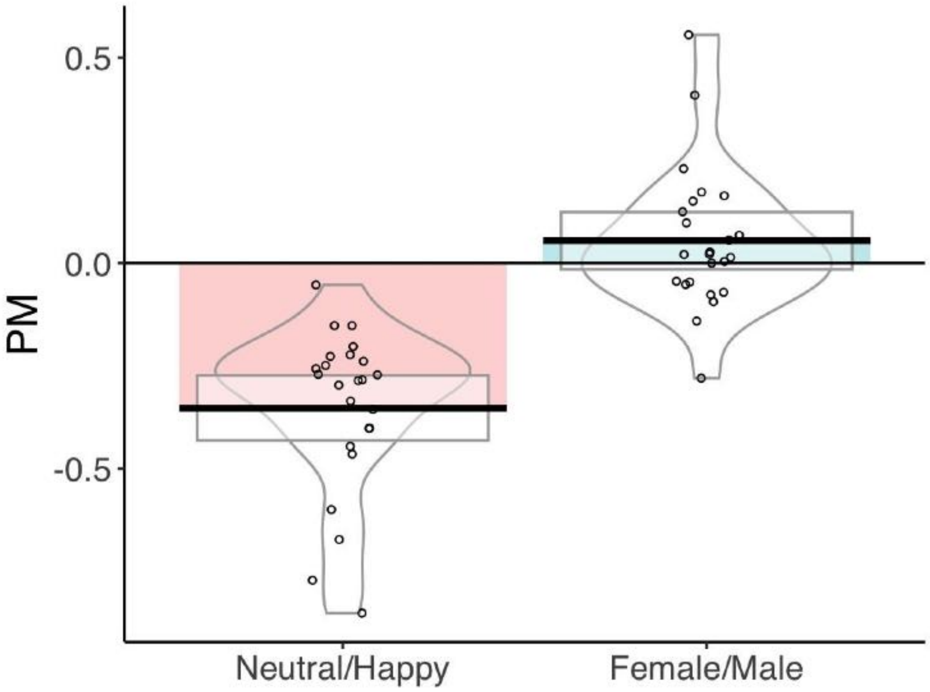

Figure 24. Colored bars show central tendencies. Rectangles, beans and points represent confidence intervals, smoothed densities and raw data respectively. PM = 0 indicates no preference between the two percepts in rivalry during the trial. Neutral/Happy PM indicates a predominance mean in favor of the happy percept. Negative values on the y axis reflect a bias for happy faces in the emotion task (and for male faces in the gender task), and positive values reflect a bias for neutral faces in the emotion task (and for female faces in the gender task).

Movement transition (MT). In emotion rivalry, a significant effect was observed for MT as a function of the type of transition (happy to neutral vs. neutral to happy) (F(1,22) = 4.8 p < .039, d = 0.93): MTs from happy to neutral were slower than MTs from neutral to happy (t(22) = -2.19 p < .0001, d = 0.47). In gender rivalry, no effects were found. See figure 25.

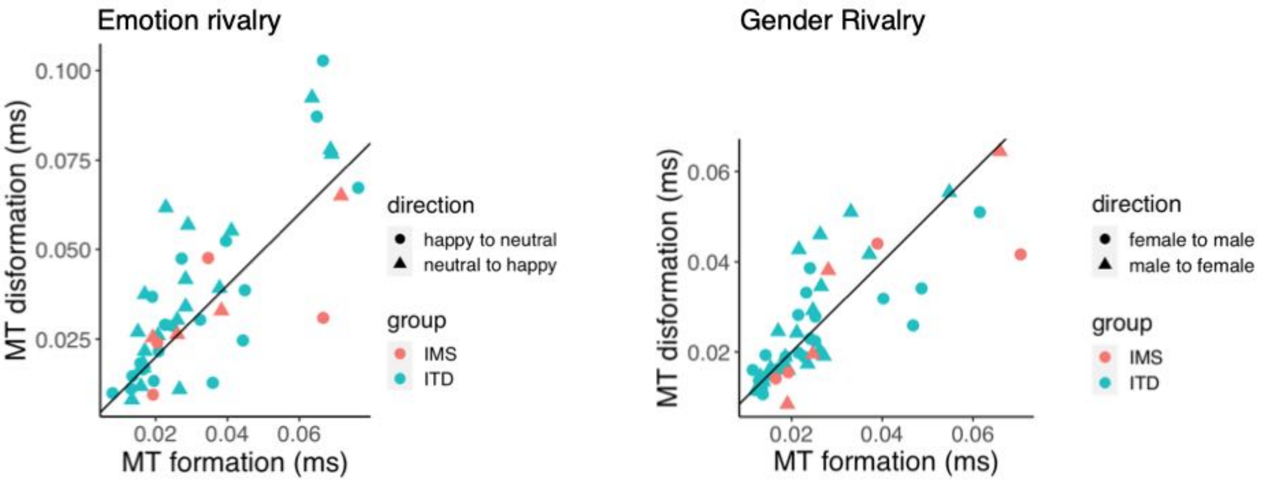

Figure 25. Each point represents a participant's mean transition (MT) for a specific dominant percept. Joystick position is projected on the x and y axes, the black line represents the axes equidistance. The MT is expressed in milliseconds.

Questionnaires. In exploratory analyses, I tested if PM and MT were correlated (Pearson, two-sided correlations) with the TAS-20 and the IRI. No correlations were significant with the IRI scores or TAS-20.

7.4 Experiments 4 and 5: Discussion

In the present investigations, I wanted to test the impact of positive emotion on the conscious time-course during a binocular rivalry task. In particular: 1) I hypothesized a slower disformation phase for conscious contents of happy facial expressions when compared to the disformation phase of neutral facial expressions, i.e. conscious happy expressions are more resistant to fading from consciousness; 2) I wanted to test whether the time-course of consciousness (in terms of speed) differs as a function of the phase (formation vs disformation); 3) I expected to observe interactions with gender factor, since in previous studies female participants have been found to be more sensitive to emotional expressions when compared to male participants; 4) I hypothesize that effects of consciousness time-course dynamics of facial expressions is less evident in participants with Moebius syndrome, because of the absence of proprioceptive signals coming from facial muscles that cannot contribute to conscious representations of happy facial expressions. I asked participants to perform a standard binocular rivalry task by presenting a happy and a neutral face (from the same identity) in rivalry and to report the conscious experience by means of a joystick.

I reasoned that disformation from consciousness is related to the sources of integrated information, and then the ‘richness’ of the conscious content. Along this line of reasoning, processing of emotional faces is the result of multiple systems, including sensorimotor and visual systems that iteratively share information. My primary outcome measure was the predominance mean (*PM*). Most importantly, I tested hypotheses through the analysis of the movement transition (*MT*) as a measure of the formation and disformation phase. I expected longer MTs for the disformation of happy faces when compared to neutral faces.

First, and importantly, as in previous experiments, I replicated previous findings (Alpers & Gerdes, 2007; Bannerman et al., 2008; Yoon et al., 2009) such that PM (i.e., equivalent measure to CT) for emotion rivalry was higher for happy faces than PM for neutral faces, while no difference was found for PM in gender rivalry, in both experiments 4 & 5.

In Experiment 4 the comparison between the type of movement transition (MTs_formation vs MTs_disformation) did yield significant differences in emotion rivalry, such that MTs_disformation are faster than MTs_formation. This result suggests an asymmetrical time course dynamic during BR in which disformation of a content is in general faster than the formation of the content. As expected in the first hypothesis, MTs_disformation of happy percept is slower than MTs_disformation of neutral percept, indicating that the disformation of the happy content fades more slowly from consciousness. With respect to the second hypothesis in which no specific effect as expected, MTs_formation of happy is faster than MTs_formation of neutral percept, indicating that the formation of the happy content access faster to consciousness. In the gender rivalry, MTs_formation of male percept coded by the female participants were slower than MTs_formation of female percept. As anticipated by the third hypothesis an interaction with gender was found, MTs_disformation from happy faces coded by the female participants were slower than MTs_disformation from neutral faces but also MTs_formation from happy faces were faster than MTs_formation from neutral faces. Interestingly, effects on the conscious time course (MTs_formation vs MTs_disformation) are related to the happy percept that in the case of the female participants, is slower to disforme and faster to form. Such difference could be explained by the diversity of involved processes in the formation and disformation phases. In this case, richness could affect differently one or the other phase of the time course. Unfortunatly, I have no information regarding the participants sexual orientation that could explain results in gender rivalry.

Assuming that formation and disformation are different processes, the effect on happy percept suggests that the disformation phase of conscious perception of facial expressions in the BR paradigm can be influenced by the stimulus richness. Such a relationship should be that richer content fades slower from consciousness. I would like to underline the fact that the principal interaction effect is driven by female participants. This result is perfectly in line with previous experiments that involved exclusively female samples.

In Experiment 5, independently of group (i.e., IHC vs IMS participants) and the type of movement transition (MTs_formation vs MTs_disformation), direction of the transition did yield significant differences for the MT, such that MTs from happy to neutral were slower than MTs from neutral to happy. This finding gives no information whether it is the disformation of happy or the formation of neutral to trigger a slower transition. It is important to remember that Experiment 5 included only male participants (IHC participants are male participants from Experiment 4). These results do not support my hypothesis. However, it is important to note that IHC and IMS are male participants in which the effect of sensorimotor simulation is not expected on the basis of all of my previous experiments. To summarize, results of Experiment 5 suggest that facial palsy or possible absence of sensorimotor simulation affects the full transition of the content (disformation and formation of the same transition) but not the emotional predominance (PM).

Finally, although exploratory, I observed noteworthy correlations between the TAS-20 and IRI scores with metrics of binocular rivalry.

8 General discussion

The present work investigated how information from different specialized modules could modulate the conscious experience of the observer in the context of emotion recognition. Information integration focused in particular on the visual and sensorimotor information by manipulating the observer's facial mimicry and somatosensory information by a facial tactile stimulation. Emotion recognition was circumscribed to neutral and happy facial expressions and the conscious experience was assessed through the binocular rivalry (BR) paradigm. As shown before, BR has the advantage of allowing to monitor the full cycle of conscious experience or time-course, that spans from the formation until the disformation stages of the content of consciousness. The experiments presented in this Thesis allowed us to investigate the different moments of the conscious time-course; in particular, with regard to the stability of the content in experiments 1-3 and with regard to the disformation of the content in experiments 4-5. No effect was found at the formation stage of the conscious content in terms of ORT and IP. With respect to the Aru and Bachmann’s functions of conscious experience that evolve over time (see figure 7), and based on the findings of the present work, I propose to add to the Aru and Bachmann’s scheme of the conscious cycle an additional stage between the formation stage and disformation stages (see Figure 26).

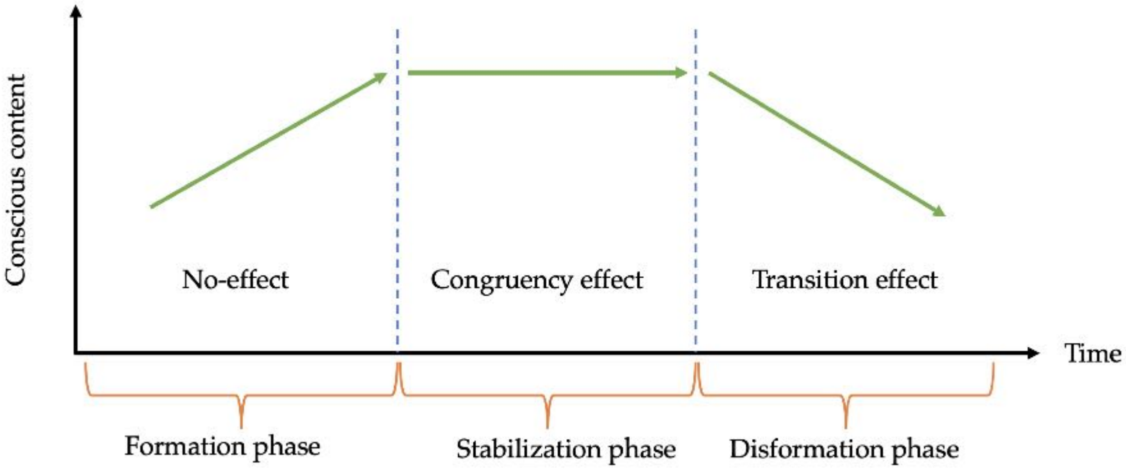

Figure 26: Implementation Aru and Backmann figure. The function of conscious experience evolving over time. In a time course perspective, at each conscious content update, the conscious content may remain in consciousness (stable) or may begin to fade from consciousness (i.e., disformation).

This upgrade is also a natural evolution of the 'early' and 'late' scenarios, as it offers a more detailed view of the 'late' scenario. The early stage was related to the BR competition and ambiguity resolution before the content became conscious. The late scenario regarded the stabilization of the representations (A-consciousness) following BR initial resolution. A comprehensive late scenario based on the present findings must include two aspects: the stabilization and the disformation of the content of consciousness. Starting from this distinction (i.e., formation, stabilization, disformation), I will now resume the effects found in this work.

8.1 The formation stage

The formation stage is the most difficult to define because it refers to two diferent BR mecanisms (selection vs transition; see figure 27). According to models of consciousness, at this stage, consciousness content is going to be build up. As I explained before, multiple modules process input information in parallel. Such information will then be selected and integrated in order to become the content of consciousness. In binocular rivalry (BR) terms, the initial percept (IP) is the first content the participant is aware of during a trial. This content requires a selection of information. The selected input becomes the dominant percept and the excluded input does not access awareness. In this context, the early scenario took in consideration a possible faster access to awareness for the dominant percept. Differently, during transition, the excluded input will replace the dominant percept, that is to say, formation of the content requires the disformation of another content.

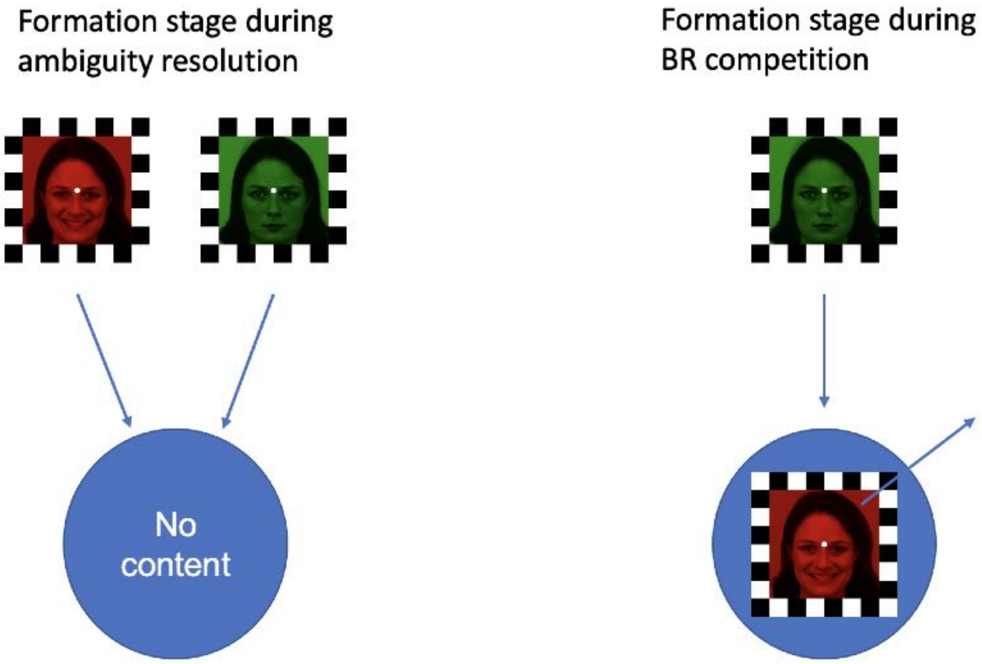

Figure 27: Formation stages. In a time course perspective, conscious content is formed. During ambiguity content is formed by selecting one of the two visual inputs. During BR competition, formation is a transition between the formed content and the disformed.

Consistently over all experiments, no effect of formation during ambiguity resolution was found. Congruent pieces of information that are processed in the visual area, sensorimotor area (Experiments 1-2; mimicry manipulation and visual emotion recognition), or somatosensory area (Experiments 3; facial tactile stimulation) did not yield a faster experience of an IP over the rival input. In other words, the conscious content access, in terms of onset reaction time (ORT), is not modulated by the available information before that such information becomes conscious. It is important to note that this conclusion does not take into account the richness of information that is integrated in the content, in opposition to the formation during BR competition. However, the possibility to quantify the conscious content is extremely limited, even impossible to apply on real data. This is probably the reason why research that tries to measure effects based on the formation stage focused on the timing aspect. This approach potentially leaves the possibility to fall in a Type 2 error. Part of the multiple processes that are involved in the information integration are parallel processes, therefore by definition they are time-optimized. The speed will consider both the quantity of information and the time in which this information arises to consciousness. According to Aru and Bachmann's consciousness time-course, for example, during the formation phase, given two contents that arise with the same timing, the content that carries more information is faster than the other content, as it reaches a "higher level" of content at the same time. The adequate measure for the formation stage remains a challenge for science of consciousness as it is dependent on the measure of conscious content richness. It is possible to exploit such richness by observing the formation stage during BR competition where one of the two rival stimuli is already part of the conscious content. Being part of the content allows the dominant percept richness to contribute to the conscious time course and should explain the results related to the formation during transitions. At this point, the conclusions on the formation stage must be interpreted according to the limits imposed by this distinction. As a side note, in addition to speed measures, further experiments should consider an eventual bottleneck effect as the observed RT of access into consciousness would depend on the slowest process involved in the formation stage. On the other hand, given the timing of the mimicry that is slower than the visual process, the results seem coherent and robust.

If no effects were found at the formation stage during ambiguity resolution, another possible effect on consciousness should be found in the late scenario; the capacity of consciousness to keep the content or to exclude it.

8.2 The stabilization stage

The stabilization stage is nested into the late scenario, that is when content is part of the conscious content. At this late stage, the subject is aware of the content and able to report it (i.e., A-consciousness), in other words the conscious content is already built up. According to models of consciousness, the brain activity underlying this stage has entered a recurrent process or/and has accessed a global workspace or/and has reached a sufficient level of activity. In BR terms, the dominant percept is the content the participant is aware of during a trial. This dominant percept remains as the content of consciousness and then leaves place to the rival percept. The cumulative time (CT) measures the time a percept remains dominant. In this context, the late scenario predicted that it is possible to modulate the CT. Intuitively the modulation could increase or decrease the CT. The effect supported by Experiments 1 and 2 suggests that the CT could increase, in other words the content is allowed to remain accessed for a longer time.

When information was congruent between sensorimotor and visual information, the content remained conscious for a longer time. When mimicry manipulation was congruent with neutral percept, the corresponding CT increased with respect to the absence of manipulation, and when mimicry manipulation was coherent with happy percept, the CT for happy percept was longer with respect to the absence of mimicry manipulation. These results indicate that the signal from the sensorimotor system is involved in maintaining content in consciousness, if and only if it is congruent with the visual representation. Here the congruence aspect of the information seems to play a crucial role in its integration. “Congruency” could be considered as a condition that triggers a logic gate (i.e., sensorimotor AND visual integration) that is involved and allows information integration. This logic gates viewpoint is actually upgraded in the IIT (see Oizumi et al., 2014 for more details), but also compatible with other theories of consciousness but at a different scales: in RPT the logic gates should be a consequence of the recurrent process itself between systems or in GNWT, a consequence of the global workspace that allows only one representation to be made conscious at a time. Allowing one representation at a time requires - as in IIT - the exclusion of incompatible information.

A second relevant aspect of the present finding is of interest for science of consciousness. If models provide information about conscious access, they also must foresee how the content is refreshed. In an iterative scenario of conscious models for example, I can imagine that conscious systems refresh some information, maybe at each iteration. There is no evidence if the whole content has to be refreshed each time (i.g., consciousness refreshes as movie frames) or if the conscious content is refreshed part by part (i.g., consciousness refreshes as a body renews its cells), even if conscious transitions in BR seem to be gradual (Naber et al., 2011). We also have no idea about the refresh time scale. IIT has no prediction but expects a timescales based on conscious experience (Tononi et al., 2016). In RPT and GNWT refresh must be probably related to the neural connectivity that is at the center of these two theories. Nevertheless these results provide evidence that sensorimotor and visual integration stabilized the conscious content. I propose to interpret this stabilization as the situation in which the system keeps the information inside consciousness during a refresh. In Experiments 1 and 2, by definition, stabilization occurred in enough refreshes to allow observing a significant effect.

It is possible that in the sensorimotor-visual integration from Experiment 1 and Experiment 2, the visual information reaches alone the conscious content as there is no early effect of mimicry. After mimicry information is processed, this new piece of information is integrated to the content during a refresh and stabilization occurs. This last interpretation requires further EMG experiments to analyze the link between stabilization timing and mimicry timing. The second alternative during a conscious content refresh I will cover, is the opposite of the stabilization: during the content refresh, when the content or part of the content is not kept, it must be excluded from consciousness, what I called, according to Aru and Backmann, the disformation stage.

8.3 The disformation stage

The disformation stage corresponds to the part in the late scenario in which content is excluded from consciousness. According to models of consciousness, the brain activity underlying this stage has stopped to be RP or/and has exited a global workspace or/and has lost a sufficient level of activity. In BR terms, the dominant percept that was the content of consciousness leaves place to the rival percept. The opposite mechanism occurs at the same time; the suppressed percept that is not conscious starts to become the dominant percept. A transition occurs when the content of the dominant percept and the "content" of the suppressed percept switch together, that is to say when the dominant percept becomes suppressed (disformation) or when the suppressed percept becomes dominant (formation). The movement transition (MT) measures the transition speed. In this context, the late scenario predicted that MT could be dissimilar between rival percepts. The effect supported by Experiments 4 and 5 suggests that different contents do not fade from consciousness in the same way.

During BR, the movement speed related to the report of disformation from a happy percept was significantly slower than neutral content. In other words, the happy percept fades slower from consciousness. At this point, two explanations are possible; this phenomenon is due 1) to the content itself that has the capacity to "disform" slowly 2) the rival percept formation that forced the disformation of the other. In experiment 4, due to the gender contrast, formation and disformation seem independent, where the happy percept with respect to the transition disformes slowly or forms faster, suggesting that the effect is percept related. In experiment 5, it is possible that the disformation of the current content has been affected by the processes involved in a parallel formation stage. In this case, a happy-related process could push neutral content away from consciousness. As said before, according to models of consciousness, the brain activity underlying this disformation stage has stopped to be RP or/and has exited a global workspace or/and has lost a sufficient level of activity. But in parallel other processes that will be linked with the new content are improving their connectivity to be RP or are increasing their activity, triggering the new content. Such competition between decreasing activity of the current content and the increasing activity from the future content leaves an open question about logic gates. It is possible that these two processes trigger an “OR” logic gate that switches part of the available information. A direct consequence of having an “OR” logic gate will allow one to experience only one content at a time contributing to the unicity of consciousness (Bayne, 2010)?

8.4 Conclusion

In summary, this work gives a theoretical contribution to embodied cognition theory and science of consciousness. Taken together, these two fields of research raise important questions regarding each field as well as their interaction.

Regarding the contribution to the embodied cognition theory, experiments using mimicry (Experiment 1 and Experiment 2), tested the model proposed by Wood and colleagues (2016). This model proposes that sensorimotor signals may feedback to visual areas and play a role in modulating the visual processing of emotional faces (see figure 1). The possible role of facial mimicry in conscious perception of emotional facial expressions was until now almost totally neglected. My findings confirm the importance of mimicry in emotional face processing. So far, integration of information between sensorimotor (i.e., mimicry) and visual areas modulates experience of emotional facial expressions.

Regarding science of consciousness, this work explored the consciousness time-course mechanisms. A particular focus was given to the mechanisms related to the content of consciousness once such content was built up. Conscious experience modulation was observed in two different ways: the stabilization effect (Experiments 1 to 3) and the disformation effect (Experiments 4 and 5). I proposed these two effects to be implemented in the consciousness time-course proposed by Aru and Backmann

(2017; see figure 7 and figure 26) as they describe the possible evolution of the conscious content (i.e., remain or leave consciousness).

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10 Figures & Tables

11 Acronyms Table

Φ	Phi
A-consciousness	Access Consciousness
b-CFS	Breaking Continuous Flash Suppression
BR	Binocular Rivalry
CT	Cumulative Time
DMCs	Difference Makers of Consciousness
EEG	Electroencephalography
ERPs	Event-Related Potentials
FFS	Fast Feedforward Sweep
GNWT	Global Neuronal Workspace Theory
IHC	Individuals Healthy control
IIT	Integrated Information Theory
IMS	Individuals with Moebius syndrome
IP	Initial Percept
IRI	Interpersonal Reactivity Index
LP	Late Positivity
M1	Primary Motor Cortex
Mbps	Megabit Per Second

ms	milliseconds
MT	Movement Transition
NCCs	Neural Correlates of Consciousness
ORT	Onset Resolution Time
P-consciousness	Phenomenal Consciousness
PM	Predominance Mean
PSC	Physical Substrate of Consciousness
RP	Recurrent/re-entrant Process
RPT	Recurrent Processing Theory
S1	Primary Somatosensory cortex
S1	Secondary Somatosensory cortex
SC	Somatosensory cortex
TAS	Toronto Alexithymia Scale
TMS	Transcranial Magnetic Stimulation
VAN	Visual Awareness Negativity

12 Appendix

12.1 Keywords

embodied cognition, mimicry, facial expression, emotion, facial stimulation, tactile stimulation, sensorimotor, somatosensory, consciousness, visual awareness, A-consciousness, P-consciousness, binocular rivalry, content of consciousness, time-course, information integration, logic-gates.

12.2 Openscience practice

The dataset and analyses reported in Experiment 1 are available at Open Science Framework repository: https://osf.io/xk25b/

Experiment 3 (pilot) data collection will continue after submission of a pre registered report.

12.3 Exploratory analysis

12.3.1 Experiment 4: IP and ORT

For each trial, I extracted the initial percept (IP, i.e., the direction of first joystick movement during the ongoing trial, namely IP_neutral or IP_happy faces in emotion rivalry and IP_female or IP_male in gender rivalry) and the onset resolution time (ORT, also named onset rivalry, i.e. the time from the beginning of trial to report the IP). Onset measures are computed in order to analyze whether IP frequencies changed as a function of the emotionality of the face and/or as a function of time (ORT).

Initial percept (IP). In terms of IPs, happy expressions were reported more frequently for both female and male participants (females: 310 trials; males: 303 trials) than neutral expressions (females: 170 trials; males: 177 trials), female identity (females: 229 trials; males: 225 trials) or male identity (females: 248 trials; males: 255 trials). The odds ratio is not statistically significant for emotion IPs, the estimated value is 0.44 ($\beta =$ 0.078, SE = 0.196, 95% CI [-0.31, 0.47], t 0.398, p = 0.69). The odds ratio is also not statistically significant for gender IPs, the estimated value is 0.22 ($\beta =$ 0.046, SE = 0.149, 95% CI [-0.25, 0.34], t 0.311, p = 0.756).

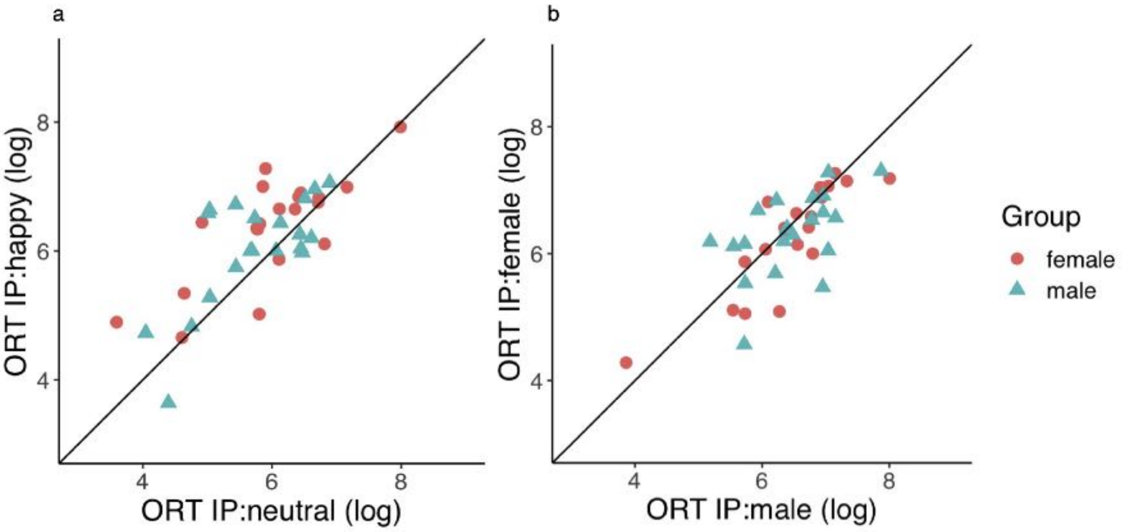


Figure 28. Each point represents a participant's onset resolution time (ORT) for a specific IP. Joystick position is projected on the x and y axes, the black line represents the axes equidistance. The ORT is expressed in milliseconds. Panel a shows emotion rivalry, panel b shows gender rivalry.

Onset resolution time (ORT). No group effect was observed for ORT (F(1,38) = 0.34 p = 0.561), meaning that there is no difference in time for participants as a function of their gender to resolve the initial BR. A significant effect was observed for ORT as a function of IP (F(2.75,104.52) = 12.30 p < .001), ORT for IP_female and IP_male were longer than IP_neutral (t(114) = 4.353, p < .001; t(114) = 5.846, p < .001) and IP_happy were longer than IP_neutral (t(114) = 3.375, p = 0.006). See figure 28.

12.3.2 Experiment 5: IP and ORT

Differences between IPs (happy, neutral and male, female) for ORT were assessed in an analysis of variance (ANOVAs) and post hoc comparisons. In order to estimate the probability of the IP as a function of group, we applied two mixed-effects logistic regression models with IP (happy vs neutral or female vs male) explained by group (IHC vs. IMS).

Initial percept (IP). In terms of IPs, happy expressions were reported more frequently in both groups (IMS: 77 trials; IHC: 303 trials) than neutral expressions (IMS: 43 trials; IHC: 177 trials), female identity (IMS: 51 trials; IHC: 225 trials) or male identity (IMS: 68 trials IHC; male: 255 trials). The odds ratio is not statistically significant for emotion IPs, the estimated value is 0.126 ($\beta = -0.063$, $SE = 0.244$, 95% CI [-0.56, 0.43], t -0.26, $p = 0.795$). The odds ratio is not statistically significant for gender IPs, the estimated value is 0.324 ($\beta = 0.127$, $SE = 0.288$, 95% CI [-0.46, 0.71], t 0.441, $p = 0.659$).

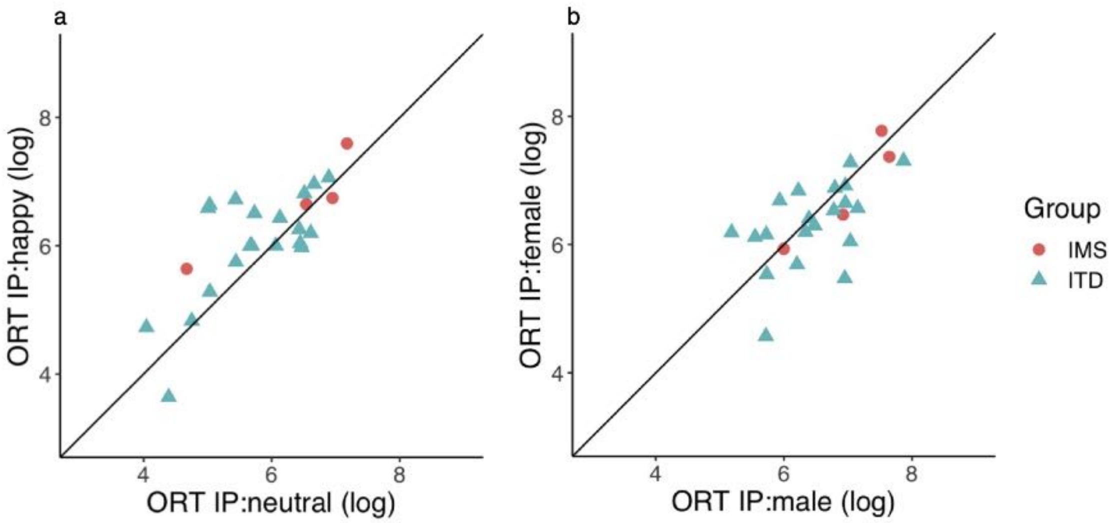


Figure 29. Each point represents a participant's onset resolution time (ORT) for a specific IP. Joystick position is projected on the x and y axes, the black line represents the axes equidistance. The ORT is expressed in milliseconds. Panel a shows emotion rivalry, panel b shows gender rivalry.

Onset resolution time (ORT). No group effect was observed for ORT (F(1,22) = 2.81 p = 0.108), meaning that there is no difference between IMS and IHC in the time needed to resolve the initial BR. A significant effect was observed for ORT as a function of IP (F(2.63,57.87) = 5.53 p = 0.003), ORT for IP_female and IP_male were longer than IP_neutral (t(66) = 3.046, p = 0.02; t(66) = 3.772, p = 0.002). See figure 29.

Movement transition (MT). In emotion rivalry, no significant effect was observed for MT as a function of the group of participants (IMS vs. IHC); (F(1,22) = 0.02 p = 0.897). In gender rivalry, no significant effect was observed for MT as a function of the group of participants (F(1,22) = 1.41 p = 0.248). See figure 30.

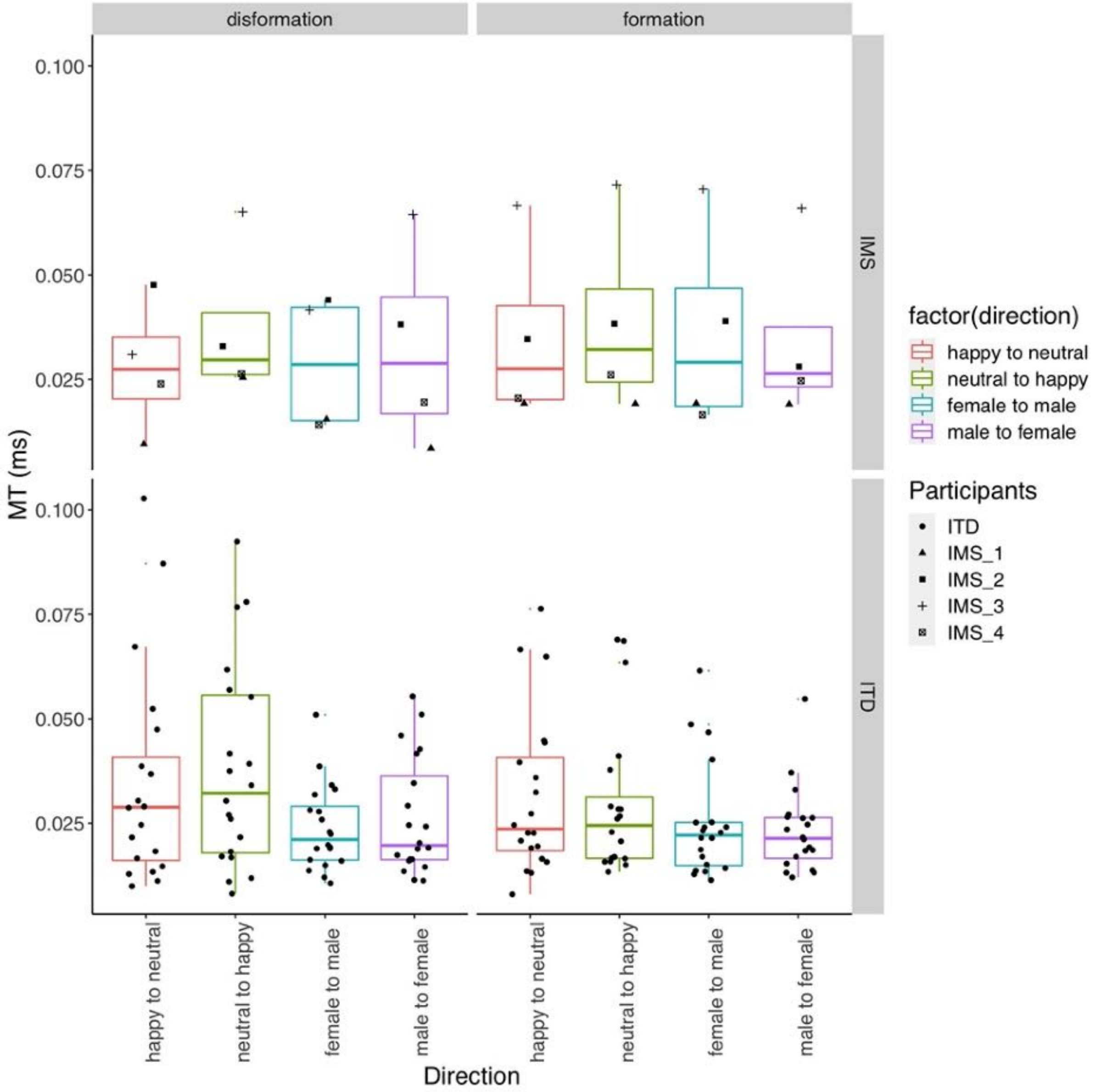


Figure 30. Boxplot. IHC and IMS means transition with respect to the transition direction and movement type.

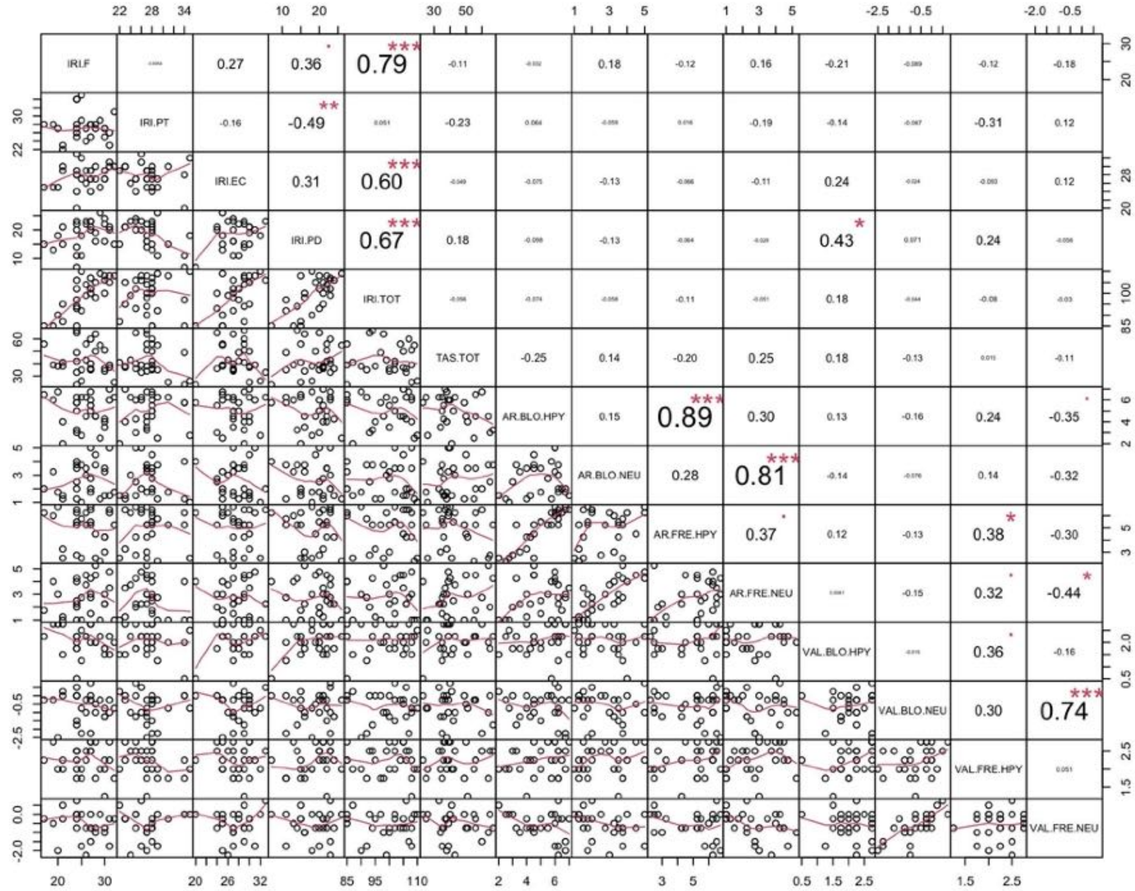
12.4 Correlation table

12.4.1 Experiment 1: IRI and TAS correlation with BR measures

IRI.F	Interpersonal Reactivity Index
IRI.PT	Interpersonal Reactivity Index
IRI.EC	Interpersonal Reactivity Index
IRI.PD	Interpersonal Reactivity Index
IRI.TOT	Interpersonal Reactivity Index
TAS.TOT	Toronto Alexithymia Scale
AR	Arousal
VAL	Valence
IP	Initial Percept
ORT	Onset resolution time
CT	Cumulative time
PM	Predominance mean
MT	Movement Transition
BLO	Blocked mimicry
FRE	Free mimicry
HPY	Happy percept
NEU	Neutral percept
MIX	Mixed percept

GEN	Gender rivalry
EMO	Emotion rivalry

Valence and Arousal.



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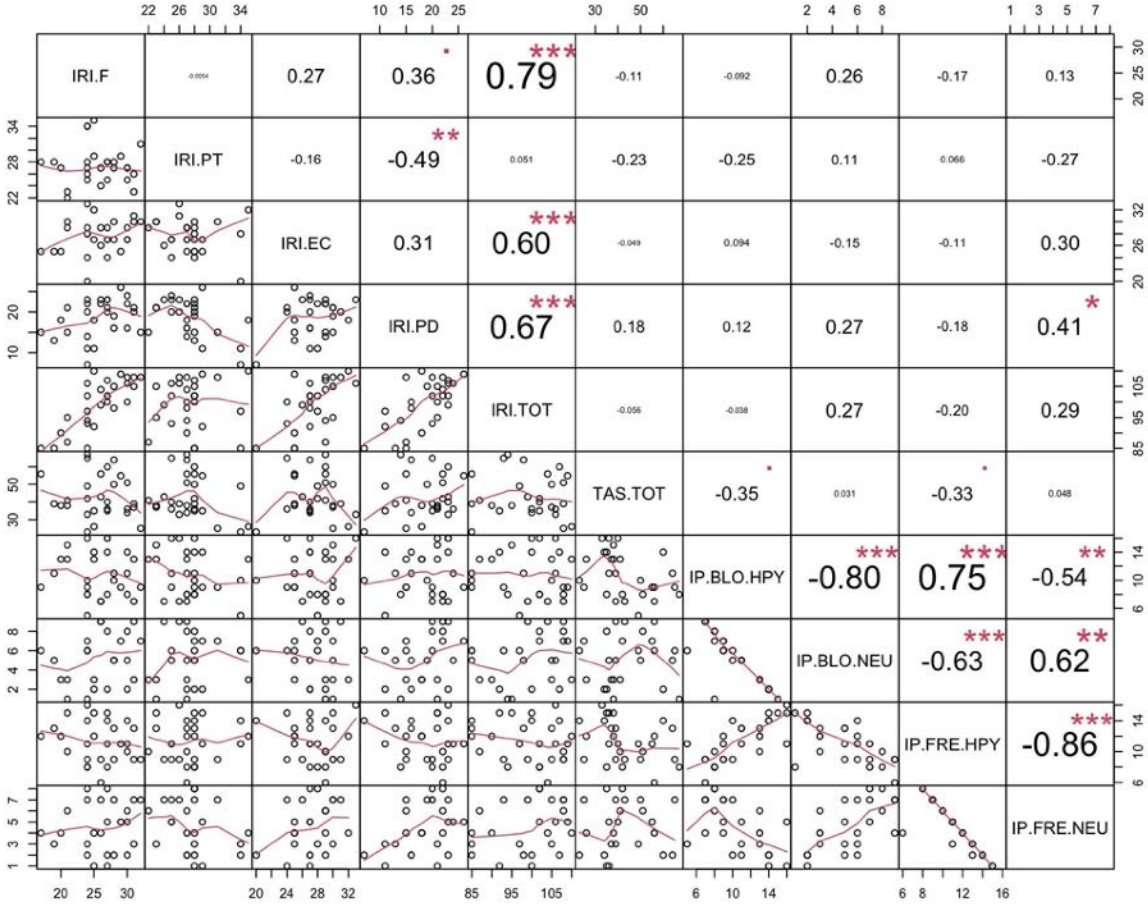
* = p < .05

** = p < .01

*** = p < .001

Initial Percept.



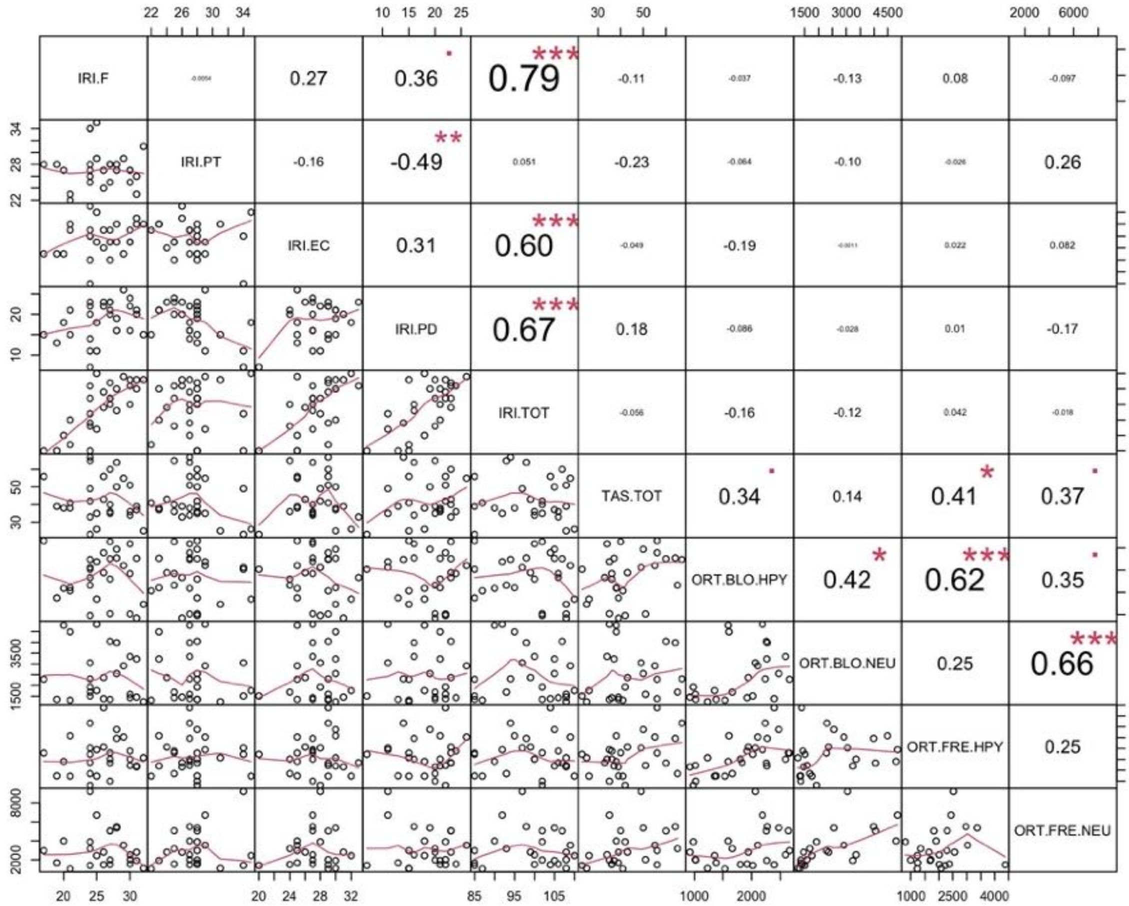
. = p < .1

* = p < .05

** = p < .01

*** = p < .001

Onset Resolution Time.



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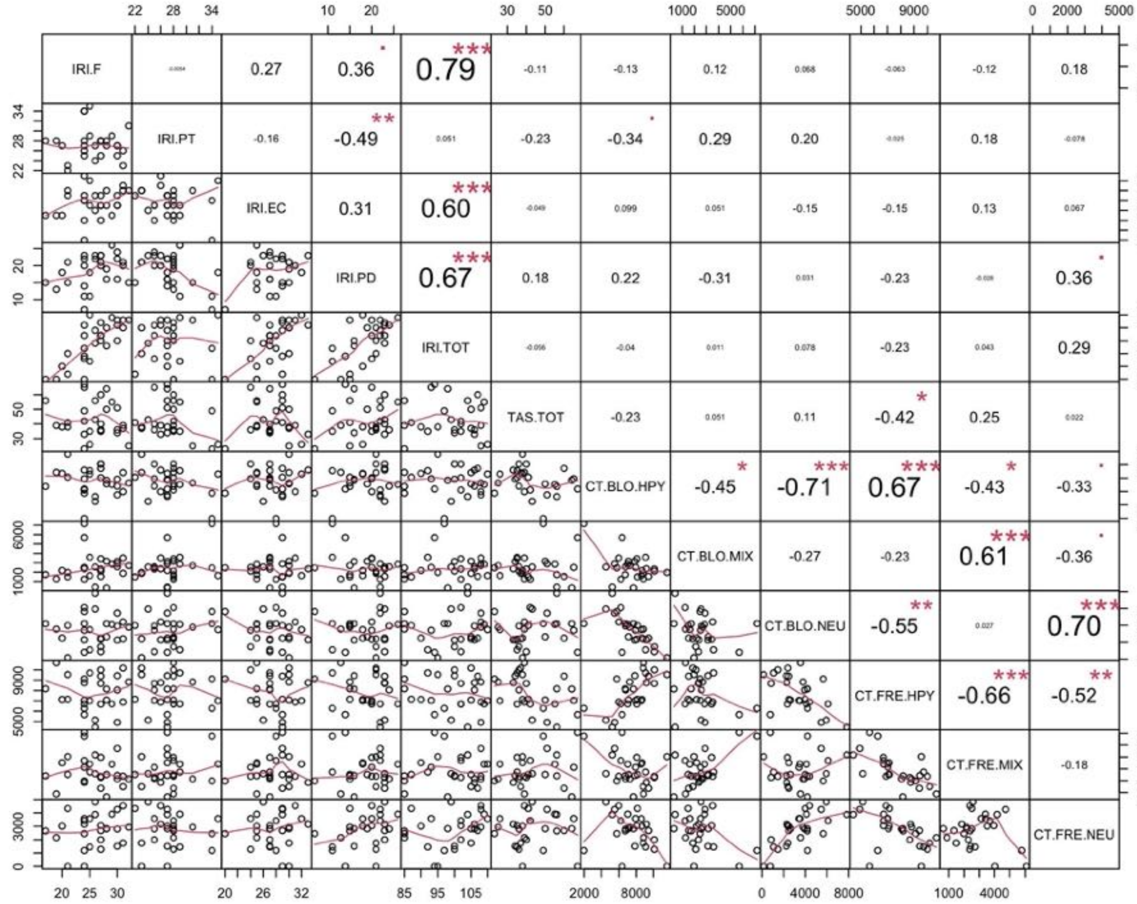
** = p < .01

*** = p < .001

Cumulative Time.



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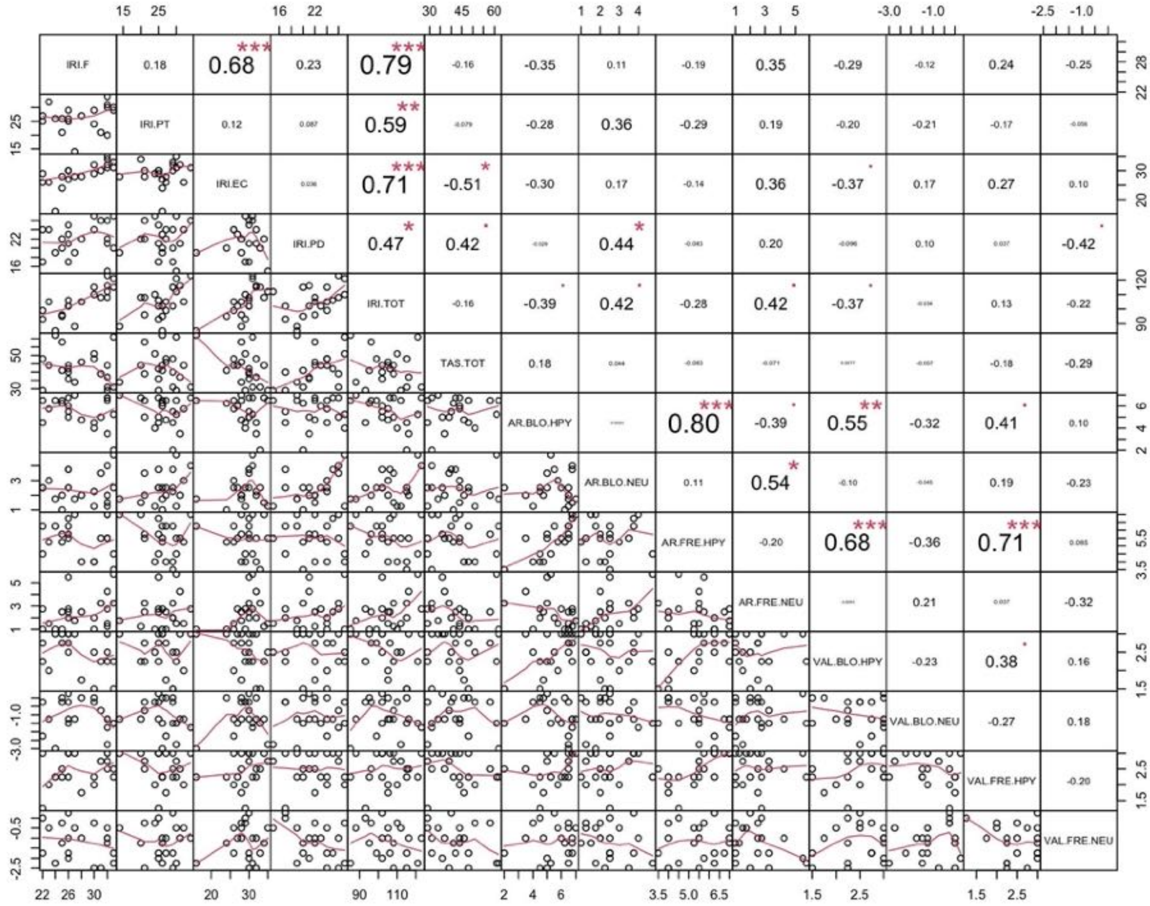
*** = p < .001

12.4.2 Experiment 2: IRI and TAS correlation with BR measures

Valence and Arousal.



. = p < .1

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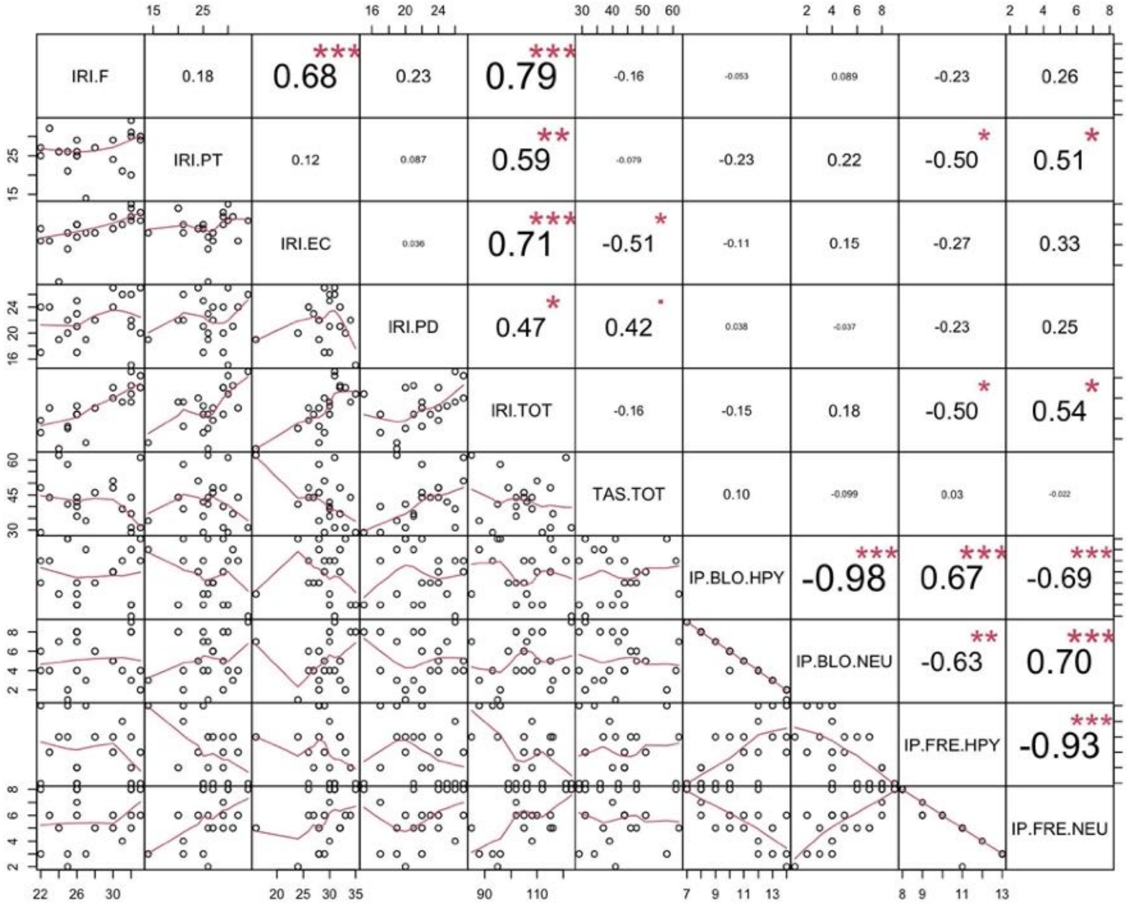
*** = p < .001

Initial Percept.



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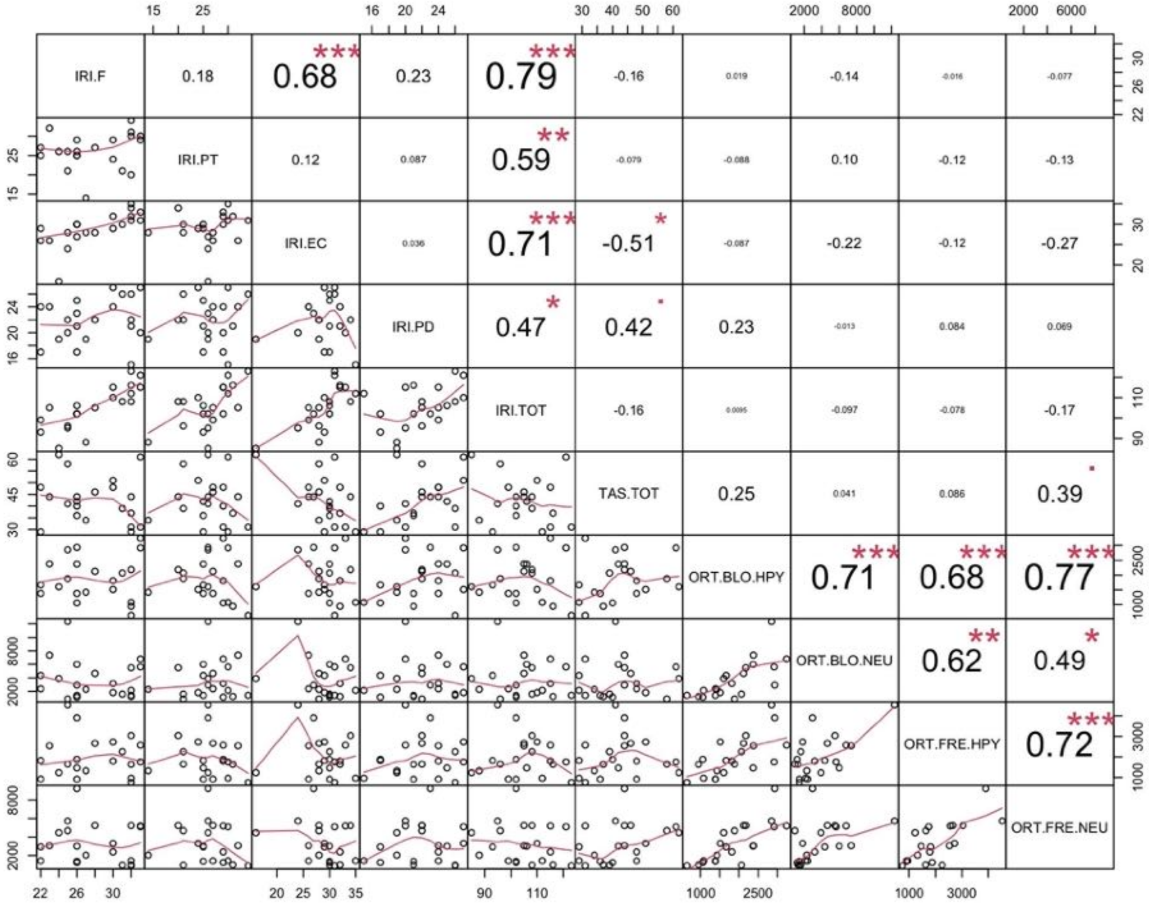
** = p < .01

*** = p < .001

Onset Resolution Time.



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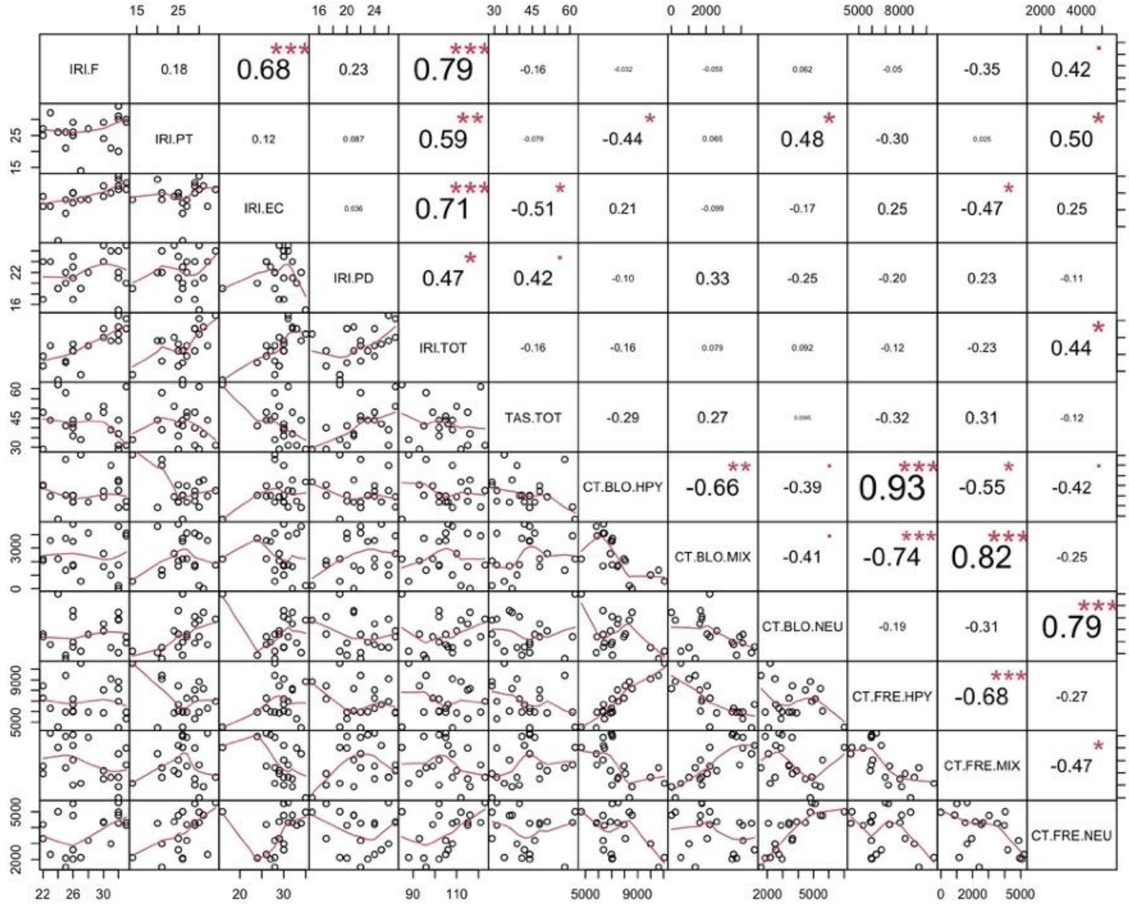
* = $p < .05$

** = $p < .01$

*** = $p < .001$

Cumulative Time.



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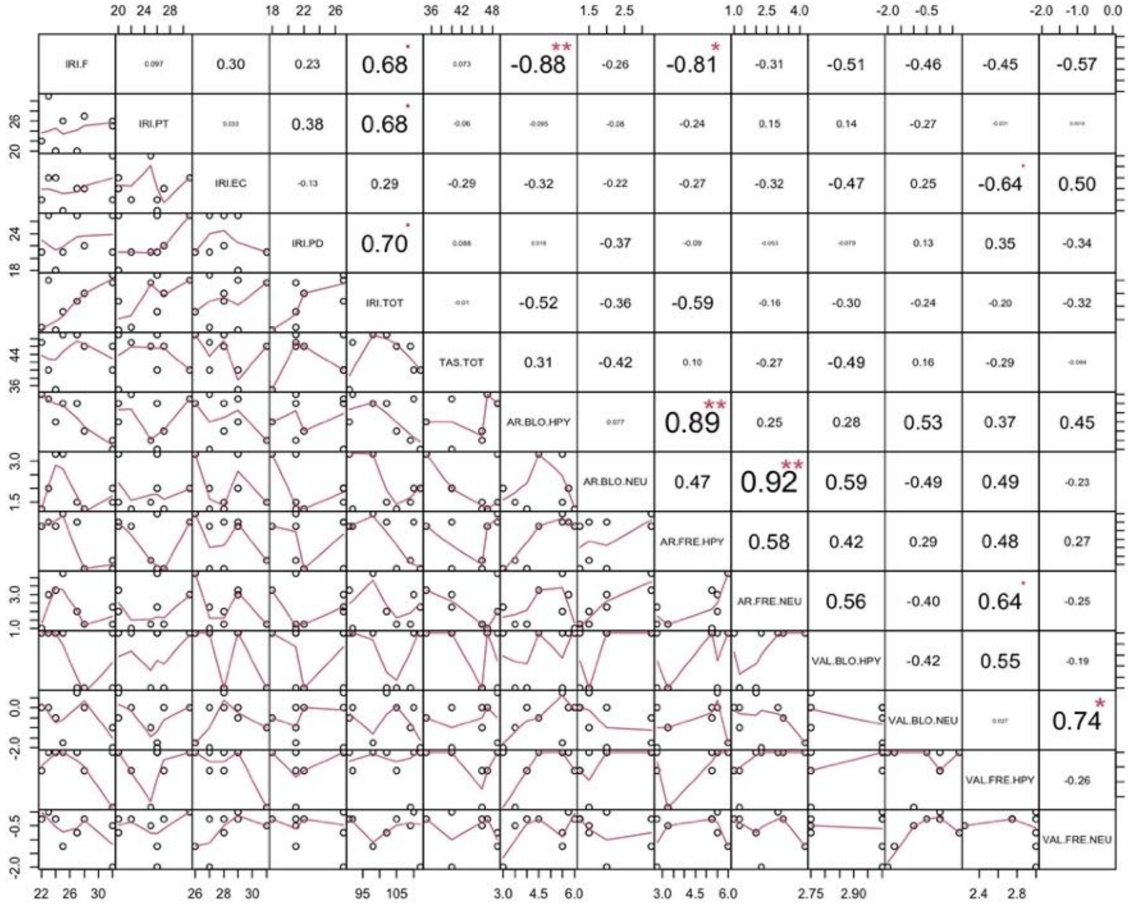
** = p < .01

*** = p < .001

12.4.3 Experiment 3: IRI and TAS correlation with BR measures

Valence and Arousal.



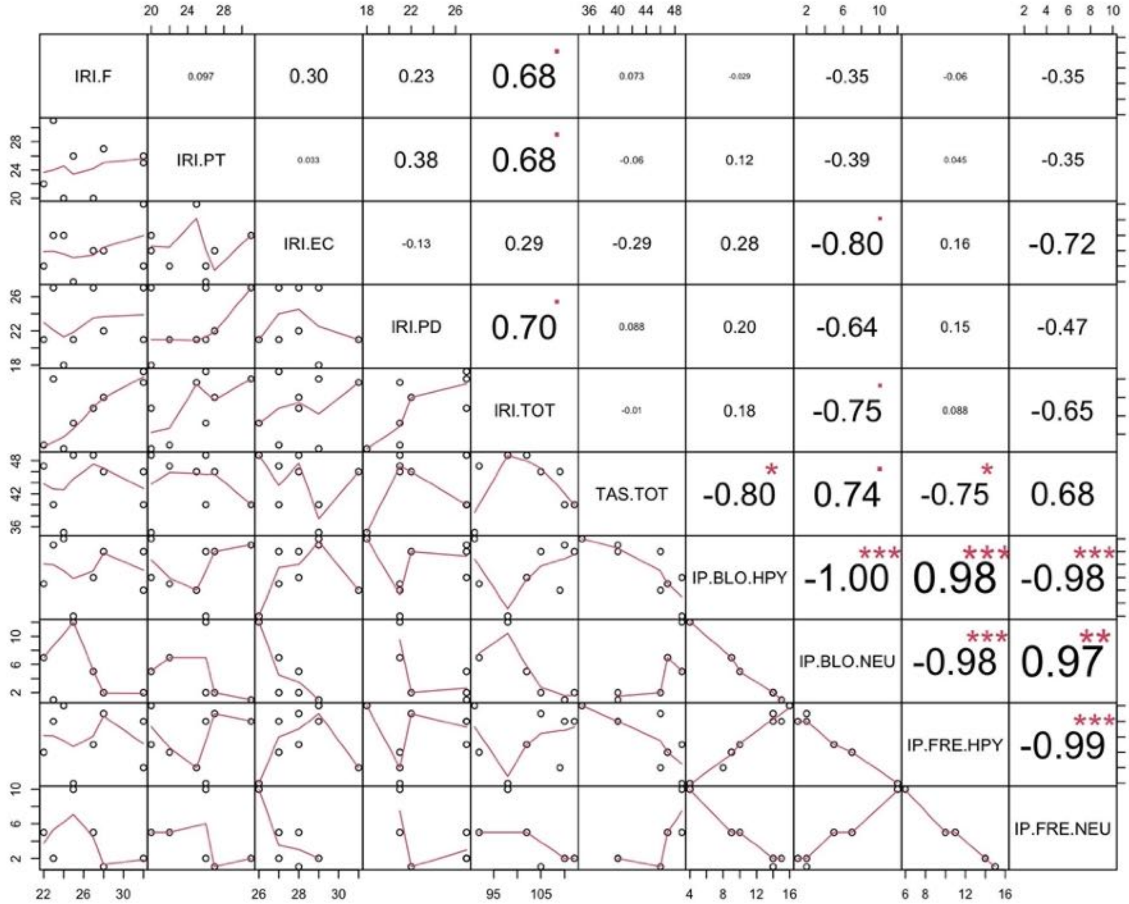
. = p < .1

* = p < .05

** = p < .01

*** = p < .001

Initial Percept.



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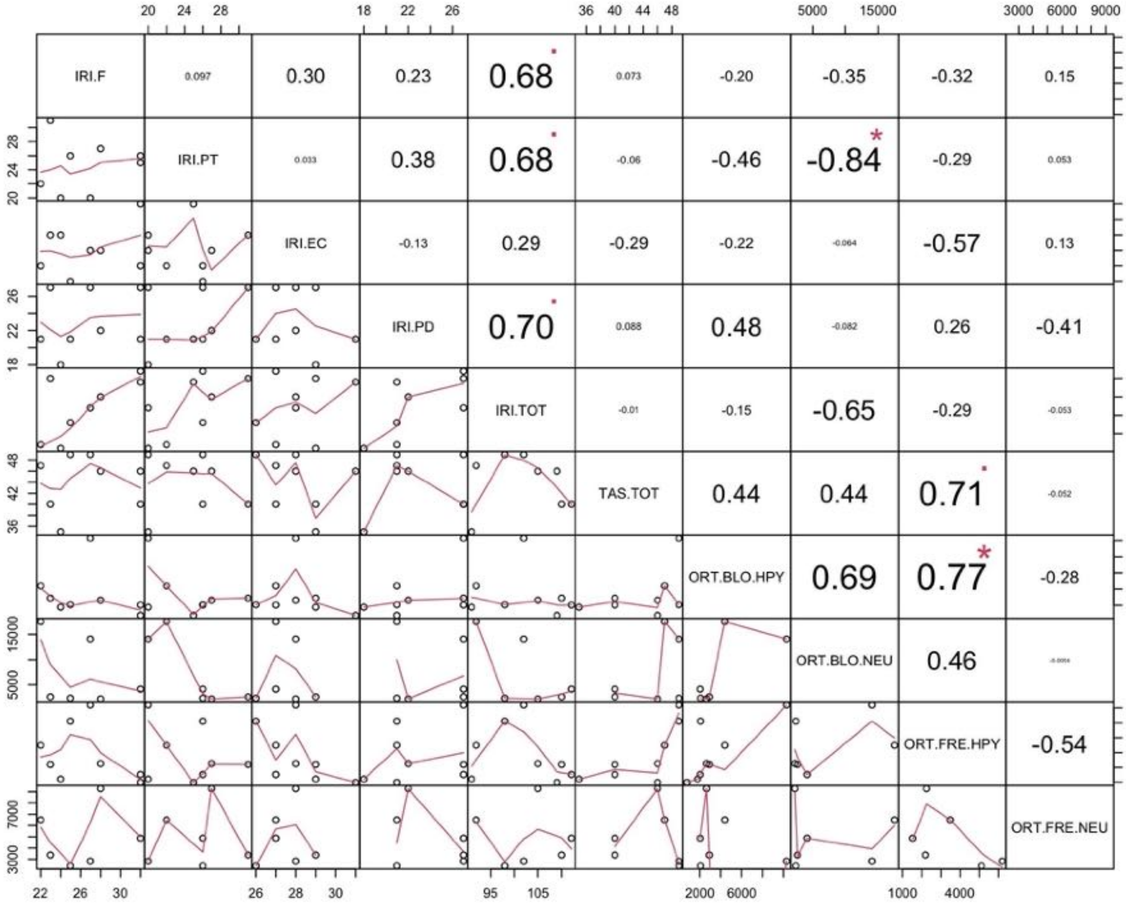
* = p < .05

** = p < .01

*** = p < .001

Onset Resolution Time.



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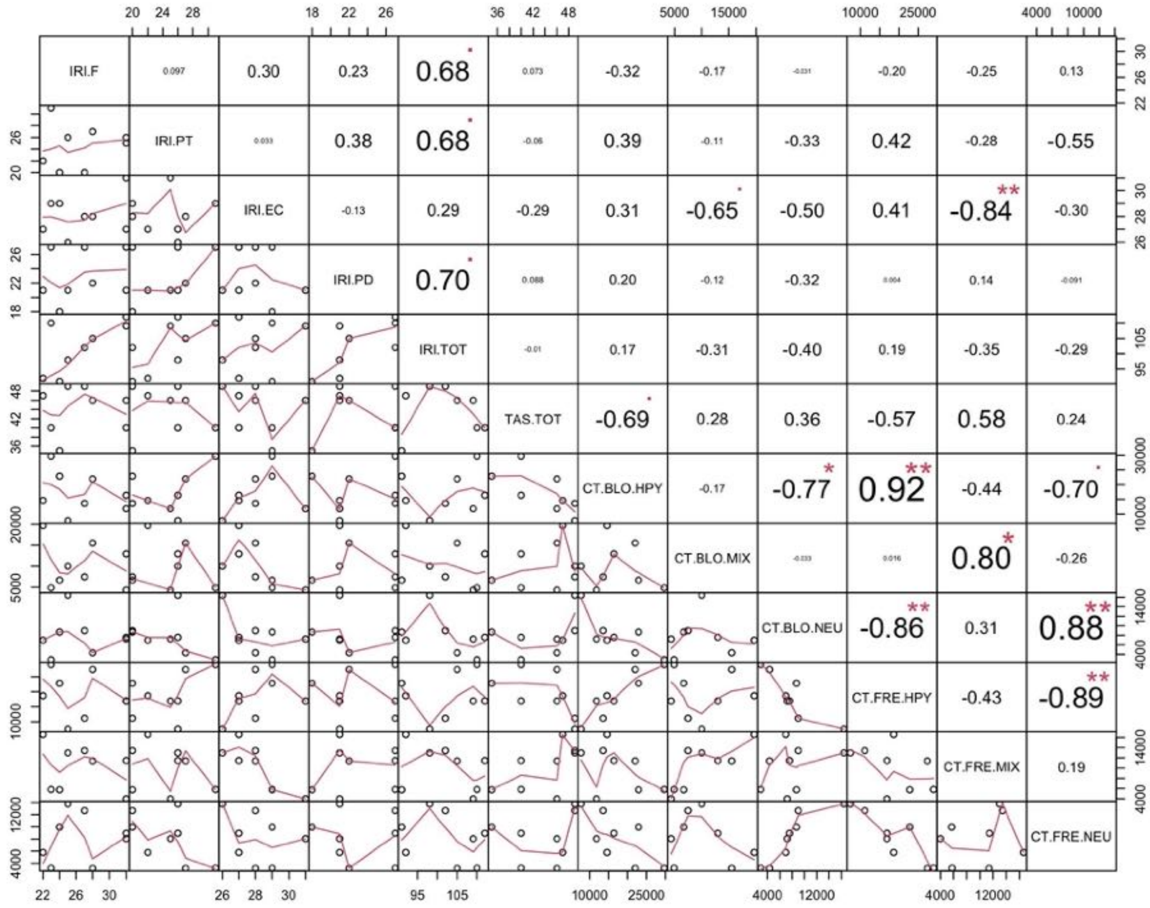
** = p < .01

*** = p < .001

Cumulative Time.



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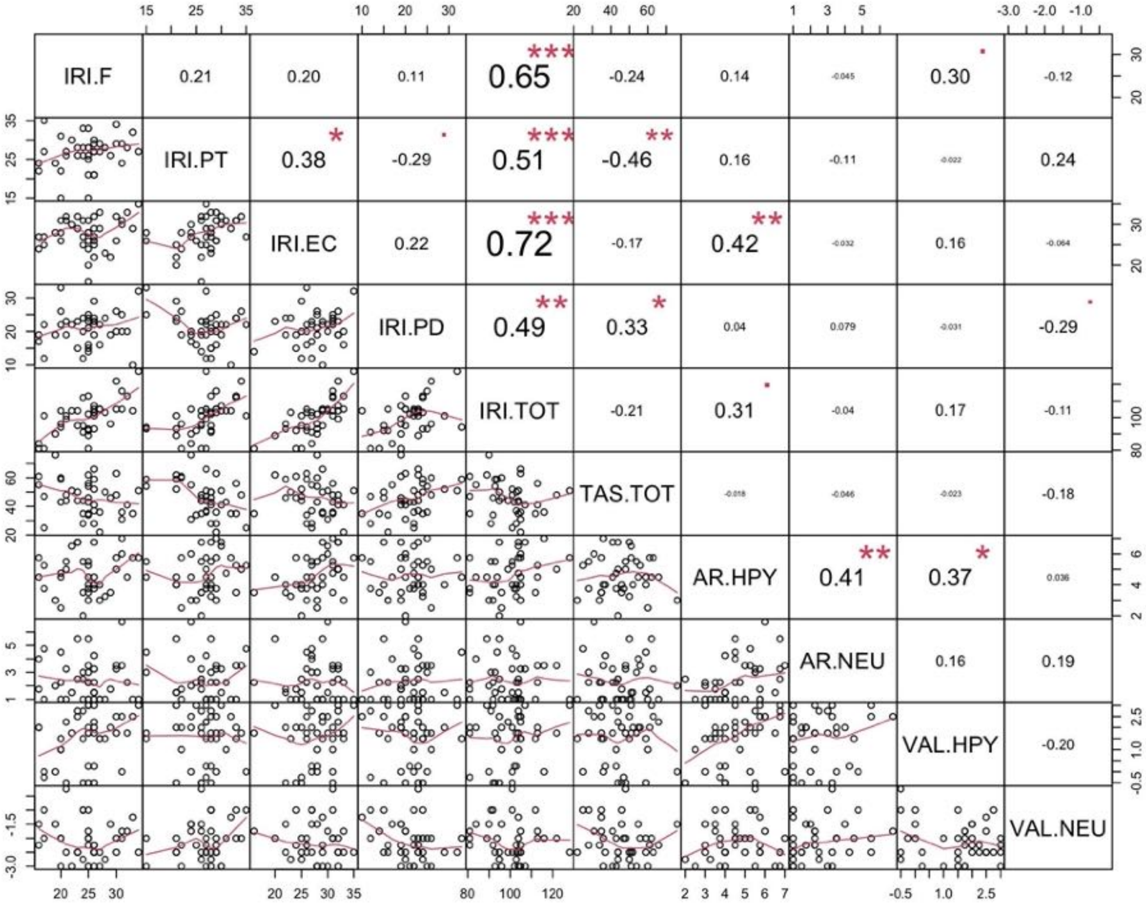
** = p < .01

*** = p < .001

12.4.4 Experiment 4: IRI and TAS correlation with BR measures

Valence and Arousal.



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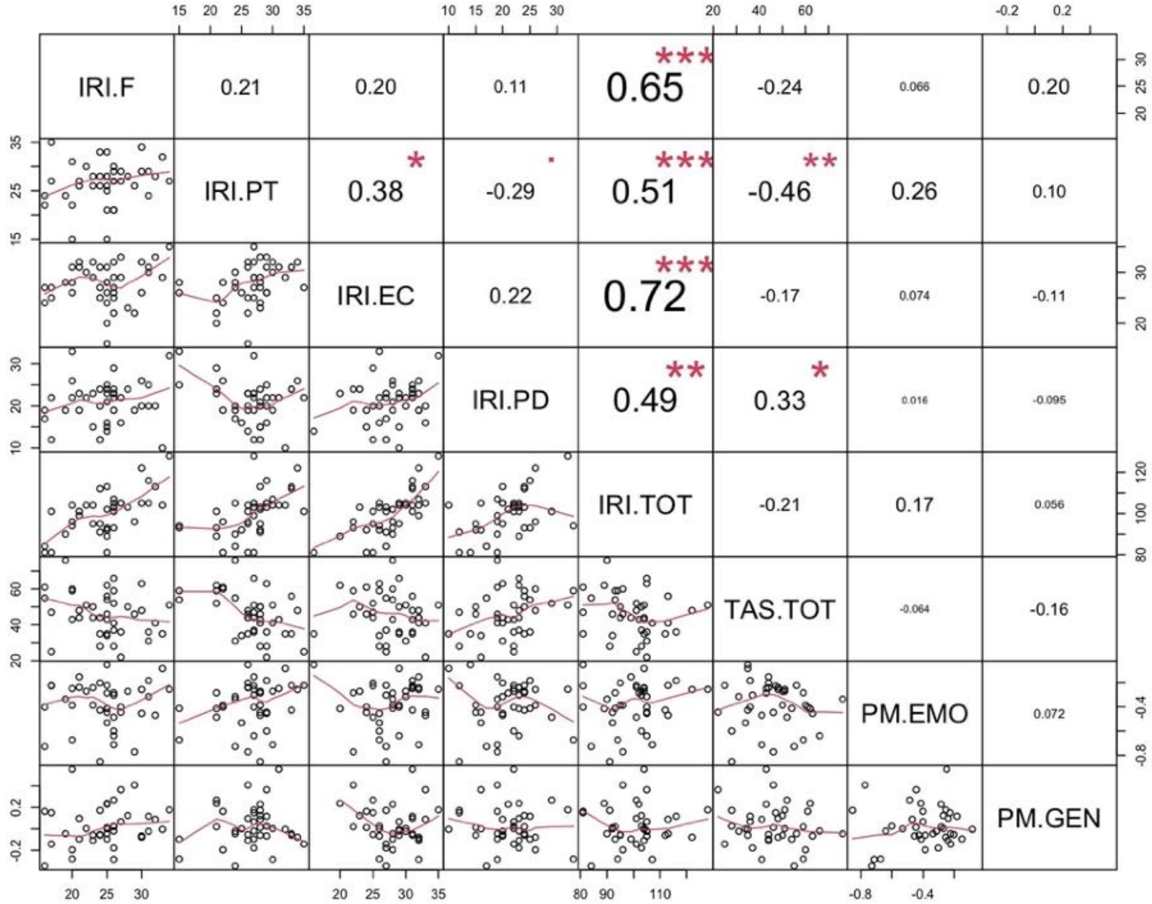
** = p < .01

*** = p < .001

Predominance Mean.



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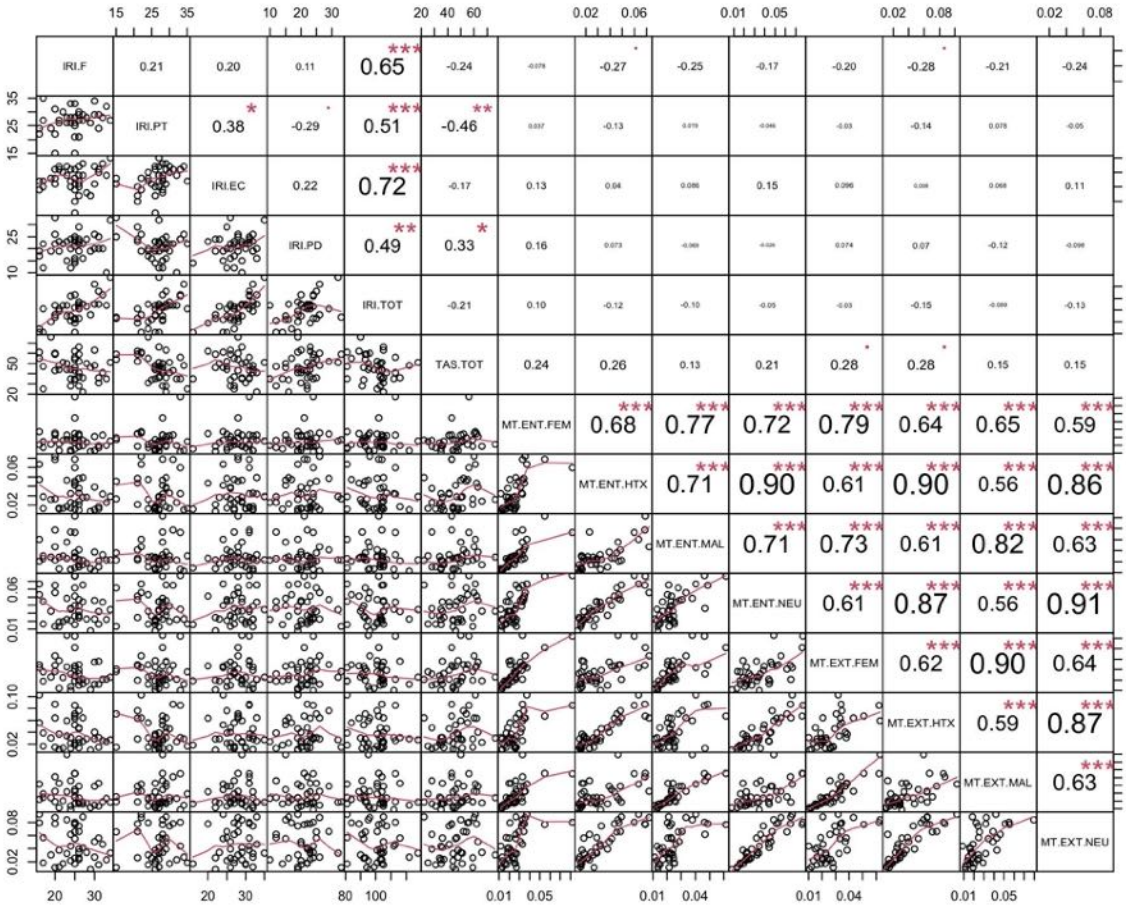
* = $p < .05$

** = $p < .01$

*** = $p < .001$

Movement Transition.



. = p < .1

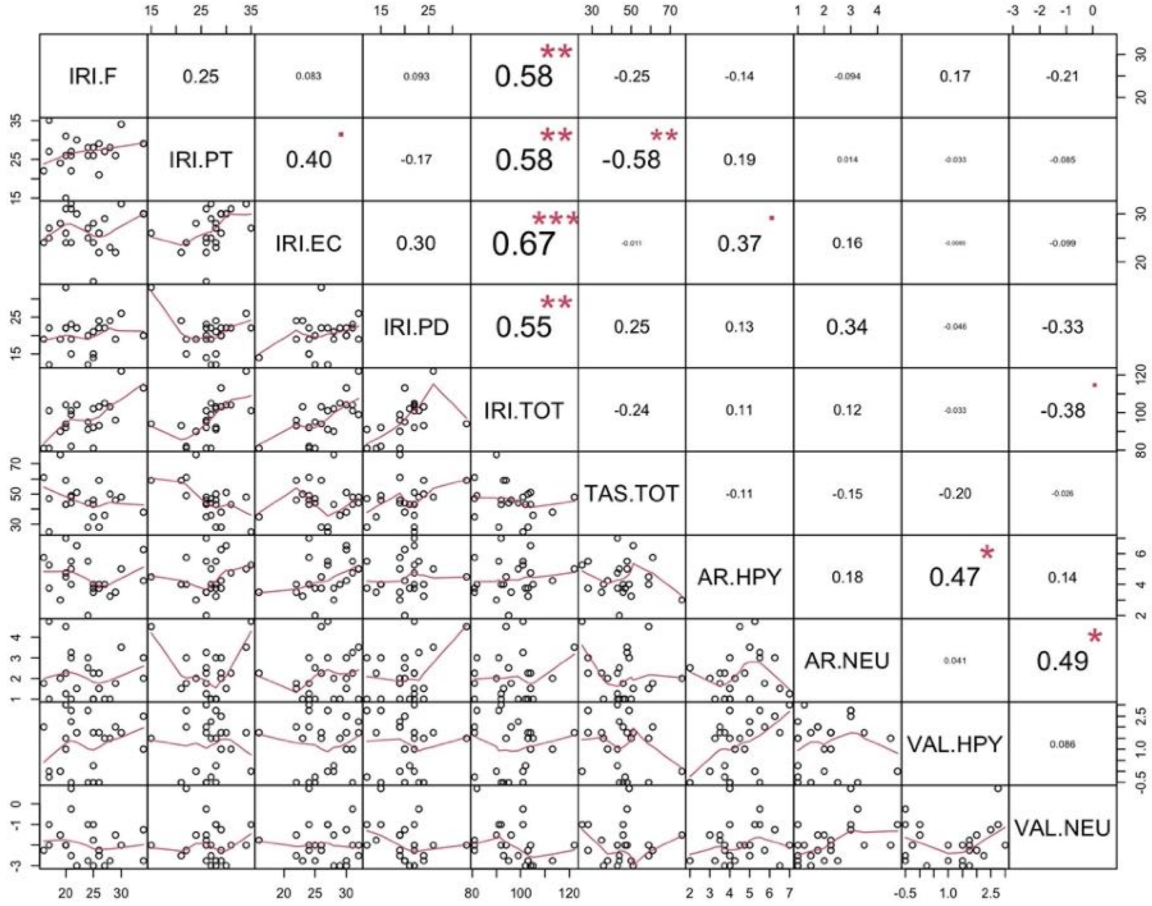
* = p < .05

** = p < .01

*** = p < .001

12.4.5 Experiment 5: IRI and TAS correlation with BR measures

Valence and Arousal.



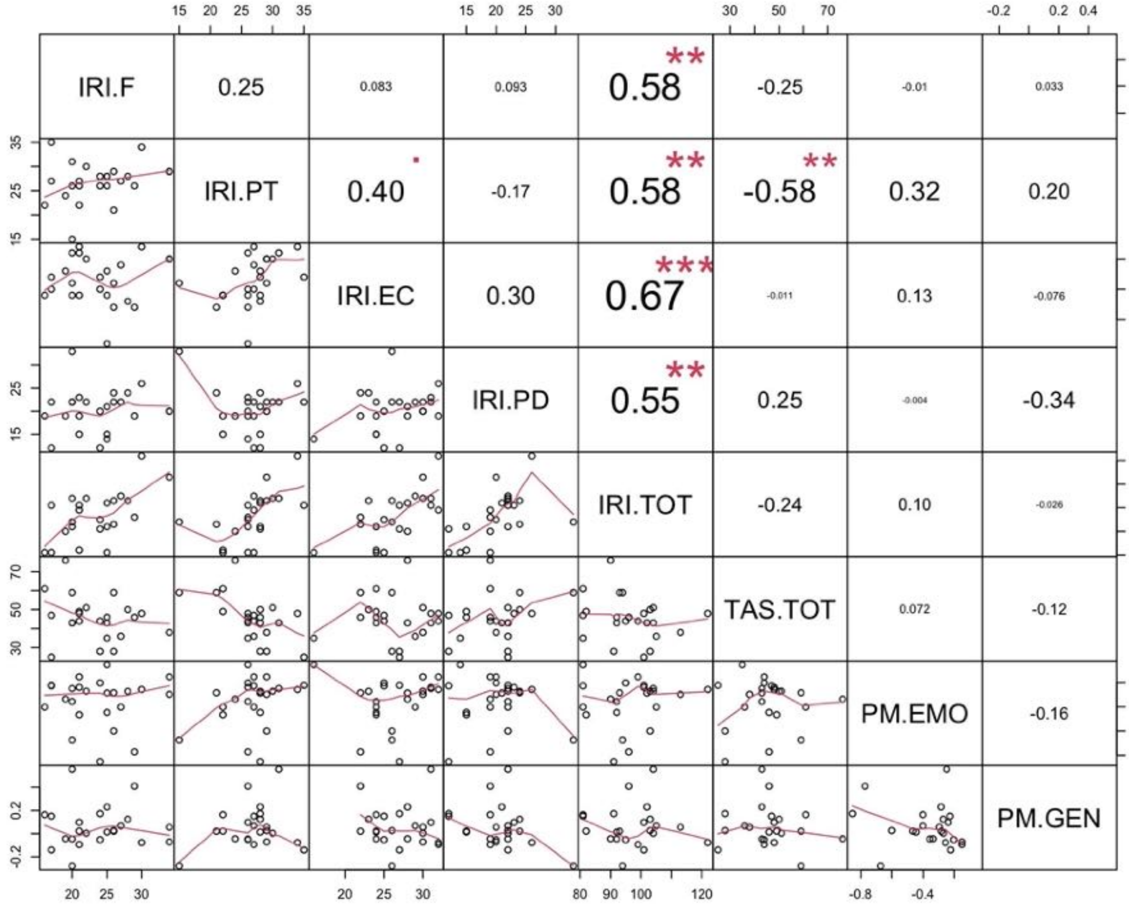
. = p < .1

* = p < .05

** = p < .01

*** = p < .001

Predominance Mean.



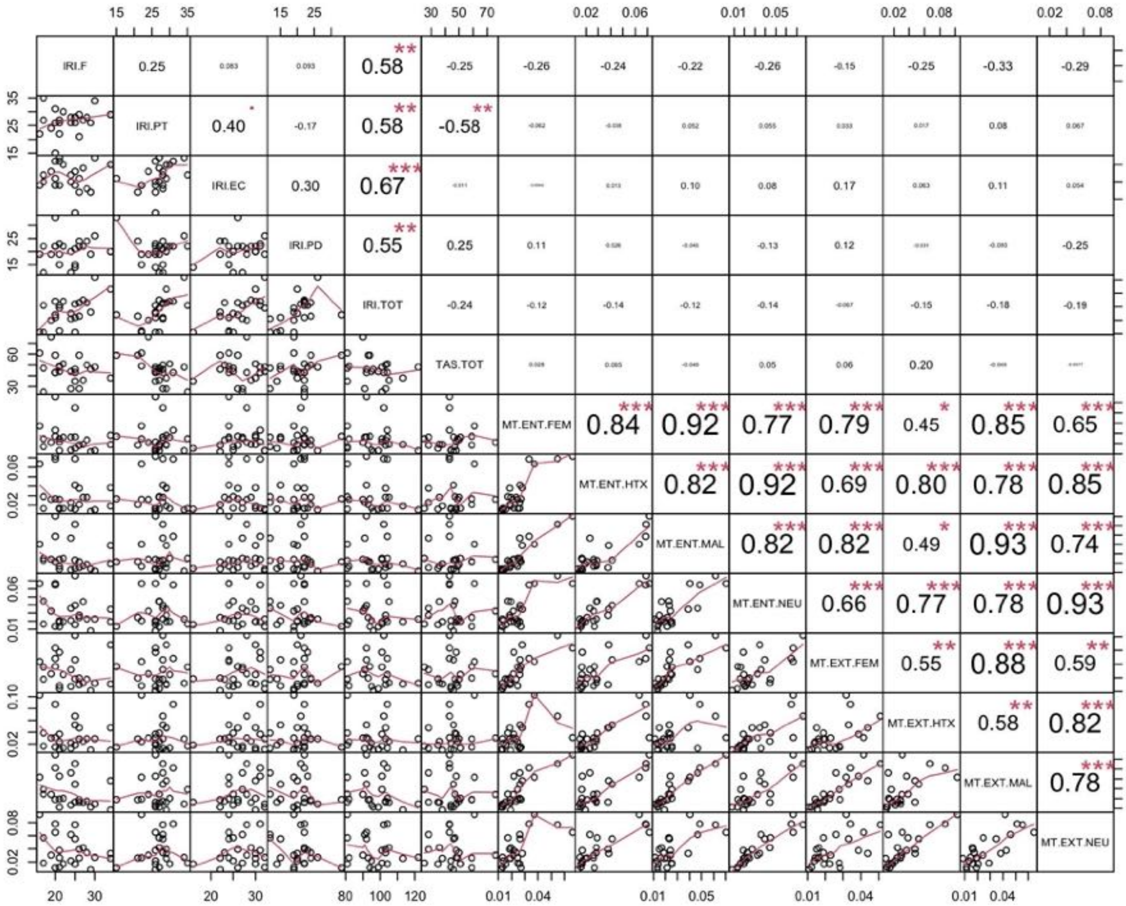
. = p < .1

* = p < .05

** = p < .01

*** = p < .001

Movement Transition.



. = p < .1

* = p < .05

** = p < .01

*** = p < .001

12.5 VR headset

The impairment of ocular abduction from Moebius participants required adaptation of the BR setting. This material allows setting images position independently, as in stereoscope. With respect to anaglyph setting here, Moebius participants experienced BR.

Figure 31. BR setting is composed of a VR headset, a monitor and a 3d printed adapter.

13 Acknowledgments

Thanks to:
Jean unfortunately gone too early to see this achievement,
Paola for her continuous and kind supervision,
Antonella for her unconditional support

For their collaboration and advice:
Prof Paola Sessa
Prof Naotsugu Tsuchiya
Prof Matthew Longo
Prof Lucia Regolin
Prof Pier Francesco Ferrari
Ph.D Arianna Schiano Lomoriello
Filippo Gambarota
MD Giacomo Minicuci

For their help in data collection:
Nicolò Di Lello
Elena Moro

For the photos:
Antonella
Fanny