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PLASTICITY AND NEUROMODULATION OF THE EXTENDED RECURRENT VISUAL NETWORK

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ABSTRACT

The extended visual network, which includes occipital, temporal and parietal posterior cortices, is a system characterized by an intrinsic connectivity consisting of bidirectional projections. This network is composed of feedforward and feedback projections, some hierarchically arranged and others bypassing intermediate areas, allowing direct communication across early and late stages of processing. Notably, the early visual cortex (EVC) receives considerably more feedback and lateral inputs than feedforward thalamic afferents, placing it at the receiving end of a complex cortical processing cascade, rather than just being the entrance stage of cortical processing of retinal input. The critical role of back-projections to visual cortices has been related to perceptual awareness, amplification of neural activity in lower-order areas and improvement of stimulus processing. Recently, significant results have shown behavioural evidence suggesting the importance of reentrant projections in the human visual system, and demonstrated the feasibility of inducing their reversible modulation through a transcranial magnetic stimulation (TMS) paradigm named cortico-cortical paired associative stimulation (ccPAS). Here, a novel research line for the study of recurrent connectivity and its plasticity in the perceptual domain was put forward. In the present thesis, we used ccPAS with the aim of empowering the synaptic efficacy, and thus the connectivity, between the nodes of the visuo-cognitive system to evaluate the impact on behaviour. We focused on driving plasticity in specific networks entailing the elaboration of relevant social features of human faces (Chapters I & II), alongside the investigation of targeted pathways of sensory decisions (Chapter III). This allowed us to characterize perceptual outcomes which endorse the prominent role of the EVC in visual awareness, fulfilled by the activity of back-projections originating from distributed functional nodes.

GENERAL INTRODUCTION

I. Information processing streams in the visual system

Vision may be considered as our predominant sense, if we reason both in terms of perception (e.g., Rock & Victor, 1964) and in terms of the volume of the brain architecture involved to it (Kaas, 2008). Parallel computing of unique visual feature information is a distinctive property of mammalian visual systems (for reviews, see Briggs, 2017; Nassi & Callaway, 2009; Seabrook et al., 2017). Concurrent channels originate in the retina with different types of bipolar cells that collect inputs directly from cone photoreceptors and transmit them to separate forms of retinal ganglion cells (RGCs), the only neurons with axons that leave the retina (for reviews, see Dacey et al., 2014; Field & Chichilnisky, 2007). From the retina, through the LGN, and to the geniculocortical input termination sites in V1, the parvocellular, magnocellular, and koniocellular streams are biologically isolated. Via a confluence of LGN afferent inputs and/or regional circuits inside V1, several more complex visual physiological features arise. Among these emergent attributes are orientation tuning, (Hubel & Wiesel, 1968); direction selectivity (Gur et al., 2005; Hubel & Wiesel, 1968); colour specificity (Conway & Livingstone, 2006; Garg et al., 2019; Johnson et al., 2001); and binocular disparity (Cumming & Parker, 1997; Hubel & Wiesel, 1968). Feedforward corticocortical projection neurons in V1 are mostly found in the superficial layers (layers 2/3 and 4B) and send fibers to the extrastriate visual cortical areas V2, V3, V4, middle temporal (MT), and V6 (Nassi & Callaway, 2007, 2009; Sincich & Horton, 2005; Yukie & Iwai, 1985).

Following Hubel and Wiesel's foundational work in 1968, it has been presumed that ascending feedforward projections and lateral (i.e., intrinsic) connections are required to generate the most elementary receptive field properties in the early visual system. Consequently, at each subsequent processing stage, both feedforward and intrinsic circuitry lead to the extraction of complex visual scene properties (Galuske et al., 2002).

Interpreting vision implies hierarchical processing. The visual system is made up of several anatomical units that are hierarchically arranged and functionally adapted for processing different features of a visual object (Felleman & Van Essen, 1991). Ascending feedforward projections, descending feedback projections, and projections from the same hierarchical level of cerebral structures connect these visual regions (Lamme et al., 1998). Despite mounting evidence that these distinct projections perform substantially distinct roles in perception, their functions in visual processing remain a topic of discussion (Lamme & Roelfsema, 2000). The connections between cortical regions lead to various functionally specialized routes for processing different components of a visual item (Van Essen & Gallant, 1994).

Inspired by the work of Rockland and Pandya (1979), plenty of connectivity studies in the cortex revealed further evidence of hierarchical organization, prompting Felleman and Van Essen to introduce the first hierarchical model of the cortex (Felleman and Van Essen, 1991), establishing the groundwork for contemporary view of feedforward (FF) and feedback (FB) mechanisms.

Hierarchy has been widely investigated in terms of cortical areas classification based on a variety of factors (Hilgetag & Goulas, 2020). Several interpretations of hierarchy' coexist in brain systems, such as distance along the brain's posterior-anterior axis, sequential variations of neural responses based on functional complexity, cortical thickness gradients, or a continuum of laminar projection patterns. The monkey visual cortical hierarchy (VCH) is a basic example of the notion. The regions are not grouped by topology, that is, synaptic proximity and distance from the retina (as in the model of Mesulam (1998)), but rather by the laminar origin and termination arrangements of projections connecting them, as depicted in Felleman's wiring diagram.

According to conventional views, basic visual elements are encoded in the primary (V1) or low-level visual cortex, whereas relatively complex sensory characteristics accumulate at higher-order visual regions for perceptual output (Briggs & Usrey, 2011; Juan & Walsh, 2003; Klink et al., 2017; Ro et al., 2003). Then, multiple sensory representations are constructed along distinct independent pathways, with object shape or form content extracted by the ventral stream from region V1;V3;V4 and motion/spatial position signals acquired by the dorsal stream from V1;V2;V5 (Brown, 2009; Kravitz et al., 2011; Lehky & Sereno, 2007; Mercier et al., 2017).

The identification of two main parallel routes of visual signal processing in the monkey's visual cortex, referred to as the dorsal magno-stream and the ventral parvo-stream, was one of the most significant advances in cerebral cortex research in the previous century. More than 30 cortical regions are implicated in these pathways, which process motion/position and shape/color visual information, respectively (DeYoe & Van Essen, 1988; Merigan & Maunsell, 1993; Mishkin et al., 1983; Van Essen et al., 1990).

Ungerleider and Mishkin (1982) presented that model of primate cortex with two visual circuits about 40 years ago. Based on lesion observations in nonhuman primates, each route was morphologically and functionally defined. The ventral route runs parallel to the ventral brain surface and is responsible for determining the identity of visual items (e.g., faces, animals, cars, or tools). The dorsal pathway, also known as the vision for action pathway (Milner & Goodale, 2006) flows along the surface of the dorsal cortex. While subsequent updates have taken into account a multitude of additional research (Kravitz et al., 2011, 2013), currently evidence state for the plausibility of an additional third visual pathway on the lateral brain surface (Pitcher & Ungerleider, 2021).

II. Recurrent communication and feedback pathways in visual networks

Across multiple feedback projections, the early visual cortex (EVC) gathers signals from higher cortices, at least as numerous as feedforward projections from lower to higher regions (Markov et al. 2011). Several feedback connections to the primary visual cortex, for instance, derive from the visual system [e.g., V2–V4, V5 (or MT)], other sensory cortices (e.g., the primary auditory cortex), but also from non strictly sensory centres in the parietal and frontal cortices (Markov et al., 2011; Muckli & Petro, 2013). Axonal termination patterns in the visual system exhibit numerous arborization structures, comprising axon branches that spread across considerable brain distances with diffused or clustered terminals, according to data from morphological analyses of corticocortical feedback (Kathleen S. Rockland & Virga, 1989; Kathleen S Rockland & Knutson, 2000). Excitatory neurons that establish synaptic interactions with both excitatory and inhibitory cells in their targeted area, actually mediate corticocortical feedback (Anderson & Martin, 2009; Angelucci et al., 2017; Angelucci & Bressloff, 2006). As a consequence, the early visual cortex communicates with a number of different cerebral circuits, although the relevance of feedback pathways is yet elusive. Retrograde tracing experiments in the monkey brain have revealed feedforward and feedback circuits between the striate, extrastriate, and parietal areas (Clavagnier et al., 2004; Markov et al., 2014; Muckli & Petro, 2013). Their functional connectivity research corroborates the hypothesis that regions across the visual computation stream are functionally independent albeit strongly associated. Researchers observed persistent and reciprocal connectivity between the early occipital cortex and higher visual areas, as well as top-down signals from parietal lobes. They found bidirectional interaction between areas of the occipital visual cortex and top-down transmission from fronto-parietal regions inside the visual pathways. Earlier anatomical investigations demonstrated a bottom-up hierarchy along the visual pathways, while latest evidence has highlighted the relevance of feedback communication over early visual regions. Compared to feedforward thalamic afferents, the early sensory cortex catches significantly more feedback and lateral information (Budd, 1998; Muckli & Petro, 2013). This is accomplished by a complex system of cortico-cortical interconnections (Felleman & Van Essen, 1991), with feedback signals originating from both extrastriate and parietal cortices (Barone et al., 2000; Lewis & Van Essen, 2000a). Morphological evidence, from nonhuman primate research, showing wide bidirectional connections along the extended visual decoding network, markedly constituted the findings. Top-down transmission may also represent a broader sense of cortical feedback's unrecognized importance, especially on the early visual cortex (Anderson et al., 2011; Gilbert & Li, 2013). Considering corticocortical routes, a recent research discovered twice as many feedback connections than feedforward pathways, as well as the observation that feedback connections were most long-range, whilst feedforward paths are relatively short-range (Markov et al., 2014).

A conceptual model exists in which feedback connections allow the early visual cortical areas to operate as an adaptive blackboard (Bullier, 2001; Cavanagh, 2011; Kosslyn et al., 2001; Mumford, 1992; van der Velde & de Kamps, 2006), highlighting task-relevant attributes with increased synaptic activity. Long-distance combination of several stimulus characteristics can be handled, based on Bullier (2001), by retroinjecting the overall calculations performed by higher order regions into V1 and V2, wherein they drive the fine-detail processing. The notion that extrastiate-V1 interconnections are crucial for the interpretation of fine details has actually become a core component of Hochstein and Ahissar's Reverse Hierarchy Theory (2002). Approximately 55–70 ms after the onset of a sensory signal, the human primary visual system is engaged (H. A. Baseler & Sutter, 1997; Foxe & Simpson, 2002; Vanni et al., 2001). Once the feedforward flow begins, recurrent activity between extrastriate and striate regions takes place soon. The timing of V1 involvement through recurrent computation can be approximated to initiate about 10–40 ms after the start of the feedforward course, based on TMS experiments on motion perception (Koivisto et al., 2010; Pascual-Leone & Walsh, 2001; Silvanto, Lavie, et al., 2005) and magnetoencephalographic (MEG) recordings (Boehler et al., 2008). These results suggest that immediately after neural activation crosses V1, feedforward and regional looping operations are coupled concurrently. While the activity continues to be transmitted forward to higher brain locations, the initial recurrent processes begin.

Feedforward transmission would be fundamental for communicating and converting sensory information. Feedback processing, on the other hand, might be essential to the intriguing idea that the brain predicts its environment (Clark, 2013; Park & Friston, 2013). Predictive coding could be crucial for organizing cognition and behaviour, and it could represent the cortex's dominant processing. In addition to sensory-specific feedback signals with complex characteristics, these network systems are pivotal to the discussion of what is communicated via top-down signaling (Petro et al., 2014). Researchers can reasonably infer what evidence is entailed in human feedback signals, such as estimates of high-level attributes of external environments (Morgan et al., 2016) and gratings (Chong et al., 2016). Researchers also presume that feedforward and feedback waves operate on distinct receptors and exhibit specific oscillatory rhythms (Bastos et al., 2015; Self et al., 2012; Van Kerkoerle et al., 2014).

During the decision-making process, activity in the parietal and prefrontal cortices intensifies, and this activation hits a characteristic peak right before movement initiation, when the neurons have achieved a threshold of activity. Sensory neuron firing, on the other hand, does not always follow an escalating pattern and is often only a poor indicator of the final choice (Britten et al. 1996, Shadlen et al. 1996). As a result, some studies have indicated that sensory areas' function is limited to supplying momentary evidence (Law & Gold 2008), which then accumulates downstream to lead to a choice. Further research has shown distinct markers of decision result in the early visual cortex. When monkeys undergo a curve-tracing task, for example, the activity of the V1 neurons that encode the traced curve is amplified, even if the monkeys draw the incorrect curve (Roelfsema & Spekreijse, 2001). Choice probabilities were employed by Nienborg & Cumming (2009) to show a significant relationship among neural activity in the occipital lobe and the perceptual coding of the sensory aspects of a stimulus. In humans, functional brain imaging experiments have also shown that sensory judgments have an impact on activity in the early visual cortex. In particular, anticipatory cues or certain sensory input characteristics affect perceptual choice and, on the same time, alter decision-related patterns in early visual cortex regions (Kok et al., 2012, 2014). Additionally, altering respondents' beliefs about the expected direction of motion influences both the perceptual judgement and the neural representations in the early visual cortex which can be retrieved via BOLD activation profiles (Kok et al., 2013). The above findings converge to characterize decision-making as a stochastic inference process involving a multilayered and dynamic interaction between sensory and choice-related neurons (Haefner et al., 2016; Nienborg & Roelfsema, 2015; Summerfield & de Lange, 2014). Wimmer et al. (2015) applied neurocomputational simulation to explain how the interplay between choice and sensory neurons might lead to the observable patterns of choice probabilities and evidence consolidation. Further precise assessments of the active blackboard theory involve causal strategies to alter response variation in visual processing regions avoiding disrupting the early transmission of signals from lower to higher areas following the exposition to a novel sensory input. TMS pulses were used to impair functioning of the early visual cortex synchronously to the occurrence of visual information in higher visual regions. The above TMS research has indicated that interruptions of V1 function negatively impacts precision in a set of cognitive operations that might depend on the blackboard, such as texture segregation (Heinen et al., 2005), scene perception (Koivisto et al., 2011), visual search (Juan & Walsh, 2003), imagery (Kosslyn et al., 1999), and working memory formation (van de Ven et al., 2012).

On this topic, monkey neurons in the lateral intraparietal region (LIP) were found to fire around 50 milliseconds after the incoming visual presentation, suggesting that LIP acquires a fast sensory input that could be deployed to influence the current activity in the early visual areas (Bisley et al., 2004). TMS administered to the parietal cortex alters the excitability of the early visual cortex and even the activity degree of the occipital lobe during visual exposure (Leitão et al., 2013). Kanai et al. (2008) found that TMS applied on intraparietal sulcus (IPS) prior to the occurrence of a visual input amplified the receding of the stimulus from awareness. The posterior intraparietal region (IPS1, IPS2) is a key area potentially transmitting top-down input to the early visual cortex and may have an involvement in conscious experience (Lauritzen et al., 2009).

TMS was also used to induce moving phosphenes by Pascual-Leone and Walsh (2001). They discovered that a second TMS pulse administered on the early visual cortex diminished the experience of phosphene moving. V5/MT activation seems to affects awareness through V1 involvement, based on the latency of the disruptive impact of TMS pulses over V1 (see also (Silvanto, Cowey, et al., 2005). It has also been proven that reentrant connections are required for conscious perception of visually displayed motion (Silvanto, Lavie, et al., 2005). That was obtained by tracing the signal processing that leads to visual awareness by utilizing TMS either over V1/V2 or V5/MT at distinct timescales following the display of a motion stimuli. The findings revealed two crucial windows of V1 activation, one prior and the other subsequent to the V5/MT major involvement, implying that, while V5/MT acquires sensory input via V1 feedforward activity, backprojections from V5/MT to V1 are ultimately necessary for motion awareness. Those latter studies are supported by a large body of electrophysiological research on the modulatory influence of extrastriate feedback on neuronal activation in V1 (e.g., Hupé et al., 2001; Hupé et al., 1998; Lamme et al., 1998; Zipser et al., 1996). V5/MT receives visual data via V1 feedforward spreading, which is then transmitted back to V1 as target-related firing (e.g., Lamme, 2001). Specifically, silencing the area MT in monkeys results in considerable reductions of activation in neurons in areas V1, V2, and V3 (Hupé et al., 2001; Hupé et al., 1998). Such findings confirm the assumption that cortical feedback connections drive circuits in the lower cortical regions. The magnitude of the regulatory influence on the receptive field periphery, related to the response induced by activating the receptive field centre, is amplified by the feedback connections from MT to regions V1, V2, and V3. This phenomenon is proved to be exclusive for low-salience stimuli, like low-contrast moving line on a crowded screen, and not for high-salience stimuli (Bullier, 2001; Hupé et al., 2001). Generally, both conscious and unconscious motion perception appears to involve recurring interaction across V5/MT and V1 (Koivisto et al., 2010, 2011).

In a similar way, current white matter evidence contradicts conventional hierarchy and claims that face analysis operates in a simultaneous and interactive manner rather than in a strict order. Multiple direct fibers routes connecting primary visual cortices and FFA/STS face region have been identified, bypassing the involvement by the OFA (Gschwind et al., 2012; Pyles et al., 2013); additional fibre clusters inside the face network have indeed been found enabling adaptability after brain injury/disease (Grill-Spector et al., 2017). For bottom-up and top-down computation, there are numerous interconnections among face and non-face areas (Kay & Yeatman, 2017).

The utilization of multimodal data to understand the architecture of relationships between modules inside the core and expanded face networks is developing rapidly (Grill-Spector et al., 2017; Wang et al., 2018, 2020; Wang & Olson, 2018). Especially within the right hemisphere, there is both a feed-forward and feed-back flow of information (Wang et al. 2020) relative to the left one, indicating the significant bottom-up and top-down communication processes inside the right hemisphere face network.

The overall network patterns revealed that the early visual cortex projects to the majority of the face sensitive regions, emphasizing that there is no single entry point (or gateway) for FFA and STS. Furthermore, the dynamic configurations of functional connectivity reflect how face processing occurs in a parallel and mutual manner rather than in a fixed order. Face patches in macaque monkeys are richly and reciprocally linked, which contradicts a sequential hierarchy (Grimaldi et al., 2016; Kravitz et al., 2013). According to a recent literature survey, the inferior longitudinal fasciculus (ILF) and inferior fronto-occipital fasciculus (IFOF) are the two most commonly documented long-range fibre routes implicated in face processing. This alternative structure might offer robustness to the face network in the eventuality of brain damage or disorder, which could clarify why prosopagnosia is so infrequent (Grill-Spector et al., 2017; Wang & Olson, 2018).

The resilience of downstream face-selective areas that persist the resection is compatible with notions for a multi-track face system with nonhierarchical components (Atkinson & Adolphs, 2011; Duchaine & Yovel, 2015; Pitcher, Walsh, et al., 2011; Rossion, 2008). Despite the fact that areas within the face network are functionally and anatomically interconnected (Fairhall & Ishai, 2007; Gschwind et al., 2012; Pyles et al., 2013; Tavor et al., 2014; Turk-Browne et al., 2010; Zhu et al., 2011), the network is not organized in a rigid hierarchy in which data is invariably sequentially transferred in a defined order. Moreover, DWI analyses (Weiner et al., 2016) demonstrate several white matter connections from retinotopic areas to the face network, that also supports latest reported models (e.g., Duchaine & Yovel, 2015), and these alternative pathways could assist two purposes. Firstly, by permitting nonserial computing, they may improve the performance of routinely operating networks. They could, for instance, act as recursive connections that enable coarse-to-fine processing (Goffaux et al., 2011; Jiang et al., 2011; Rossion et al., 2003; Rossion, 2008), reverse hierarchical processing (Ahissar & Hochstein, 2004; Bullier, 2001; Mumford, 1992), or recurrent processing (Kravitz et al., 2013). A few of these frameworks additionally allow for feedback routes among face-sensitive regions (Haxby et al., 2000; Moeller et al., 2008). As for this theory, preliminary face classification in the right hemisphere cortical face network may be centred on a global and coarse face representation, that would subsequently be improved via a neural reentrant circuit to lower regions like the OFA (see Mumford (1992) for a proposed reverse hierarchy in the visual system; also Hochstein and Ahissar (2002)). The emergence of selective responses to faces in the right FFA, as observed in the above-mentioned studies, is consistent with a perspective of face perception by microgenesis, referring to the phenomenon by which the initial identification of a face as a face is realized by summarizing the global facial configuration instead of classifying the attributes as spatially independent units. In accordance with the "reverse" hierarchical interpretation of visual perception (e.g., Bullier et al. 2001; Galuske et al. 2002; Hochstein and Ahissar 2002; Hupé et al. 1998; Lamme and Roelfsema 2000; Mumford 1992; see also (Bar, 2003), lower order visual areas showing subsequently face responsiveness, such as the OFA, may be implicated in optimizing the early coarse representation that emerges in higher order regions (Rossion, 2008; Rossion et al., 2010; Schiltz & Rossion, 2006), in order to achieve a finer classification of the faces.

Reentrant connections may perhaps incorporate lower order visual regions in visual processing and interpretations that entail high-resolution elements (Rossion et al., 2003; Rossion, 2008). This latter cognitive perspective is mainly based on theoretical and empirical research on object identification, particularly on how neural activity in higher order visual areas can affect response characteristics in early visual regions (Mumford, 1992; Hupé et al., 1998; Lee et al., 1998; Lamme and Roelfsema, 2000; Bullier et al., 2001; Galuske et al., 2002; Hochstein and Ahissar, 2002).

Moreover, the selective response to faces in higher order visual regions like the FFA may occur in the typical brain separately from putative face sensitive information from the inferior occipital cortex (OFA), presumably involving direct pathways from early (non-face-sensitive) visual areas (Rossion, 2008). This interpretation is supported by the existence of substantial cortical bidirectional connections (Felleman and Van Essen, 1991) and the model of recursive phasic transmission among visual cortical regions (Edelman, 1993; Mountcastle, 1978). Indeed, a critical face decoding area which correspond to the superior temporal sulcus (STS) proved to be connected reciprocally with the visual occipital cortices in monkeys (Seltzer & Pandya, 1994).

In line with a non-hierarchical system (Rossion, 2008, 2011), the initial face representation developing in advanced areas consequent feedforward processing might be holistic and coarse (Goffaux et al., 2011; Sugase et al., 1999) as already found from electrophysiological evidence in the temporal cortex of non-human primates (Sripati & Olson, 2009). This general representation could then be refined by a subsequent wave of signals and/or reentrant functional exchanges with lower visual areas.

The rationale for a detail- or channel-specific feedback arrangement would be to minimize dispersion of feedforward sensory inputs. Cortical feedback may govern the timing and accuracy of feedforward visual information flow, and this could be done differentially regarding the information inside every stream. Several authors believe that cortical feedback is critical in probabilistic computation or predictive coding (for a review, see Cumming & Nienborg 2016; Edwards et al., 2017; Pennartz et al., 2019; Rao & Ballard, 1999). Top-down inputs conveying data on a subject's prior knowledge of a task, decisions on previous trials, or cognitive state are sent by corticocortical feedback in such circumstances, and then integrated with feedforward visual sensory input inside the target neuronal region. Relative on the task, cortical backward signals might modulate correlated variability over target neurons (Bondy et al., 2018).

In conclusion, what functions does recurrent processing (RP) accomplish, and how is this achieved anatomically? Three key functions have been suggested, these we will illustrate: (i) contextual regulation of sensory processing; (ii) high-level information feedback; and (iii) Predictive Processing (PP) (Pennartz et al., 2019). The activity of primary sensory neurons that encode the spatial position or other physical properties of objects is modulated by high-level information including value-related (Goltstein et al., 2013; Shuler & Bear, 2006; Stanisor et al., 2013), attentional (Herrero et al., 2008; Luck et al., 1997; Motter, 1993), and choice-related signals (Lorteije et al., 2015). The generative neural network theories of visual information processing described in (Rao & Ballard, 1999) are usually related to predictive coding. Researchers adopt the term PP to indicate the broad concept of learning and inferring via generative models in the brain, as defined by (Clark, 2016). According to PP, the brain limits redundant information transfer by allowing a higher area to anticipate the predicted sensory signal and transfer this to a downward area, which therefore calculates the discrepancy between expected and objective inputs. A higher area provides expectations regarding the causal representations observed in a lower brain area through feedback pathways. A prediction error is computed in the bottom layer (V1) and delivered to the higher area using feedforward interactions (from V1 to V2). Rodents (Attinger et al., 2017; Leinweber et al., 2017) and primates (Schwiedrzik & Freiwald, 2017) have already been reported to exhibit PP. On the other hand, perception, intended as the conscious sensory interpretation of environmental variables, has been related to corticocortical RP (Lamme et al., 1998; Wokke et al., 2012). Thus, RP is suggested to combine high-level information with sensory-detailed representations to determine awareness. Additional bottom up/top-down cycles can implement the first phase of RP, resulting in further adjustments of perceptual characterization (Olcese et al., 2018; Vetter et al., 2014).

Within this framework of neural arrangement, it will be portrayed below how different kind of stimuli and perceptual processes might be resolved by considering an iterative network of visual areas which interact in a non-hierarchical way.

III. Cortical networks involved in dynamic social stimuli perception

For more than 40 years, nodes in the face processing network have been thoroughly explored in cognitive neuroscience and neuropsychology (Duchaine & Yovel, 2015; Freiwald et al., 2016; Haxby et al., 2000; Kravitz et al., 2013; Ku et al., 2011). Faces elicited selective brain activation in numerous areas of the occipital-temporal cortex. These face-selective encoders are generally reported in the inferior occipital cortex (OFA – occipital face area), the fusiform gyrus (FFA – fusiform face area), and the posterior section of the superior temporal sulcus (pSTS). The Haxby model (Gobbini & Haxby, 2007; Haxby & Gobbini, 2011; Haxby et al., 2000), a widely prominent model of face processing, presumes a serial-hierarchical architecture in which information travels systematically from face patch to face patch, across posterior brain regions towards anterior regions (e.g., the OFA FFA; OFA STS).

Further later models have expanded on the Haxby model by proposing two face computing pathways — a dorsal stream and a ventral stream – with some reciprocal transmission within each (Duchaine & Yovel, 2015; Grimaldi et al., 2016; Pitcher, Walsh, et al., 2011). Diffusion imaging studies focused on a subset of face-sensitive areas (Gschwind et al., 2012; Pyles et al., 2013) and confirmed the plausibility of two face processing streams.

Both models suggest that the face system is divided into two pathways: one dorsal that extends from the occipital face region to the superior temporal sulcus and one ventral that flows from the occipital face area to the fusiform gyrus. In conclusion, both face neural frameworks imply two clusters of facial decoding, in which the FFA is specialized in the processing of face identification from static face pictures while the pSTS is engaged in the computation of changing attributes of faces like those of expression, eye gaze, and lip movement. Face processing in real life entails the continuous evaluation of a number of dynamics, short-term social indicators, including emotional expressions and social attention (direction of gaze). The superior temporal sulcus is a region linked with multisensory integration (Beauchamp et al., 2004), the processing of biological motion (Bonda et al., 1996), facial motion (Puce et al., 1998), and social attention (Allison et al., 2000) and is also part of the core face network. From the early visual cortex to the superior temporal cortex, the lateral stream develops. It is formed of an area in the posterior superior temporal sulcus (pSTS-faces, Haxby et al., 2000; Weiner & Grill-Spector, 2015) and a region on the STS's main branch (mSTS-faces), which ultimately projects to the anterior STS (aSTS-faces, Pyles et al., 2013; Weiner & Grill-Spector, 2015).

There is considerable evidence that the pSTS plays a key role in the perception of facial expressions (Adolphs, 2002; Calder & Young, 2005; Engell & Haxby, 2007; Furl et al., 2007; LaBar et al., 2003; Narumoto et al., 2001; Said et al., 2010; Schultz & Pilz, 2009). The STS serves an essential part in the processing of dynamic facial stimuli (face motion) (Adolphs, 2009; Bartels & Zeki, 2004; Blake & Shiffrar, 2006; Fox et al., 2009; LaBar et al., 2003; Peelen et al., 2006; Aina Puce & Perrett, 2003; Schultz et al., 2005). As a result, researchers believe that the major functional distinction between the face perception circuits is the separation of kinetic and shape signals (see also Gilaie-Dotan et al., 2015; Pitcher et al., 2014). It is proposed that the pSTS is implicated in the processing of flexible facial information such as head rotation, eye gazing, and facial emotions, yet it also might extract motion information from fixed face characteristics such as face identity (O’Toole et al., 2002). The pSTS detects facial expression in static faces as well as moving face details. Researchers claim that the pSTS is sensitive to inferred motion as well as true motion (i.e., active faces), suggesting that the pSTS-FA achieve motion from shape analysis. Still images of facial expression or averted eye gaze imply facial motion, similar to still images of moving people, which activate motion areas such as MT (Kourtzi & Kanwisher, 2000) or biological motion areas along the STS (Kourtzi et al., 2008). This because faces rarely convey static facial expression or averted eye gaze for an extended period of time.

Hence, the posterior STS is a crucial component of the face network, especially when dealing with changing social signals (Gobbini & Haxby, 2007; Haxby et al., 2000). The STS has long been thought to enclose domain-specific units specialized for processing social cues, such as cortical ensembles that represent dynamic characteristics of faces (e.g. eye gaze and emotional expression; Grossman & Blake, 2002; Hoffman & Haxby, 2000; Puce et al., 1998). The idea of a modular arrangement on the pSTS is compatible with an intricate activation patterns that can be distinguished using multivariate techniques (Deen et al., 2015; Isik et al., 2017). Across the posterior-to-anterior axis of the right STS, appeared a marked division of activity: a) the posterior and middle sectors of the STS were most responsive to gaze-related activity, b) the middle region of the STS was most sensitive to emotional expressions, c) and the anterior STS was most sensitive to speech-related activity (Schobert et al., 2018).

Despite reactions to various types of social stimuli appear to overlap in pSTS over several studies, some degree of non-overlap may exist, reflecting a local segregation of multiple functions along the whole-STS area. Some pioneering research has examined STS activity in response to a plethora of stimuli. Pelphrey et al. (2005) assessed responses with eye, mouth, and hand movements and observed overlapping and non-overlapping activations across these scenarios. Engell and Haxby (2007) contrasted response with averted gaze and emotional facial expressions in the right STS and discovered discrete (although partially overlapping) patches, with a posterior– anterior partition for averted gaze and expression activations, respectively. Additionally, when comparing responses to a wide range of socially relevant paradigms, Deen et al. (2015) revealed a posterior-to-anterior gradient, with the posterior section mostly implicated in theory of mind and biological motion, the middle portion in face and voice perception, and the anterior patch in language (see also Allison et al., 2000, for an earlier review of STS activation sites). Voxels susceptible to eye-gaze were traced in the posterior/superior cluster, close to parietal regions involved in spatial attention and/or eye movements (Corbetta et al., 1998). The mid STS may contain separate projections to limbic regions involved in emotion processing, such as the amygdala, and to frontoparietal areas involved in emotion regulation, emotions, or imitation, according to the intermediate position of voxels responsive to emotion expressions (Phelps & LeDoux, 2005; Vrticka et al., 2013).

Evidence from neuropsychological lesion studies casts doubt on the hierarchical organization, because information within the core face network may be crossed between the ventral and dorsal visual streams, bypassing the inferior occipital area (Atkinson & Adolphs, 2011; Rossion, 2008; Weiner et al., 2016). Based on multimodal evidence from nonhuman primates, a new paradigm has added a third visual pathway to the scheme, where information from V1 travels via MT/V5 to the STS (Pitcher and Ungerleider 2021).

The existence of a social pathway, is in line with the neuroanatomical and functional projections from the early visual cortex to the STS through the motion-selective middle temporal (MT) region in both human and non-human primates (Boussaoud et al., 1990; Desimone & Ungerleider, 1986; Gschwind et al., 2012; Pitcher et al., 2014, 2020; Sliwinska, Bearpark, et al., 2020; Ungerleider & Desimone, 1986b). From a physical and functional perspective, the third visual pathway is substantially independent from the ventral and dorsal visual pathways, according to findings. The ventral and dorsal routes are generally related with the 'what, where, and how' of visual object recognition, whereas the third route is primarily associated with the dynamic features of social perception (Allison et al., 2000; Hein & Knight, 2008; Perrett et al., 1992). Nonhuman primate neuroanatomy provides the most persuasive evidence for a cortical pathway into the STS that skips the ventral pathway. The existence of a corticocortical link projecting directly from the primary visual cortex (V1) into the motion-selective region MT was discovered through tracing research in macaques. The anterior visual motion regions in the medial superior temporal (MST) and fundus of the superior temporal (FST) cortices have direct anatomical linkages with MT (Boussaoud et al., 1990; Ungerleider & Desimone, 1986). The FST then supplies into the dorsal bank and fundus of the STS. This network is physically distinct from corticocortical connections between V1, V2, and V4 that project directly into the ventral pathway's inferior temporal cortex (Boussaoud et al., 1991). In humans we do not have such explicit neuroanatomical findings, however tractography investigations have revealed a white matter tract flowing into the STS that is structurally distinct from white matter pathways on the ventral surface (Babo-Rebelo et al., 2021; Finzi et al., 2021; Gschwind et al., 2012). The existence of a direct route into the STS (the dorsal bank and fundus of the STS in macaques) from early visual cortex, outside of the ventral pathway, is supported by this convergence of human and non-human findings. The inclusion of MT in the third pathway underlines the importance of motion. As a result, the use of moving visual stimuli is required to define the functional features of the third circuit. Neuropsychological research constitutes a critical method for causally proving that the third pathway has independent structural and functional connection in the human brain. The possibility of a direct stream into the STS was first hypothesized based on observations from a prosopagnosic patient, but the proposal remained questionable due to the lack of structural brain imaging (Bauer, 1984). Despite having lesions spanning the brain area in which the FFA and OFA are generally located, functional brain imaging investigations have discovered several patients with prosopagnosia who display face-selective responses in the STS (Dalrymple et al., 2011; Gao et al., 2019; Rezlescu et al., 2012; Steeves et al., 2006). Moving faces are processed via a route that passes from early visual cortex into the STS via V5/MT, according to an influential alternative model (O'Toole et al., 2002). This network is physically and functionally separate from the ventral face-processing pathway (for structural face information), which starts in the OFA and continues through the FFA to the anterior temporal lobe.

The STS and, by analogy, the third route, play a key role in social cognition. The strongest proof derives from a large body of work that shows how the STS responds to a range of social stimuli (Calder et al., 2007; Phillips et al., 1997; Pitcher, 2014; Sliwinska, Elson, et al., 2020; Winston et al., 2004), and primates use these information generated by behaviours to calculate the values and intentions of others. Critically, neuropsychological and transcranial magnetic stimulation (TMS) research have shown which brain areas are required for tasks of social cognition and have helped to causally define the behavioural functions associated with specific damaged areas (Bauer, 1984; Milner & Goodale, 2006; Pourtois et al., 2004; Sliwinska et al., 2020; Van de Vliet et al., 2018).

However, distributed face regions do not work in confinement, but are combined together to build a face-processing network via specific long-distance channels (Moeller et al., 2008). As a consequence, facial signal analysis is implemented not just regionally, but also over longer range across face-selective hotspots (Bernstein & Yovel, 2015).

The overall connectivity patterns revealed that the early visual cortex provides inputs to the majority of the face sensitive regions, implying that there is no gateway (or single entrance point) for FFA and STS. The dynamic patterns of effective connectivity depict that face perception occurs in a parallel and interactional way rather than sequentially. Findings are more compatible with previous research in macaques, which found that face patches are densely and reciprocally related, challenging a serial hierarchy (Grimaldi et al., 2016; Kravitz et al., 2013). From behavioural performance (Levine et al., 1988), neural activity (Bukowski et al., 2013), electrophysiological measures (Eimer, 2011), intracranial stimulation effects (Rangarajan et al., 2014), and prosopagnosia patients (Duchaine & Yovel, 2015), right hemispheric dominance has been frequently reported. Face regions in the right hemisphere are far more structurally interconnected, more synchronized, and more actively coupled with each other during face perception as compared to the left hemisphere (Wang et al., 2020).

Overall, we might think the lateral stream being a network for dynamic (Duchaine & Yovel, 2015; Fox et al., 2009; Pitcher et al., 2011; Weiner & Grill-Spector, 2011), social (Andrews & Ewbank, 2004; Freiwald et al., 2016; Pitcher & Ungerleider, 2021) and multimodal (Beauchamp & Martin, 2007; Weiner & Grill-Spector, 2011) perception, since it integrates transient (Stigliani et al., 2019) features of faces such as motion, expression, and gaze (Calder et al., 2007; Fox et al., 2009; Pitcher et al., 2014).

Several previous imaging findings have shown that the pSTS responds more to moving faces than static faces (Pitcher et al., 2019; Pitcher, Dilks, et al., 2011; Schultz & Pilz, 2009), implying that the motion-selective area hMT (O’Toole et al., 2002) is a potential source of functional input (Ungerleider & Desimone, 1986a; Boussaoud et al., 1990). Moreover, neuropsychological patients exhibiting lesions spanning the cortical region in which the FFA and OFA are generally sited, with a spared pSTS, suggest that the area has independent neural inputs from other face-selective areas (Steeves et al., 2006; Dalrymple et al., 2011), in accordance with the notion that there is a specialized functional route from early visual cortex to the pSTS, possibly via hMT (O'toole et al., 2002; Gschwind et al., 2012; Pitcher, 2014; Duchaine & Yovel, 2015; Pitcher et al., 2017).

Even if the possible role of the MT area in the social pathway that includes pSTS is still to be confirmed in a conclusive way, what has already been abundantly established is its dominant role in sensory decisions involving the elementary motion stimuli.

In the next paragraph, it will therefore considered the cortical network, entailing MT, which underpin perceptual decision-making and the plausibly neural mechanisms which lead to its awareness.

IV. Cortical networks involved in perceptual decisions

Visual input feeds a network of roughly 30 associated brain nodes in macaques, which is arranged into a modular system based on laminar connectivity patterns (Barone et al., 2000; Felleman & Van Essen, 1991; Kravitz et al., 2011; Markov et al., 2014; Maunsell & Van Essen, 1983; Merigan & Maunsell, 1993; Shipp, 2007; Ungerleider & Desimone, 1986a; Zeki & Shipp, 1988). V1, at the beginning of the architecture, transmits substantial fibers to regions V2, V3, V4, V5/MT, and V6; these V1-receiver cerebral areas are also interconnected with one another. V1, V2, and V5 are all involved in early visual computation and are interlinked. These regions exhibit a range of base and intermediate visual stimulus characteristics at different scales, which are required for visually oriented behaviour (Born & Bradley, 2005; Hegdé & Van Essen, 2003; Sincich & Horton, 2005; Vidyasagar & Eysel, 2015; Zeki, 2015). V1 and V2 are evolutionarily stable in mammals, whereas V5 is present in all primate species investigated (Kaas, 1995; Large et al., 2016; Vanni et al., 2020), this indicates that all these regions serve a critical role in the cortical decoding of sensory input.

Area MT is widely recognized as a primary node for visual motion analysis (Albright, 1984; Britten et al., 1992; Dubner & Zeki, 1971). Movshon and Newsome (1996) proposed that neurons of MT acquire their directional sensitivity from V1, V2, and V3. Their opinion is that the cells in these three MT-projecting regions already express direction of stimulus motion. Obviously, following V1 deactivation, MT neurons' general susceptibility and direction specificity are considerably diminished (Girard et al., 1992; Rodman et al., 1989). Nevertheless, findings that MT feedback projections can significantly affect the orientation/direction selectivity of an upstream early visual area (e.g., V2) provide an alternative account to the hypothesis that sequential hierarchical processing and lateral communications are the exclusive pathways accountable for the emergence of receptive field properties. Consequently, if cortical interactions are characterized by recurrent dynamical networks, many cycles of feedforward and feedback loops between V1, V2, V3, and MT (and maybe V4) may play a key role in the emergence of responsiveness to orientation and direction throughout several neural structures (Correia et al., 2021).

Making a sensory decision is an essential cognitive activity. Prior research has looked at the processes underlying single perceptual judgements and discovered that they entail operations in multiple brain areas. Sensory cortices encode information about potential responses (Fetsch et al., 2014; Salzman et al., 1990), and regions of the parietal and frontal cortices process the information as sustained activity during motor planning (Churchland et al., 2011; Kim & Shadlen, 1999; Roitman & Shadlen, 2002; Shadlen & Newsome, 2001).

From their famous and comprehensive research of the function of the middle temporal (MT) region in motion direction discrimination, the Newsome group was the first to describe LIP activity during visual motion decision-making (Britten et al., 1996; Britten et al., 1992; Britten et al., 1993; Newsome & Pare, 1988). Shadlen & Newsome (1996, 2001) extended over MT's sensory involvement in the detection of a noisy moving dot stimulus to either trace from monkeys LIP during the motion discrimination task. MT provides anatomical input to LIP (Lewis & Van Essen, 2000a, 2000b; Ungerleider & Desimone, 1986b), which then projects to frontal structures (Ferraina et al., 2002).

Inside the regions of MT and MST, a neuronal reflection of the available evidence has been found (Celebrini & Newsome, 1994; Ditterich et al., 2003; Salzman et al., 1990). LIP is recognised to reflect the cumulative data, in combination with other elements that impact the choice, such as past likelihood, value, and costs connected with the options (Drugowitsch et al., 2012; Hanks et al., 2011; Rorie et al., 2010; Seo et al., 2009).

The comparative outcomes of microstimulating MT and LIP on choice precision and latencies are likewise consistent with modeling techniques that improve the speed of sensory input entry or increase the accumulated signal count, respectively (Ditterich et al., 2003; Hanks et al., 2006). Thus, one approach to describe confidence would be that choice evidence is carried out from the reference frame of decision (e.g., likelihood of left vs right) and transcoded in a different set of brain structures in the reference frame of precision (probability of correct versus error) (Insabato et al., 2010).

Identifying and dissociating "sensory evidence" and "decision variable" signals has been one of the primary focuses of decision making studies (Gold & Shadlen, 2007). When monkeys execute a motion discrimination trial, the discharge patterns of motion tuned cells in the middle temporal region (MT) show considerable levels of "choice probability," i.e. they accurately anticipate a monkey's direction selection even though there is no significant motion direction (Britten et al., 1996; Parker & Newsome, 1998). Microstimulation proximal to sensory neurons tuned in one of two directions elicits a variation in a monkey's sensory responses in that direction (e.g. Salzman et al., 1990). In accordance with research on monkey neurophysiology (Britten et al., 1996), it has been demonstrated that activation patterns in hMT+, the human homologue of area MT, can predict perceptual reports of motion direction including for sensory input representing no evident motion in any specific direction, indicating that hMT+ represents a pure sensory evidence signal which reflects perception. On the other hand, the human cortical sites involved in decision-making are usually the posterior parietal cortex (Tosoni et al., 2008), the intraparietal sulcus, unitedly with other frontal regions (Kayser et al., 2010; Liu & Pleskac, 2011).

In primates, the brain circuits implicated in metacognitive aspects of decision have been explored widely. Kiani & Shadlen (2009) discovered that neurons in the lateral intraparietal (LIP) cortex in rhesus monkeys exhibited activation that mirrored the monkey's decision confidence. When the stimulus was highly relevant, such that, when sensory noise was minimal or when the stimulus length was extended, nuclei in region LIP raised their firing. This discharge improved even if a monkey was less prone to choose the opt-out alternative. These findings show that the same neural region is engaged in perceptual decision and confidence judgement since LIP neurons were also implicated in the accumulation of evidence representations (Roitman & Shadlen, 2002). Microsimulation experiments added to the hypothesis that LIP neuron firing is directly connected to confidence. Following stimulus display, microstimulating LIP neurons had the same impact as shifting evidence in favour of one sensory option and modulate confidence (Fetsch et al. 2014).

A considerable amount of experimental studies, however, proposes that the quantification of confidence is not necessarily serial. Once an observer performs to a sensory decision, confidence can incorporate additional information (Baranski & Petrusic, 1994; Pleskac & Busemeyer, 2010), and although this ongoing evidence accumulation might only include sensory data, it denotes that confidence quantification does not explicitly pursue the perceptual choice determination (and therefore involves at least partially dissociable neural processes). Perceptual confidence can also be based on non-perceptual sources of evidence including decision time (Kiani et al., 2014) and attentional signals (Denison et al., 2018). This shows that the mechanisms required to determine perceptual certainty may not be the same as those engaged in making a perceptual choice. The use of tasks in which the subject may implement further evidence for confidence once they have made their sensory judgement (Fleming et al., 2018; Murphy et al., 2015), which conceivably depends on autonomous processing of the perceptual decision, has been used to disentangle the dynamics of metacognition from sensory processing. The extent of post-decisional increases in confidence correlates with signals from the posterior medial frontal cortex, according to these research, suggesting an extended network. However, the neural underpinnings of confidence amplitude have been discovered from EEG markers that are identical to those associated with the buildup of underlying perceptual choice evidence: the P300 (Desender et al., 2016, 2019; Gherman & Philiastides, 2015; Rausch et al., 2020) and Central Parietal Positivity (CPP, Boldt et al., 2019; Herding et al., 2019). The activity in posterior parietal cortex found more recently (Balsdon et al., 2021) might be reconducted to electrophysiological studies that indicate how confidence is reliant upon signals coded in the parietal cortex, that is where the internal perceptual evidence is consolidated (Kiani & Shadlen, 2009; Rutishauser et al., 2018). Throughout the course of constructing a perceptual judgement, these brain fingerprints of confidence evidence encoding seem to be detectable. This is consistent with data showing how confidence could be estimated online beside sensory evidence accumulation (Balsdon et al., 2020; Gherman & Philiastides, 2015; Zizlsperger et al., 2014), rather than evaluating the information in favour of the perceptual judgement merely after committing to it. The ideal explanation of confident behaviour could be an accumulation mechanism that is quite independent from the accumulation of perceptual data (Balsdon et al., 2020). The current discussion between single-channel (Maniscalco & Lau, 2016) and dual-channel (Charles et al., 2014) might be synthesized by the results of partial dissociation in Balsdon (2021) since it explain confidence through perceptual suboptimalities since enabling supplemental computation to affect the certainty computation separately.

It follows that, the brain might not conceivably operate in a strictly serial and pre-set fashion but would be characterized by a set of interactive and recurrent processes, partially independent from the functional point of view, which allows to effectively process the stimuli and guarantee an adequate perception of the environment. Moreover, this architecture should be plastic and receptive to environmental and developmental changes in order to be functionally adaptive, which is a crucial attribute of the nervous system.

V. Induction of neural plasticity in cortico-cortical streams

The nervous system's capacity to adapt and maximize its limited energy in reaction to neurobiological alterations, traumas, changing environmental pressures, and perceptual experiences is referred to as neuroplasticity (Pascual-Leone et al., 2005). The scarcity of experience-dependent modifications after the critical window termination misled researchers to believe that the visual system, especially the early visual cortex, was hard-wired and had no residual plastic ability. Numerous contemporary sources of evidence, conversely, have pushed this concept into discussion: Confirmation of residual visual plasticity in healthy adults has been proven by behavioural and physiological changes attributed to perceptual learning (Beyeler et al., 2017; Dosher & Lu, 2017; T. Watanabe & Sasaki, 2015), temporary visual deprivation (Binda et al., 2018; Binda & Lunghi, 2017; Lunghi et al., 2011; Lunghi & Sale, 2015; Zhou et al., 2013); chronic blinding diseases and visual restoration treatments (Aguirre et al., 2016; Burton, 2003; Castaldi et al., 2016; Dormal et al., 2015; Heimler et al., 2014). Chemical signals that control neuronal migration and the development of synaptic connections, along with activity-dependent processes that fine-tune and regulate the density and strength of synaptic contacts through Hebbian plasticity, govern neural wiring in evolving brain substrates (Levelt & Ḧubener, 2012). Long Term Potentiation and Depression (LTP/LTD) processes regulate all of this, and are also essential to learning and memory (Malenka & Bear, 2004).

Hebbian associative plasticity has shown to be a basic form of plasticity in the nervous system of biological organisms from its original conceptualizations in 'The organisation of behaviour' (Hebb, 1949). According to Hebbian associative plasticity, (a) temporal and (b) causal contingency between the signals of two neurons (or two neural systems) gives rise to LTP and/or LTD of their synaptic efficiency over time (Buonomano & Merzenich, 1998; Caporale & Dan, 2008; Song et al., 2000). Whenever an axon of cell A is close enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change occurs in one or both cells, increasing A's efficiency as one of the cells firing B, according to Donald Hebb's notable synaptic plasticity rule. Albeit not stated clearly, the sentence "takes part in firing it" strongly indicates that the arrival of the input (A) and the firing of cell B are directly associated in time.

The significance of chronological association between neurons firing could ultimately be proven as an essential parameter for the successful induction of Hebbian associative plasticity. Animal studies investigations from the 1980s and 1990s (e.g. (Levy & Steward, 1983)) found that if synaptic input A preceded cell B firing, synaptic strengthening developed, however if the order was inverted, synaptic depression prevailed. These are acknowledged as Spike-timing dependent plasticity's (STDP) main significant principles. In other words, LTP can be established in a homosynaptic circuit whenever the pre-synaptic cell is continuously excited before the post-synaptic cell, whereas LTD can be established when the processes are reversed. Synaptic learning is one of the principal forms of plasticity occurring in mammalian nervous systems, following Hebb's classic theory [for reviews on STDP neurophysiological substrates, see: (Caporale & Dan, 2008; Feldman, 2012; Markram et al., 2012)].

As an effective tool for studying cortical plasticity phenomena in humans, TMS has proven to be fundamental over the years. Stefan and colleagues (2000) first published a study on paired associative stimulation (PAS) in the human motor system. This allowed for the assessment of the behavioural implications in conscious, awake humans. TMS of the primary motor cortex (M1) in combination with an afferent input to M1 (such as somatosensory feedback via peripheral nerve stimulation, e.g. median nerve stimulation - MNS) causes alterations in the intensity of motor evoked potentials (MEP) (Carson & Kennedy, 2013; Müller-Dahlhaus et al., 2010; Stefan et al., 2000). As already mentioned, that pattern of timing-dependent plasticity in aware individuals has been ascribed to STDP in a multitude of model systems (Caporale and

Dan, 2008), including cultured neurons (Bi & Poo, 1998), cortical slice preparations (Magee & Johnston, 1997; Markram et al., 1997), and healthy animals (Zhang et al., 1998). Remarkably, TMS enables researchers to explore the characteristics of regional interneuronal pathways regulated by distinct neurotransmitters (Ziemann et al., 2015) including its capacity to induce cortical plasticity (Huang et al., 2005; Suppa et al., 2016). Some researchers have developed novel PAS protocols based on neuronal input to M1 originated from other cortical regions such as the contralateral M1 (Koganemaru et al., 2009; Rizzo et al., 2009, 2011; Rizzo et al., 2009), the ventral premotor cortex (PMv) (Buch, Johnen, Nelissen, O'Shea, et al., 2011), the supplementary motor area (SMA) (Arai et al., 2011), and the posterior parietal cortex (PPC) (Chao et al., 2015; Koch et al., 2013; Veniero et al., 2013). These paradigms above are identified as cortico-cortical PAS (ccPAS), that are reconfigured PAS protocols in which both paired stimulations are administered on the cortical surface, causing the cortico-cortical route interconnecting two distinct sites to be physically activated (Guidali et al., 2021). The opportunity to causally assess the malleable characteristics of cortical pathways and their efficiency is well-known. The cc-PAS protocols have been mostly designed to investigate the interconnectivity of motor networks (motor cc-PAS) and only recently a version of cc-PAS for the visual system (sensory ccPAS) has been implemented. Non-homologous sites of the motor system, such as the ventral premotor (PM) cortex and the caudal section of SMA, that are extensively linked with M1 [e.g., (Kim et al., 2010; Matsumoto et al., 2007; Quessy et al., 2016; Rizzolatti & Luppino, 2001)], have also been targeted employing ccPAS protocols [e.g., (Buch et al., 2011)]. The PM-M1 PAS seems to determine also a behavioural impact, enhancing manual dexterity (Fiori et al., 2018). The PM-M1 PAS has been shown to affect MEP magnitude with an ISI of 40 ms (Chiappini et al., 2020), which corresponds to long-latency inhibitory PM-to-M1 communications (Fiori et al., 2017), implying that this ccPAS has the possibility to increase interactions inside motor circuits by manipulating indirect routes.

The posterior parietal cortex (PPC) is yet another cortical area that is interconnected to M1 both directly and indirectly, and Koch et al. (2013) conceived the first cc-PAS that selected this cortico-cortical circuit. The excitatory approach is able to boosts alpha-band synchronization between the two designated areas through EEG-TMS co-registration (Veniero et al., 2013), whereas the inhibitory protocol improve coherence exclusively in the beta-band. PPC-M1 PAS appeared to increase phase coupling among these two regions, which might, consecutively, enhance the efficiency of cortico-cortical interaction in the parieto-motor pathway, given that such signals mirror the activity of M1 and PPC (Rosanova et al., 2009; Salmelin & Hari, 1994).

On the other hand, the V5-V1 PAS is the only cc-PAS targeting sensory regions that sheds light on the communication between the visual motion area (V5) and V1 (Romei, Chiappini, Hibbard, Avenanti, et al., 2016). Visual motion awareness is mediated by back projections from extra-striate regions to V1 [e.g., (Pascual-Leone & Walsh, 2001; Silvanto, Cowey, et al., 2005)], which is why Romei et al. applied the V5-V1 PAS to strengthen visual motion sensitivity. V5-V1 PAS was also used by Chiappini et al. (2018) in a state-dependent fashion. During the PAS, individuals were exposed to motion stimuli with a defined direction to recruit direction-specific V5 cells. When the motion direction was equivalent to the one applied during the procedure, the V5-V1 PAS improved motion sensitivity selectively.

Finally, over the high-order cognitive domain, there are limited findings (Kohl et al., 2019; Nord et al., 2019). Researchers documented potential cortico-cortical and cortico-subcortical consequences of ccPAS on the pre-supplementary motor region and inferior frontal cortex, affecting inhibitory behaviour dependently on the age, as the first evidence of ccPAS in the cognitive domain (Kohl et al., 2018). This was pursued by a subsequent study of ccPAS in the cognitive context, that either discovered impacts on attentional bias and reciprocal modifications in frontal interhemispheric communication contingent on the sequence of stimulation (Zibman et al., 2019), mimicking the order-dependent outcomes shown through motor ccPAS (Veniero et al., 2013). Bidirectional influences on normal and task-evoked circuits (default mode and task-related) were discovered in a novel ccPAS research which applied resting-state connectivity parameters to derive tailored parietal and prefrontal stimulation sites (Santarnecchi et al., 2018). Taking into account fronto-parietal network, electrophysiological (but not behavioural) outcome indicators have been traced by a ccPAS investigation with parietal and prefrontal targets (Casula et al., 2016). This was prior to a similar study, where researchers also observed that ccPAS designed to sequentially stimulate the IPS and the LPFC, altered control more towards a goal-directed strategy, although this result was exploratory (Nord et al, 2019). They failed indeed to trace a LPFC/IPS impact on decision-making, and any influence on working memory. However, recent interesting results showed how a relatively brief cc-PAS protocol over associative cortical regions of the fronto-parietal system might be able to increase cognitive abilities such as logical and relational reasoning in humans (Momi et al., 2020).

Apart from their methodological variations, the neurophysiological and behavioural effects induced by all PAS protocols are marked by timing dependency, target specificity, regularity, and reversibility, implying a shared neurophysiological mechanism at the origin of the plastic effects induced by PAS (Carson & Kennedy, 2013; Dan & Poo, 2004; Suppa et al., 2017).

The plethora of evidences regarding the possibility of inducing plasticity in cortical network and evaluate the physiological and behavioral consequences, motivate the investigation of how specific connections subserve a specific hypothesized function. Consequently, the ccPAS emerge as a promising instrument to explore the significance of reentrant visual networks.

i. *Exploring the role of reentrant cortico-cortical visual pathways in perception*

Long-distance connections across brain structures are assumed to be essential in cortical operations that combine multiple sources of signals and information extracted over several cortical regions (Sato, 2021). Cross-regional PAS, which focuses on long-distance communication spanning various cortical systems, provides a potentially helpful way to investigate the functional aspects of these interactions (Guidali et al., 2021).

Stated this, and considering all the previously reported notions, the purpose of this research can be outlined. Overall, the aim of the present thesis consists in the application of a neurostimulation protocol, namely ccPAS, which is capable of inducing cortical plasticity, for understanding and probing the functions of re-entrant connectivity within the extended visual system. This is achieved by modulating the efficiency of specific networks involved in the perception of complex social attributes and low-level sensory information, investigating the perceptual and behavioural consequences expected from the stimulation. The general hypothesis is that the visual system works in a recurrent way and is not strictly hierarchical and sequential, so that the early visual areas play a key role in the construction of the percept and in determining an actual awareness of this. Within this theoretical framework, the feedback pathways would acquire a crucial role in the transmission of signals from functionally specific "higher" areas to allow a bidirectional interaction that leads to accurate perception.

The first two chapters treat a series of experiments aimed at investigating the role of connections in the temporal-occipital visual network in the perception of dynamic social stimuli, followed by an in-depth study in the appendix (A). In the third chapter, on the other hand, the parieto-temporo-occipital network involved in sensory decision-making and motion perception is explored; complemented by an additional study reported in the appendix (B).

CHAPTER I

Empowering temporo-occipital back projections boosts visual perception of emotions

Introduction

The face is a rich source of social signals about the emotional state of an individual. The ability to decode observed facial expressions is fundamental for social interactions and humans have evolved a highly sensitive cortical visual system that allows one to identify and judge others' expressions even in extremely difficult conditions, e.g. when faces are experimentally presented for less than one tenth of a second (Bar et al., 2006; Olson & Marshuetz, 2005; Pessoa et al., 2005; Willis & Todorov, 2006). Decades of research in neuroscience have highlighted two key components of the cortical neural network involved in the recognition of emotional facial expressions: early visual cortices (V1/V2), which act as the bottleneck for visual information passing into the cerebral cortex and send direct and indirect projections to face-selective regions in occipito-temporal ventral areas; and the posterior superior temporal sulcus (pSTS) which possesses face-selective patches involved in processing dynamic aspects of facial expressions and represents a major hub for linking emotion perception to social cognition (Fusar-Poli et al., 2009; Grèzes et al., 2007; Hein & Knight, 2008; Lahnakoski et al., 2012; Peelen et al., 2007) possibly through projections to the subcortical (e.g. amygdala) and fronto-parietal brain networks (e.g., mentalizing network and mirror neuron networks). Neuroanatomical studies have clarified that V1/V2 and pSTS are mostly indirectly interconnected (Blank et al., 2011; Ethofer et al., 2011; Gschwind et al., 2012; Pyles et al., 2013). Yet, these regions show intense intrinsic functional connectivity at rest (Turk-Browne et al., 2010). Such functional coupling is enhanced during perception of emotional expressions (Fairhall and Ishai, 2007) and remarkably, its strength at rest predicts inter-individual differences in emotion recognition accuracy (Wang et al., 2016). But *how* pSTS-V1/V2 coupling does exactly give rise to accurate emotion recognition remains an open and unaddressed question.

In contrast to traditional hierarchical feedforward models of visual processing, which suggest that visual recognition is mediated by visual information flows from early visual cortex to higher order regions such as the STS, increasing evidence points towards a reverse process, in which backward projections (i.e., from higher- to lower-order visual areas) play a key role in visual perception, attention and awareness (Gilbert & Li, 2013; Lamme et al., 1998; Wyatte et al., 2014). Transcranial Magnetic Stimulation (TMS) has supported such theoretical models thanks to the possibility to investigate temporal dynamics of functional connections between distinct visual areas. In this respect, a seminal investigation (Pascual-Leone & Walsh, 2001) confirmed by subsequent TMS studies (Koivisto et al., 2010; Silvanto, Lavie, et al., 2005) demonstrated the causal involvement of back-projections from V5 to V1 for TMS-induced motion perception to consciously arise. Moreover, recent developments have allowed not only for the direct evaluation of back-projections' functional relevance in different domains but crucially, by capitalizing on their potential malleability, boosting their connectivity. To this purpose, a new neurostimulation protocol named cortico-cortical paired associative stimulation (ccPAS) has been recently developed (Arai et al., 2011; Buch et al., 2011; Casula et al., 2016; Johnen et al., 2015; Koch et al., 2013; Koganemaru et al., 2009; Rizzo et al., 2009, 2011; Romei, Chiappini, Hibbard, Avenanti, et al., 2016; Veniero et al., 2013). It involves repeated paired stimulation of two interconnected brain areas with the aim of inducing spike-timing-dependent plasticity (STDP), a form of synaptic plasticity meeting the Hebbian principle that synapses are potentiated if the presynaptic neuron fires repeatedly before the postsynaptic neuron (Caporale & Dan, 2008; Jackson et al., 2006; Markram et al., 1997). In the ccPAS protocol, pre- and post-synaptic coupling is achieved by repeatedly administering pairs of TMS pulses. In each pair, a first pulse over a target area is followed by a second pulse over an interconnected target area with an interstimulus interval (ISI) consistent with the activation of latency connections between the two areas. Most of the existing ccPAS studies have focused on the motor system (Koganemaru et al., 2009), and have targeted monosynaptic connections (but see Chiappini et al., 2020). They have consistently shown a causal and directional change of influence of the first higher order targeted brain region (e.g., the premotor cortex) over a second anatomically connected lower level region (e.g., the motor cortex) (Buch et al., 2011). Two recent studies have assessed whether similar neurophysiological principles may apply also to the visual system (Romei et al., 2016). In keeping with previous literature (Pascual-Leone et al., 2001; Silvanto et al., 2005; Koivisto et al., 2010) they have shown that strengthening the reentrant connections between V5 and V1 led to the enhanced ability to perceive coherent visual motion stimuli, providing further causal evidence that V5-to-V1 back-projections are instrumental to motion perception and crucially, are functionally malleable.

These recent advances extending the ccPAS efficacy in promoting plasticity of functional connections from the motor to the visual system have prompted the surging of new information-based attempts (Romei, Thut, et al., 2016) exploiting this novel approach for the study of complex brain networks which are functionally relevant (e.g. supporting emotion recognition) but not directly connected, such as STS-V1. A main challenge faced with the application of ccPAS protocols when testing indirect complex networks is the identification of a critical timing accounting for the indirect long-distance connection between the two targeted nodes. When little or no direct monosynaptic connections are present, as in the case of STS-V1, a first empirical question to be addressed in order to meaningfully apply the ccPAS protocol is how long does it take for a neural signal located or generated in pSTS to reach V1? Under these circumstances the adoption of very short inter-pulse timing of 8-20ms used in previous studies assessing monosynaptic connections would not serve the purpose as not respecting the Hebbian principle of consequentiality (the signal generated in STS would not have yet reached V1 at the time of V1 stimulation). A way of investigating the temporal profile of signal propagations in complex indirect networks such as STS-to-V1 is through the combined use of TMS-EEG. By applying single TMS pulses over the right pSTS while concurrently recording EEG activity over the more distant early visual areas we were able to characterize the temporal profile of signal propagation in the STS-V1 network. Whether such temporal profile reflects feedback connectivity of this complex network and is therefore instrumental to functionally convey emotion value to visual processing will be addressed in the current work.

Specifically, we sought to investigate the functional relevance and plasticity of reentrant connections from STS-to-V1 in the ability to perceive the emotions of others by combining the ccPAS protocol, with two behavioural tasks. Based on the notion that the STS is involved in the processing of emotional facial expressions (Candidi et al., 2015; Pitcher, 2014) and that the STS-V1 connectivity seems to be related with the ability of facial expression recognition (Wang et al., 2016), we hypothesized that administering a ccPAS protocol aimed at enhancing STS-to-V1 connectivity would improve performance in an emotion discrimination task while no such improvement was expected when controlling for the effectiveness of stimulation, the directionality and timing of the stimulated pathway, as well as the specificity of the task.

Methods

Participants

109 healthy participants were involved in the study. Thirty-nine participants (17 men, mean age ± S.D.: 23.6 y ± 2.8) were randomly assigned to one of the three experimental groups of the Experiment 1 in which we control for the current direction specificity, forty-two (20 men, 23.9 y ± 2.2) were randomly assigned to one of the three experimental groups of the Experiment 2 in which we tested the time specificity and twenty-eight participants (9 men, mean age ±

S.D.: 22.8 y ± 2.5) were randomly assigned to one of the two experimental groups of the Experiment 3 in which we tested the task specificity. All the participants were right-handed according to a standard handedness inventory (Briggs & Nebes, 1975), had normal or corrected-to-normal visual acuity in both eyes, and were naive as to the purposes of the experiment. None of the participants had neurological, psychiatric, or other medical problems or any contraindication to TMS (Rossi et al., 2009). Participants provided written informed consent, and the procedures were approved by the ethics committee at the Department of Psychology and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. No discomfort or adverse effects during TMS were reported or noticed.

Visual Stimuli

Pictures were presented on a 19-inch screen located about 70 cm away from the participant. Thirty-two emotional (fear and happy) faces (16 belonging to eight different male actors) were selected from the Nimstim database (Tottenham et al., 2009). Mirror-reflected copies of the stimuli were also created, so that the total amount of stimuli was 64. Each face was cropped using an elliptical stencil to exclude hair, ears and neck part to rule out an effect of other physical component except a facial expression (Goshen-Gottstein & Ganel, 2000; Lee et al., 2011; Martin & Greer, 2011; Sweeny et al., 2009). Mosaic pattern pictures made up of fragments of each prime face were created, by means of MATLAB software, to be employed as masks stimuli, each preserving the elliptical form, the color and the spatial frequency of the original picture (Martens et al., 2006; Sato & Aoki, 2006; Yang et al., 2011).

Experimental and control tasks

The experiments were programmed using Matlab software to control picture presentation and to trigger TMS pulses. In Experiment 1 and 2, participants performed an emotion discrimination task, in which they were presented with facial expressions, and were asked to discriminate between happy and fearful. Each emotion discrimination block included 192 trials, and each trial consisted of a gray screen (600 ms duration) indicating the beginning of the trial, followed by a forward masking (17ms duration) that preceded the test picture presented at the centree of the screen. Stimuli were presented for 17, 33 or 50 ms, immediately replaced by a backward masking, which remained on the screen for 50, 33 or 17 ms respectively, to keep a constant stimulus onset asynchrony (SOA) of 67 ms. A black screen was presented till the participant's answer. Participants were asked to discriminate the target's face emotion, by pressing two different keys on a keyboard (forced choice: "happy" or "fear") with the index and middle right-hand fingers. They were asked to be as fast and as accurate as possible. Response–button correspondence was randomized across participants. Each block lasted approximately 5 minutes.

During Experiment 3, participants were exposed to the same procedure of Experiment 1 and 2 with the exception that they were requested to discriminate the target's gender (forced choice: "female" or "male").

Experimental design

In this study, participants were randomly assigned to the different groups according to the cortico-cortical Paired Associative Stimulation (ccPAS) protocol they would undergo. To test the effect of ccPAS on emotion perception, participants performed the emotion or the gender discrimination task before (i.e., at baseline, BSL) undergoing their assigned ccPAS protocol and immediately after the ccPAS phase (T0) and after 20 (T20), 40 (T40), 60 (T60) and 80 (T80) minutes after the ccPAS.

ccPAS protocol

ccPAS was delivered by means of a Magstim BiStim2 machine (Magstim Company, UK) via two 50 mm figure-of-eight coils. 90 pairs of stimuli were continuously delivered at a rate of 0.1 Hz for ~15 min (Veniero et al., 2013), each pair of stimuli consisted of two monophasic transcranial magnetic pulses. The pulses were triggered remotely using a computer that controlled both stimulators. The first targeted area was right posterior temporal sulcus (pSTS) while the second targeted area was V1. For both areas intensity of TMS was set at 60% of the maximum stimulator output. The ccPAS protocol was manipulated in different groups of participants in three different Experiments.

Experiment 1: TMS-EEG experiment

The inter-stimulus interval (ISI) for the ccPAS protocol was selected on the basis of TMS-EEG data recorded in a preliminary experiment. This experiment was part of another study that aimed at investigating STS connectivity during action observation and execution. Ten participants (6 females, mean age = 22y, range 21-27 y) received 60 active TMS pulses and 60 sham TMS pulses at rest, over the right pSTS (mean ± sd coordinates in Talairach space: x = 56.1 ± 2.2, y = -50.0 ± 2.1, z = 9.1 ± 1.6). TMS intensity was set at 70% of the rest motor threshold. EEG data were preprocessed to remove noisy epochs and correct muscular or eye artifacts with independent components analysis (for details, see Zanon et al., 2018). TMS-evoke responses were analyzed at the source level to identify peaks of activity in V1 after pSTS stimulation. Current source densities were estimated by projecting scalp potentials to source space by using standardized low resolution brain electromagnetic tomography (sLORETA) (Busan et al., 2012; Nunez et al., 1994; Pascual-Marqui et al., 2002), as implemented in the LORETA-key software (v20171101). Both Active and Sham TMS responses were projected in a realistic head model based on the MNI152 template and restricted to the cortical gray matter. A region of interest (ROI) approach was applied to measure cortical responses in V1. Specifically, a spherical ROI with a 20 mm radius was centred on V1 stimulation coordinates (V1-ROI) see paragraph Neuronavigation below) and mean activity was extracted across voxel comprised in the ROI. In order to rule out a possible contamination due to the spread of local activation in the TMS target area, mean activity after both active and sham TMS was extracted from a spherical ROI (20 mm radius) centred on pSTS coordinates (STS-ROI). Sham-corrected TMS responses in both V1-ROI and STS-ROI were computed by subtracting sham responses from active responses and mean signal across participants were inspected to identify discrete peaks in the evoked activity. Peak latencies for relevant components were measured for each participant and ROI and further analysed by mean of a repeated-measures ANOVA with LATENCY and ROI as within subject factors to assess significant differences between ROIs and to select the ISI for the ccPAS protocol.

Experiment 2: control for stimulation directions.

Experimental group ($\mathrm{Exp2}_{\mathrm{STS\text{-}V1}}$): the first pulse was given to pSTS followed by another pulse, delivered to V1 with an ISI of 200 ms in accordance with the EEG pilot study. Thus, this timing was critical to repeatedly activate presynaptic and postsynaptic neurons in reentrant V5-V1 connections in a way that is consistent with spike timing-dependent plasticity (STDP), i.e., a form of synaptic plasticity meeting the Hebbian principle and predicting that synapses are potentiated if the presynaptic neuron fires repeatedly before the postsynaptic neuron (Caporale & Dan, 2008; Jackson et al., 2006; Koganemaru et al., 2009; Markram et al., 1997). Thus, ccPAS in the STS-V1 group was aimed at strengthening re-entrant connections from pSTS to V1.

Control group 1 ($\text{Ctrl}_{\text{V1-STS}}$, control for direction): in this control group we switched the direction of the associative pulses: the first pulse was given to V1 and the second pulse to pSTS at the same ISI as the experimental condition (200 ms). The $\text{Ctrl}_{\text{V1-STS}}$ group controlled for direction dependent effects, i.e., we verify that any effect as found in the STS-V1 group is the result of enforced feedback connections (pSTS to V1) and should not be found when feed-forward connections (V1 to pSTS) are instead stimulated.

Control group 2 ($\text{Ctrl}_{\text{Sham}}$, control for unspecific effects): stimulation in this group was identical to that of the STS-V1group except for the fact that the TMS coils were tilted at 90 degrees so that no TMS pulses were effectively applied throughout the ccPAS session.

Experiment 3: control for stimulation time.

Experimental group ($\text{Exp3}_{\text{STS-V1}}$). This ccPAS group was identical to Experiment 1.

Control group 1 (Ctrl_{0ms}, control for timing). In this group both pulses were delivered simultaneously (ISI = 0 ms). According to the Hebbian principle (Caporale & Dan, 2008; Markram et al., 1997), synapses increase their efficiency if the synapse persistently takes part in firing the postsynaptic target neuron. However, if two neurons fire at the same time, then one cannot have caused, or taken part in firing the other. Thus, although I-wave interactions may occur during simultaneous TMS pairing (Prabhu et al., 2009), no net STDP is expected.

Control group 2 ($\text{Ctrl}_{\text{100ms}}$, control for timing). Stimulation in this group was identical to that of the STS-V1 group except for the fact that pulses were delivered at a non-optimal ISI of 100 ms. This ccPAS condition controlled for timing dependent effects, i.e., we verify that any effect as found in the STS-V1 group is timing dependent and not provoked by a mere consistent stimulation pairing of the targeted areas.

Experiment 4: control for task.

Experimental group (STS-V1$_{\text{Gender}}$). This experimental group underwent the same experimental manipulations as the Experimental group (STS-V1). However, they have been performing a gender discrimination task, instead of an emotion discrimination task.

Control group 2 (Ctrl$_{\text{ShamGender}}$, control for unspecific effects). TMS coils were tilted at 90 degrees so that no TMS pulses were effectively applied throughout the ccPAS session. Participants were requested to perform a gender discrimination task.

Neuronavigation

In order to select the right pSTS coordinates we employed an activation likelihood estimation (ALE) which is a quantitative meta-analysis method that was developed concurrently but independently by (Turkeltaub et al., 2002) and (Chein et al., 2002). To qualify for inclusion in the meta-analysis, studies must have: (1) been an original paper appeared in a peer-reviewed journal; (2) have used a variant of the emotional bodies paradigm in healthy subjects (single group data, see below); (3) have studied subjects using fMRI; (4) have used the image subtraction methodology to determine activation/deactivation foci (i.e. happy vs. fixation or neutral) in whole brain analysis; (5) have reported data in standard stereotactic coordinates (either Talairach or Montreal Neurological Institute [MNI] space) (Laird et al., 2005; Turkeltaub et al., 2002). Studies which did not specify whether the reported coordinates were in Talairach or MNI space were excluded since it was not possible for such cases to apply the ALE analysis. Studies reporting single group data only (i.e., relative to healthy volunteers) were included. Thus, spatial coordinates reporting a main effect of emotional faces processing across the control and a clinical group were not considered. Coordinates relative to functional psychophysiological or psychopathological correlations were not considered. fMRI studies investigating processes other than emotional processing (i.e., working memory, attention) by using similar emotional faces stimuli were not included. To exclude an unwanted systematic confounding effect, emotional faces other than human faces such as the schematic faces were excluded. PET studies were not included to prevent the methodological heterogeneity underlying these different functional imaging techniques. Eight studies met these criteria and were included in the present meta-analysis (de Gelder et al., 2004; Grèzes et al., 2007; Peelen et al., 2007; Pichon et al., 2008, 2009, 2012; Sinke et al., 2010; van de Riet et al., 2009). A total of 187 activation foci representing regions of significantly greater activation for emotional bodies as compared with neutral bodies were compiled from these studies. These peak activations were then used to generate an ALE map (Turkeltaub et al., 2012), using Ginger ALE software (http://www.brainmap.org/ale/) to identify brain regions that are frequently implicated in emotional bodies observation. The output of this analysis then was used to threshold our whole-brain ALE map to achieve a P value of 0.01 while controlling for false discovery rate and an extent threshold of 25 voxels. The resulting coordinates for pSTS were x = 52; y = - 48 z = 8. These coordinates were similar to the ones already found in other two ALE metanalyses on emotional faces (x = 56; y = - 44; z = 4 and x = 53; y = - 50; z = 4) (Fusar-Poli et al., 2009; Sabatinelli et al., 2011, respectively).

Coil position was identified on each participant’s scalp with the SofTaxic Navigator system (Electro Medical Systems) (Avenanti et al., 2012; Bertini et al., 2010; Serino et al., 2011; Urgesi, Calvo-Merino, et al., 2007; Urgesi, Candidi, et al., 2007). Skull landmarks (nasion, inion, and 2 preauricular points) and ~100 points providing a uniform representation of the scalp were digitized by means of a Polaris Vicra digitizer (Northern Digital). Coordinates in Talairach space were automatically estimated by the SofTaxic Navigator from an MRI-constructed stereotaxic template. The right pSTS scalp location was identified by means of the SofTaxic Navigator system and marked with a pen. Mean coordinates ± standard deviation corresponded to Brodmann area 21 in the posterior part of the right pSTS (Experiment 1: x = 59 ± 3, y= -49 ± 2 z = 9 ± 1; Experiment 2: x = 58 ± 3, y= -50 ± 2, z = 9 ± 2; Experiment 3: x = 57 ± 2, y= -50 ± 2, z= 9 ± 1). For the stimulation of V1 we identified the scalp location that corresponded best to the visual cortex (x = 19, y = −98, z = 1, (Serino et al., 2011)). Mean coordinates ± standard deviation corresponded to Brodmann's area17, in the middle occipital gyrus (Experiment 1: x = 19 ± 1, y = -96 ± 1 z = 1 ± 2; Experiment 2: x = 19 ± 1, y= -96 ± 1, z = 1 ± 1; Experiment 3: x= 18 ± 1, y= -97 ± 1, z = 0 ± 1).

Data analysis

Behavioural data were processed offline. Response times were calculated removing trials that were incorrect (12%) and slower than 1 sec (3%). Accuracy was converted into measures of sensitivity (d') and response bias (β) in accordance with signal detection theory (Macmillan & Creelman, 1991). Two types of responses were scored as correct: a "fear/man" response to a fearful/man expression (hit) and a "happy/woman" response to a happy/woman expression (correct rejection). Two types of responses were scored as incorrect: a "fear/man" response to a happy/woman expression (false alarm) and a "happy/woman" response to a fearful/man expression (miss).

In order to readily compare performance across the 3 Experiments as a function of time (T0, T20, T40, T60 and T80), variations in emotion discrimination performance were baseline corrected such that the values obtained in the performance at each time after the stimulation were divided from the value obtained in the performance at baseline. In this way, any value > 1 reflects enhancement in performance, while values < 1 reflect reduction in performance, compared to baseline values.

Mixed factors ANOVAs were performed on d’, β and RT with Groups as a between-subjects factor and Exposition Time and Time from ccPAS as a within-subjects factor were computed. Post-hoc analysis was performed using the Duncan test to correct for multiple comparisons. Partial eta^2 was computed as a measure of effect size for the main effects and interactions.

Results

Experiment 1: TMS-EEG

A first TMS-EEG study was designed with the specific aim of investigating the time window at which effective connectivity from STS to V1 could be measured. To this aim, we administered active and sham single-pulse TMS over the right pSTS in a group of 10 participants while EEG was continuously recorded. We analyzed the time-course of TMS-evoked responses at the sensor level (occipital electrodes O1, Oz, O2) and the source level over a region of interest (ROI) centered over the right occipital pole, corresponding to V1/V2 location. Following pSTS stimulation, the maximal EEG peak of TMS-evoked activity was recorded over occipital electrodes (Figure 1A) and V1/V2-ROI (Figure 1B) after ~200 ms, consistent with the recruitment of long-range and polysynaptic reentrant temporo-occipital connections

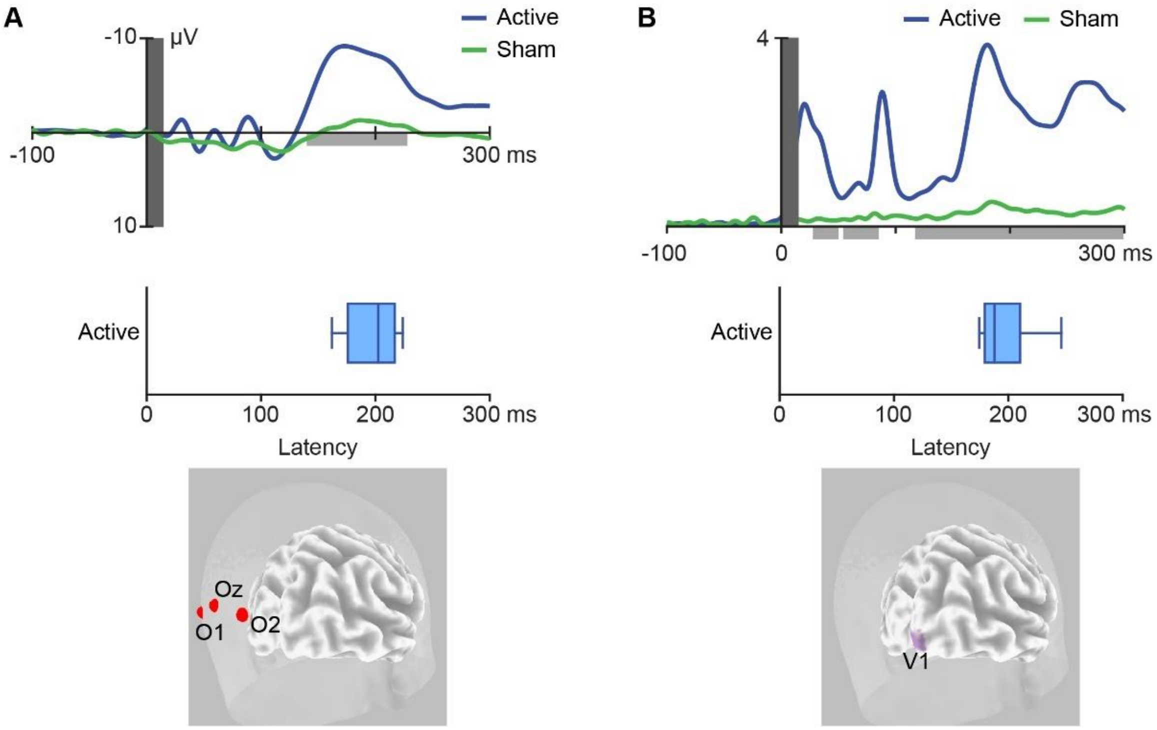


Figure 1*. The figure shows the time-course of TMS-evoked responses at the sensor (A) and source (B) levels. Top panels show TMS-evoked responses following active (blue) and sham (yellow) stimulation of pSTS. Shaded light grey areas reflect significant difference between active and sham stimulation (p < 0.05 for at least 20 consecutive time points, corresponding to 20 ms). The 20-ms time interval removed and interpolated due to the TMS artifact is shaded in dark grey. Mid panels show the mean latency of the main TMS-evoked components peaking at ~200 ms following pSTS stimulation. Error bars denote standard error. The bottom insert shows the target sensors (O1, Oz, O2) and the extent of the cortical regions included in the V1-ROI (Talairach coordinates: x = 19, y = –98, z = 1).*

Smaller and shorter-lasting activations were also observed in both V1/V2 and pSTS after ~80 ms (Figure 2). To test whether the activation observed in V1 is independent from that observed in STS and exclude that it is due to a spreading effect (i.e., volume conduction effect), we extracted peaks latencies at subject level and carried out a repeated-measured ANOVA with ROI (V1, STS) and LATENCY (80, 200) as within-subjects factors. The ANOVA showed a significant main effect of LATENCY ($F_{1,9} = 425.01$, $p<0.001$) and a significant LATENCY x ROI interaction ($F_{1,9} = 5.53$, $p = 0.043$). Duncan's Post-hoc tests showed that the latencies significantly differed between the two ROIs at about 200 ms (mean ± SE latencies: V1-ROI = 199.7 ± 8.6 ms; STS-ROI = 179.9 ± 3.5 ms, $p = 0.018$) thus showing time-specific activation of V1/V2 following pSTS stimulation. No latency difference between ROIs was observed at

80 ms (mean ± SE latencies: V1-ROI = 83.7±2.6 ms; STS-ROI = 86.7 ± 6.2, *p* = 0.672). Based on these findings, in Experiments 2-4 we selected 200 ms as the critical ISI for targeting pSTS-to-V1/V2 back-projections and thus designed a novel long-latency (200-ms) ccPAS protocol (Chiappini et al., 2020). An ISI of 100 ms was used as the most conservative control for testing the protocol's temporal specificity.

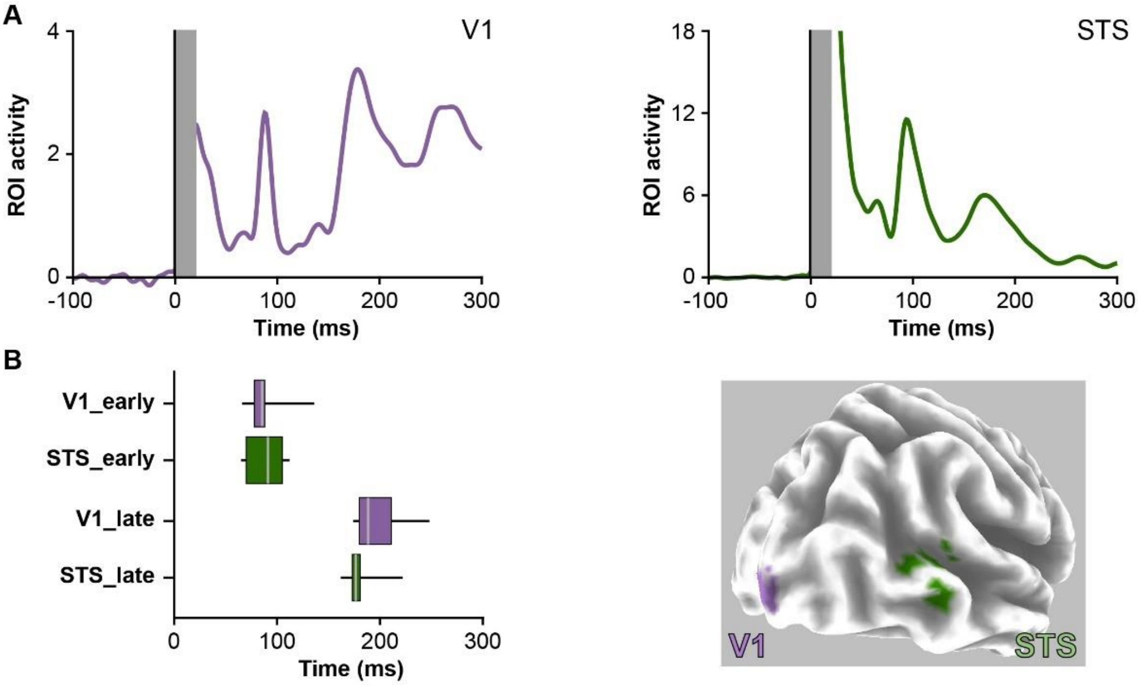


***Figure 2**. The analysis of TMS-evoked activity at the source level showed two peaks of activity over V1-ROI V1/V2: a small and short-lasting peak at ~80 ms from TMS and a later peak with maximal amplitude at ~200 ms. Similar activity was detected over a ROI centred over the targeted pSTS site (STS-ROI).*

Experiment 2-4: ccPAS

In Experiment 2, 39 participants were evenly assigned to three different groups according to the particular ccPAS protocol assigned. In the Experimental group (EXP1STS-V1), the first TMS pulse was given to STS followed by another pulse, delivered to V1 with an ISI of 200 ms (see TMS-EEG study), aimed at strengthening re-entrant connections from STS to V1. In a first control group (CtrlV1-STS, controlling for directionality) we switched the direction of the associative pulses: the first pulse was given to V1 and the second pulse to STS at the same interstimulus interval (ISI) as the experimental condition (200 ms), aiming at strengthening feedforward connections from V1 to STS. In a secondo control group (CtrlSham, controlling for unspecific TMS effects) the ccPAS stimulation was delivered using the same parameters as in the experimental condition but with the coil titled at 90 degrees so as not to induce active current in the brain areas under the coils.

In Experiment 3, 42 participants were evenly assigned to three different groups. The Experimental group (EXP3STS-V1) was identical to the one described in Experiment 2 and aimed at replicating the effects observed in Experiment 2. In a first control group 1 (Ctrl0ms, controlling for timing), both pulses were delivered simultaneously (ISI = 0 ms). In a second control group (Ctrl100ms, similarly controlling for timing), the parameters of stimulation were identical to those implemented in EXP2STS-V1 and EXP3STS-V1 groups except for the ISI set at an arbitrary value of 100 ms, which according to our TMS-EEG study should not to be effective to impact functional connectivity between STS and V1 since no V1 activation was found at 100ms after pSTS stimulation.

In Experiment 4, 28 participants were evenly assigned to two different groups. The stimulation parameters for the gender task group (GenderSTS-V1) and the sham group (GenderSham) were identical to those of EXP2STS-V1/EXP3STS-V1, and CtrlSham, respectively (Figure 3A), beside the fact that the experimental instructions prompted the participants to answer to the same stimuli as in the previous experiments by performing a gender discrimination task, instead of the emotion discrimination task (Figure 3C). To test for the specific effect of the different ccPAS conditions on emotion perception, we compared participants performing the emotion discrimination task (Experiment 2 and 3) with those performing the gender discrimination task (Experiment 4). Participants were tested before undergoing their assigned ccPAS protocol (i.e., at baseline, BSL), immediately after the ccPAS (T0) and again at 20 (T20), 40 (T40), 60 (T60) and 80 (T80) minutes following the ccPAS procedure (Figure 3B). Performance obtained at baseline was comparable across all groups and experiments.

The experimental procedure and stimuli were identical across groups and experiments. Each trial consisted of a gray screen (600 ms duration) indicating the beginning of the trial, followed by a forward masking (17 ms duration) that preceded the test picture presented at the centre of the screen (Figure 3B). Stimuli were presented for 17, 33 or 50 ms, immediately replaced by a backward masking, which remained on the screen for 50, 33 or 17 ms respectively, to keep a constant SOA of 67 ms.

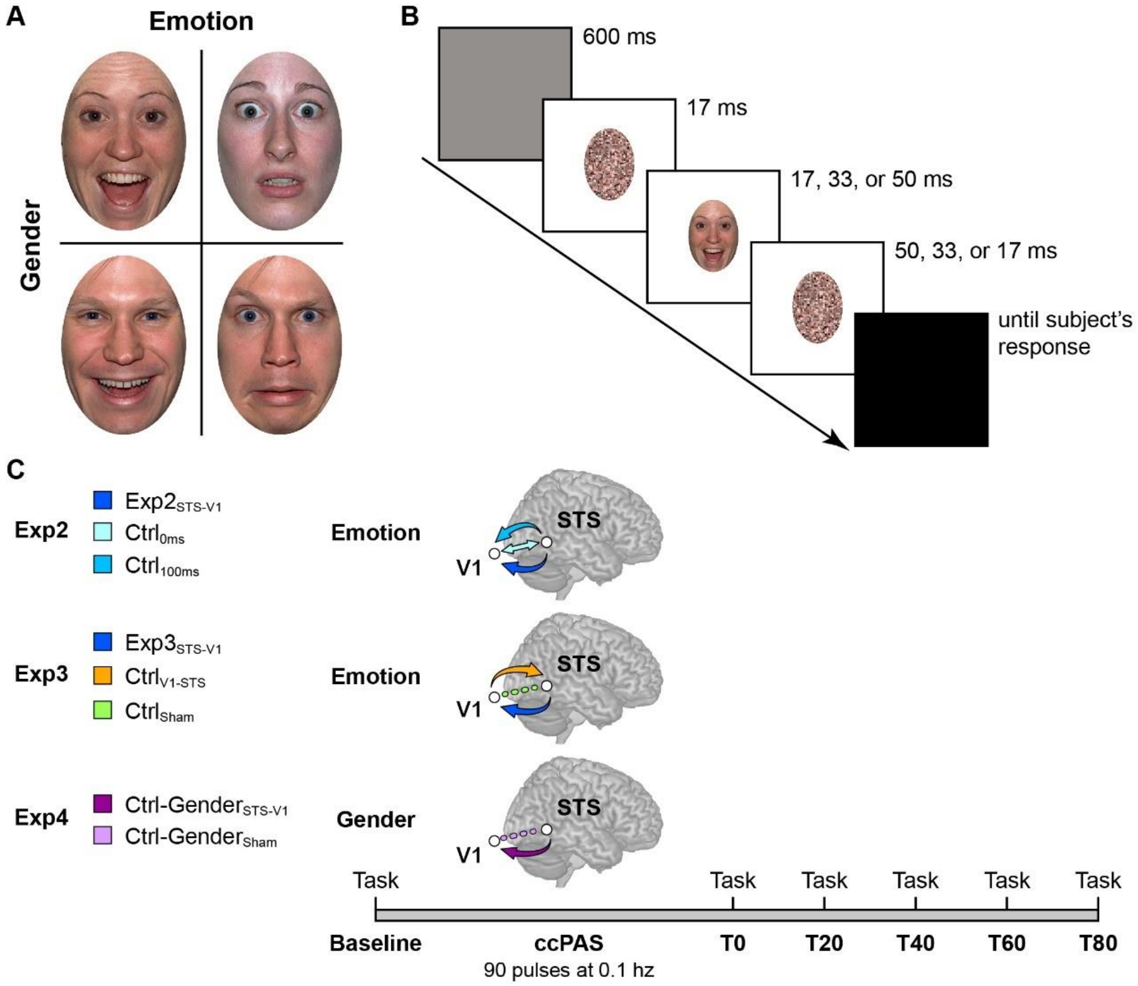


Figure 3. ***A***. *Stimuli examples, depicting a male and a female target showing happy and fearful expressions.* ***B***. *Trial structure showing sandwich presentation of face stimuli.* ***C.*** *ccPAS protocols and time course of the experimental session.*

Experiment 2 – functional relevance of STS-to-V1 back-projections in emotion perception

The Group x Exposition Time x Time from ccPAS ANOVA on d' showed a main effect of Exposition Time ($F_{2,72} = 4.32$; $p = 0.02$; $eta^2 = 0.11$) and, more importantly, a significant Group x Exposition Time interaction ($F_{4,72} = 2.64$; $p = 0.04$; $eta^2 = 0.13$). Post hoc analysis showed that following the ccPAS protocol, participants assigned to the $EXP2_{STS-V1}$ group, only when exposed to facial target for 17 ms (but not 33 or 50ms), showed increased performance relative to all the other groups and exposition times (all $p < 0.04$). No other comparisons were significant (all $p > 0.09$). No other main effects or interactions reached significance (all $F < 1.55$; all $p > 0.14$) **(**Figure 4).

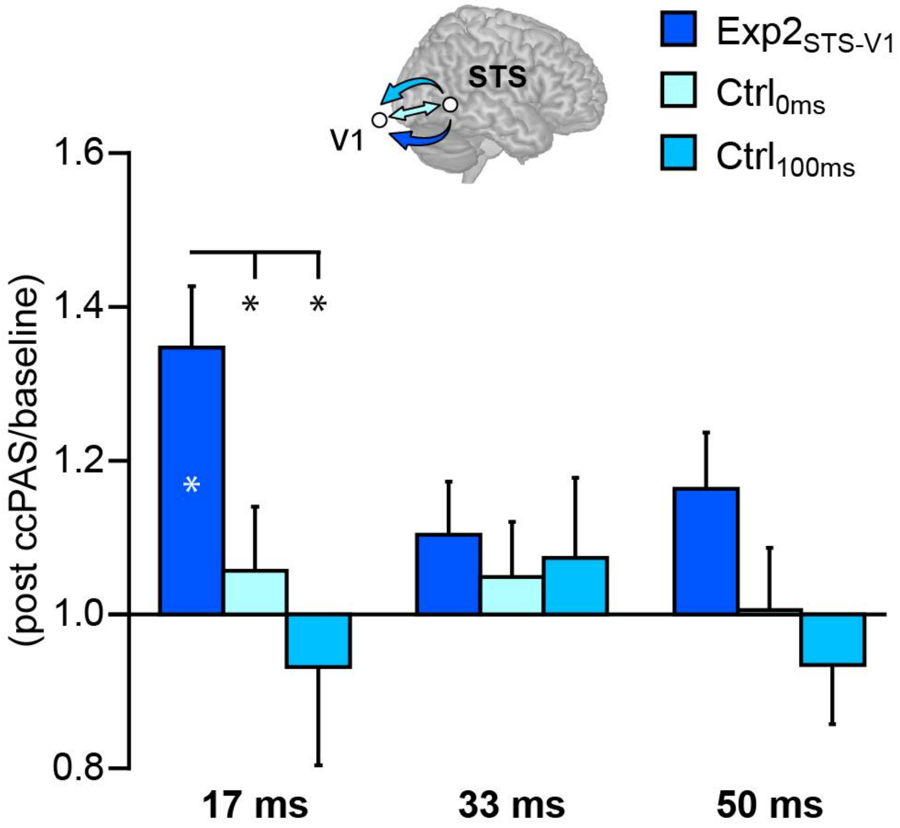


Figure 4. *Experiment 2 results showing a selective increase in visual sensitivity (d') to emotional facial expressions when faces are exposed for ~17 ms. The increase is specific to the ccPAS protocol that targets long-latency pSTS-to-V1/V2 backward connections using the critical ISI of 200 ms (i.e., $Exp2_{STS-V1}$ ccPAS). No change is observed following ccPAS protocols controlling for timing of the paired stimulation with an ISI of 0 ms ($Ctrl_{0ms}$) or 100 ms ($Ctrl_{100ms}$). Mean d' values across the post-ccPAS time points (average of T0, T20, T40, T60, T80) are expressed relative to baseline values. White and black asterisks indicate significant increase relative to baseline and all the other post-ccPAS conditions, respectively. Error bars denote standard error.*

The Group x Exposition Time x Time from ccPAS ANOVA carried out on response times showed only the non-surprising main effect of Time from ccPas ($F_{4,144} = 16.64$; $p < 0.0001$; $eta^2 = 0.32$) accounted for by faster responses, as time passes (T0 > all others Time from ccPAS; all $p < 0.02$). No other main effects or interactions reached significance (all $F < 1.48$; all $p > 0.17$) (Table 1). The Group x Exposition Time x Time from ccPAS ANOVA carried out on response bias showed no significant main effects or interactions (all $F < 1.77$; all $p > 0.08$) suggesting that better performance of the STS-V1 group could not be ascribed to changes in response bias (Table 1).

Measure	**Protocol**	**17 ms**	**33 ms**	**50 ms**
Response bias (β)	$Exp2_{STS-V1}$	0.13 ± 0.18	–0.01 ± 0.17	–0.28 ± 0.21
	$Ctrl_{0ms}$	–0.13 ± 0.17	–0.30 ± 0.23	–0.32 ± 0.21
	$Ctrl_{100ms}$	–0.07 ± 0.11	–0.37 ± 0.30	–0.39 ± 0.19
Response times (RTs)	$Exp2_{STS-V1}$	0.88 ± 0.33	0.87 ± 0.30	0.85 ± 0.32
	$Ctrl_{0ms}$	0.82 ± 0.40	0.83 ± 0.44	0.83 ± 0.45
	$Ctrl_{100ms}$	0.87 ± 0.45	0.89 ± 0.41	0.88 ± 0.37

Table 1. Mean baseline-corrected changes in response bias and response time (± standard error) as a function of ccPAS protocol and exposure time in Experiment 2.

Experiment 3 - time specificity of STS-to-V1 back-projections for emotion perception

The Group x Exposition Time x Time from ccPAS ANOVA on d' showed a significant Group x Exposition Time interaction ($F_{4,78} = 2.56$; $p = 0.045$; $eta^2= 0.12$). Post hoc analysis showed that, as in Experiment 1, following the ccPAS protocol, participants assigned to the $EXP2_{STS-V1}$ group, only when exposed to facial target for 17 ms (but not 50 or 33ms), showed increased performance relative to all the other groups and exposition times (all $p < 0.04$) replicating the same pattern observed in Experiment 1. No other comparisons were significant (all $p > 0.11$).

No other main effects or interactions reached significance (all F < 1.83; all p > 0.08) (Figure 5).

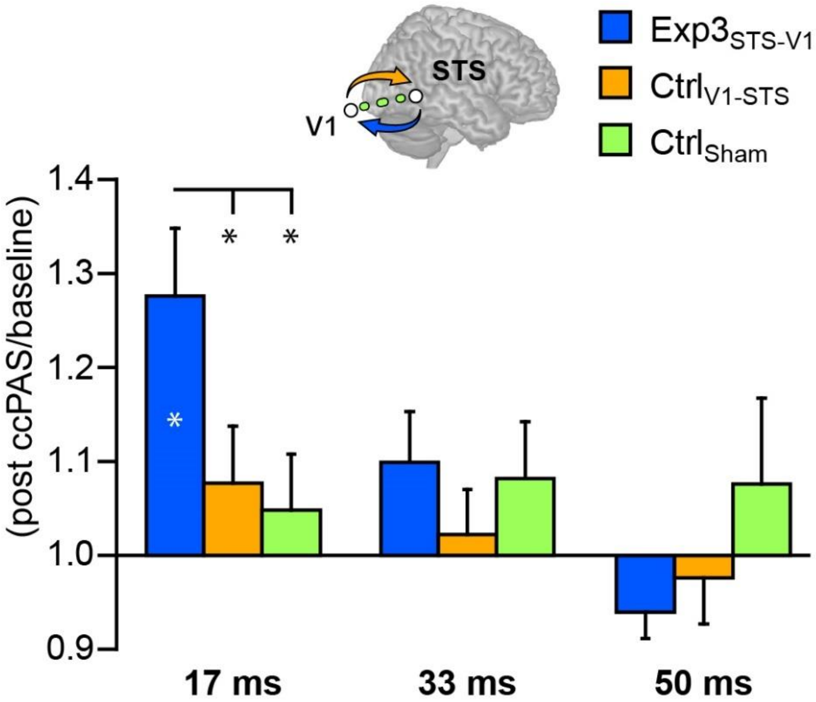


Figure 5. *Experiment 3 results replicating the selective increase in visual senstivity (d') to briefly presented emotional facial expressions (17 ms). As in Experiment 2, the increase is specific to the ccPAS protocol targeting long-latency pSTS-to-V1/V2 backward connections (i.e., $Exp3_{STS-V1}$ ccPAS). No change is observed following ccPAS protocols controlling for direction of connectivity ($Ctrl_{V1-STS}$) or unspecific effects ($Ctrl_{Sham}$). Mean d' values across the post-ccPAS time points (average of T0, T20, T40, T60, T80) are expressed relative to baseline values. While and black asterisks indicate significant increase relative to baseline and all the other post-ccPAS conditions, respectively. Error bars denote standard error.*

The Group x Exposition Time x Time from ccPas ANOVA carried out on response times showed only the non-surprising main effect of Time from ccPAS ($F_{4,156}$= 7.80; p < 0.0001; eta^2= 0.17) accounted for by faster responses, as time passes (T0 > all others Time from ccPAS; all p < 0.001). No other main effects or interactions reached significance (all F < 1.80; all p > 0.08) (Table 2). The Group x Exposition Time x Time from ccPAS ANOVA carried out on response bias showed no significant main effects or interactions (all F < 1.96; all p > 0.15) suggesting that better performance of the STS-V1 group could not be ascribed to changes in response bias (Table 2).

Measure	**Protocol**	**17 ms**	**33 ms**	**50 ms**
Response bias (β)	$Exp2_{STS\text{-}V1}$	–0.34 ± 0.18	–0.13 ± 0.16	–0.30 ± 0.26
	$Ctrl_{0ms}$	–0.26 ± 0.32	–0.39 ± 0.23	0.02 ± 0.19
	$Ctrl_{100ms}$	–0.15 ± 0.16	–0.11 ± 0.20	–0.14 ± 0.18
Response times (RTs)	$Exp2_{STS\text{-}V1}$	0.94 ± 0.55	0.96 ± 0.60	0.94 ± 0.80
	$Ctrl_{0ms}$	0.86 ± 0.40	0.86 ± 0.35	0.84 ± 0.36
	$Ctrl_{100ms}$	0.84 ± 0.24	0.86 ± 0.27	0.86 ± 0.30

Table 2. Mean baseline-corrected changes in response bias and response time (± standard error) as a function of ccPAS protocol and exposure time in Experiment 3.

Experiment 4 - task specificity of STS-to-V1 back-projections

We found no evidence that the same ccPAS protocol enhancing pSTS-to-V1/V2 connections modulates gender recognition. In fact, the ANOVA on sensitivity entering ccPAS conditions ($Ctrl\text{-}Gender_{STS\text{-}V1}$, $Ctrl\text{-}Gender_{Sham}$) x Exposition time (17, 33, 50 ms) x Time from ccPAS (T0, T20, T40, T60, T80) ANOVA showed no significant main effect or interaction (all $F \leq 3.22$, $p \geq 0.08$; Table 3). Also, the ccPAS x Exposition Time x Time from ccPAS ANOVA on baseline-corrected β values showed no significant effect (all $F \leq 2.49$, all $p \geq 0.09$), whereas the same analysis on baseline-corrected RT values showed a main effect of Time from ccPAS ($F_{4,104} = 21.19$; $p < 0.0001$; $p\eta^2 = 0.45$) accounted for by faster responses, as time passes (lower RTs in T0 relative to all others Time from ccPAS; all $p < 0.005$).

Measure	Protocol	17 ms	33 ms	50 ms
Task sensitivity (d’)	Ctrl-Gender$_{\text{STS-V1}}$	1.02 ± 0.06	1.07 ± 0.05	0.93 ± 0.05
	Ctrl-Gender$_{\text{Sham}}$	1.20 ± 0.08	1.07 ± 0.08	1.10 ± 0.06
Response bias (β)	Ctrl-Gender$_{\text{STS-V1}}$	–0.42 ± 0.1	–0.79 ± 0.2	–0.48 ± 0.2
	Ctrl-Gender$_{\text{Sham}}$	–0.41 ± 0.2	–0.81 ± 0.2	–0.43 ± 0.3
Response times (RTs)	Ctrl-Gender$_{\text{STS-V1}}$	0.75 ± 0.35	0.76 ± 0.29	0.79 ± 0.27
	Ctrl-Gender$_{\text{Sham}}$	0.75 ± 0.29	0.76 ± 0.30	0.76 ± 0.31

Table 3. Mean baseline-corrected changes in d’, response bias and response time (± standard error) as a function of ccPAS protocol and exposure time in Experiment 4.

To further assess the functional specificity of pSTS-to-V1/V2 back-projections, we directly compared the three groups that received the same pSTS-to-V1/V2 ccPAS protocol, but performed either the emotion discrimination task (in Experiment 2 and 3) or the gender discrimination task (in Experiment 4). The ccPAS (Exp2$_{\text{STS-V1}}$, Exp3$_{\text{STS-V1}}$, Ctrl-Gender$_{\text{STS-V1}}$) x Exposure time x Time from ccPAS ANOVA showed the main effects of ccPAS ($F_{2,38} = 5.53$; $p < 0.01$; $p\eta^2 = 0.23$) and Exposure time ($F_{2,76} = 11.27$; $p < 0.0001$; $p\eta^2 = 0.23$) and a significant ccPAS x Exposure time interaction ($F_{4,76} = 3.16$; $p = 0.02$; $p\eta^2 = 0.14$). Importantly, d’ values increased during emotion discrimination at 17 ms, but not during gender discrimination under identical conditions (all $p \leq 0.03$). Further post-hoc comparisons confirmed that increase in d’ for emotion discrimination was comparable across Experiment 2 and 3 ($p = 0.41$). No other effects were observed (all $F \leq 1.26$, all $p \geq 0.27$; Figure 6).

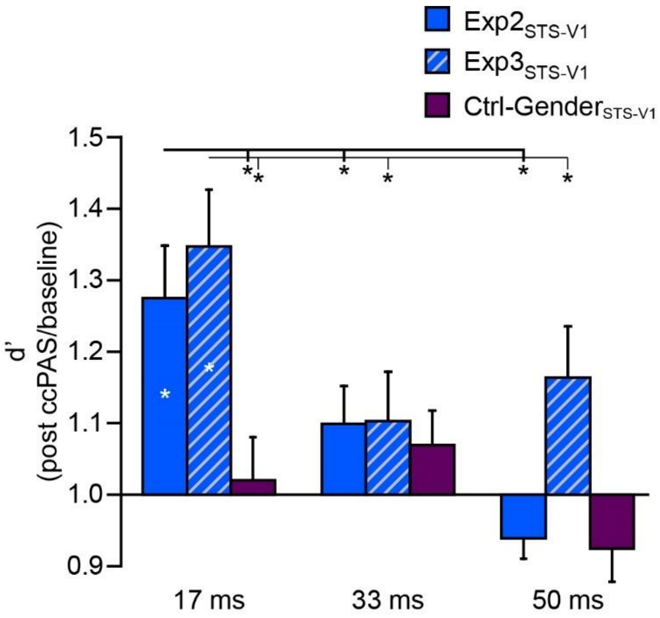


Figure 6. *Test of function specificity of long-latency pSTS-to-V1/V2 ccPAS across Experiment 2-4. The increase in visual sensitivity (d') to briefly presented emotional facial expressions (17 ms) is greater for emotion discrimination (Exp2$_{STS-V1}$ and Exp3$_{STS-V1}$) than for gender discrimination (Ctrl-Gender$_{STS-V1}$). Mean d' values across the post-ccPAS time points (average of T0, T20, T40, T60, T80) are expressed relative to baseline values. Red and black asterisks indicate significant increase relative to baseline and all the other post-ccPAS conditions, respectively. Error bars denote standard error.*

Discussion

It has long been recognized that the feedforward connections in the brain are paralleled by feedback connections from higher-order areas, but there has been little consensus as to the role of the feedback connections in perception. It has been proposed that these higher-order properties result from feedback connections from higher areas and might be required for awareness (Lamme & Roelfsema, 2000; Pollen, 1999). In support of this view, perception of moving phosphenes caused by stimulation of area V5 with transcranial magnetic stimulation (TMS) can be diminished by stimulation of V1, but only if the stimulation of V1 is applied after the TMS pulse to V5 (Pascual-Leone & Walsh, 2001). This preliminary evidence indicates that conscious perception of moving phosphenes might be contingent on feedback connections to V1 that are disrupted by the second pulse. In additional support to the role of feedback projections in visual awareness, Romei and colleagues (2016) have recently demonstrated that strengthening the V5-V1 backward connections improves the perceptual processing of coherent motion. However, all the evidence focused on rather low level visual proprieties leaving unexplored whether backprojections may play also a critical role when complex visual features need to be discriminated. Here, we have demonstrated, for the first time, that temporal to visual backprojections are critical for emotion discrimination. In particular, we showed that stimulation aimed at increasing synaptic efficacy in backprojections from STS to V1 transiently boosted visual emotion perception. Our findings provide causal evidence that strengthening reentrant STS-V1 connections can enhance emotion perception. This supports the view that reentrant connectivity from higher-order to early visual areas subserves integrative visual functions (Koivisto & Revonsuo, 2010; Lamme et al., 1998; Silvanto, Cowey, et al., 2005; Silvanto, Lavie, et al., 2005; Wyatte et al., 2014). Notably, we specifically tested for a novel account of the functionality of reentrant projections, namely the plasticity of the STS-V1 circuit, by manipulating its pre- and post-synaptic nodes according to the Hebbian rule as implemented through this novel ccPAS protocol. The most immediate consequence of this novel intervention approach is that participants in the STS-V1 group experienced an enhanced ability to discriminate facial emotional expressions. In contrast, none of the participants in the control groups (including $\text{Ctrl}_{\text{V1-STS}}$ controlling for directionality of the stimulation, $\text{Ctrl}_{\text{Sham}}$, which controls for unspecific effects, Ctrl_{0ms} and $\text{Ctrl}_{\text{100ms}}$ for timing control) improved their perception following the TMS application, thus ruling out that mere repeated stimulation of STS and V1, task practice or other nonspecific effects could explain the selective task-specific increase in performance. These findings indicate that hierarchical connections between temporal nodes of the network underlying emotion perception and discrimination (Narumoto et al., 2001; Pitcher, 2014) are functionally malleable and sensitive to ccPAS. Plastic changes critically depended on the direction of stimulation during the ccPAS; if this requirement was not met, the behavioural enhancement did not take place.

One may wonder why no change in performance was detected following ccPAS in the Ctrl$_{V1-STS}$ group. In principle, reversing the order of the stimulation (i.e., the first TMS pulse over V1, the second over STS) would strengthen feedforward rather than backward connectivity in the network. Our findings suggest that backward more than feedforward connections are amenable to plastic boosting of visual perception, which is in keeping with their top-down modulatory role (Gilbert & Li, 2013; Hupé et al., 1998; Koivisto et al., 2010; Lamme et al., 1998; A Pascual-Leone & Walsh, 2001; Silvanto, Cowey, et al., 2005; Silvanto, Lavie, et al., 2005; Wyatte et al., 2014). However, it should be noted that the ISI of the ccPAS was selected based on the timing of causal interactions demonstrated through a TMS-EEG experiment, which demonstrated that the highest peak of connectivity between STS and V1 was observed at 200 ms. However, although the combination of the two neurophysiological approaches provided precise information about the causal time-resolved connectivity (Ilmoniemi et al., 2010), other ISIs may be effective for modulating perceptual function via changes in feedforward connectivity or in affecting gender discrimination capabilities.

Interestingly, the STS-V1 stimulation selectively improved emotion facial expression discrimination when facial stimuli were presented for a short exposure time (i.e., 17 ms), while no changes in performance were recorded when facial stimuli were presented for 33 or 50 ms. This finding is in line with the considerable evidence that local recurrent processing is important when stimuli are degraded, partial, or otherwise ambiguous. The basic logic behind this proposal is that degrading a stimulus has been shown to weaken the initial responses in object-selective areas (Nielsen, 2006; Sclar et al., 1990; Williford & Maunsell, 2006), but recurrent processing over time can strengthen responses back to near threshold levels and preserve selectivity via top–down reinforcement. Single-unit recordings that use reversible cooling to temporarily inactivate a particular brain area provide further support for our hypothesis. Hupé et al., (1998) applied cooling to area V5/MT, a visual area in the superior temporal sulcus of the monkey brain that sends feedback projections to areas V1, V2, and V3. Recordings from V1 through V3 indicated that responses to moving bar stimuli were vastly weakened (fewer spikes observed per second) when V5/MT was inactive compared to control experiments in which it was active. This attenuation of lower-level responses was most dramatic in low salience conditions, such as when the bar had a very low contrast. Top–down amplification promotes visual awareness (Dehaene et al., 2006; Lamme, 2003, 2006), and there is mounting evidence that recurrent amplification also plays an important functional role in visual object recognition when stimuli are degraded or ambiguous, by promoting a complex grouping and “filling-in” process (Silverstein, 2015; Wyatte et al., 2014).

Finally, the STS-V1 stimulation selectively improved performance in an emotion discrimination task, while no differences in performance were observed when participants underwent a gender discrimination task after strengthening the very same reentrant STS-V1 pathway. This important finding demonstrated, for the first time, the high specificity of such backprojections in emotion discrimination. The involvement of the STS in emotion perception has been demonstrated widely by single-cell recording in monkeys (Hasselmo et al., 1989) and humans (Fried et al., 1982; Ojemann et al., 1992) that showed that there are independent cell populations in the STS that respond specifically to expressions. Moreover, neuroimaging (Engell & Haxby, 2007; Fusar-Poli et al., 2009; Ishai et al., 2005; Johnston et al., 2013; LaBar et al., 2003; Narumoto et al., 2001; W. Sato et al., 2004; Zhu et al., 2013) and magnetoencephalographic (Liu & Ioannides, 2010; Streit et al., 1999) studies have reported increased activation in this area during emotion discrimination tasks. Importantly, a recent TMS study has demonstrated that pSTS plays a critical role for facial expression discrimination (Pitcher, 2014). The pSTS represents a fundamental hub in the face processing network, since it receives visual information from V1 and extrastriate regions and is functionally bi-directionally connected with the amygdala, a key subcortical structure fundamental for emotion processing (Allison et al., 2000; Amaral & Price, 1984; Bickart et al., 2012; Davies-Thompson & Andrews, 2012; Foley et al., 2012; Furl et al., 2013; Grèzes et al., 2014; Hein & Knight, 2008; Herzog et al., 1976; Liu et al., 2015; Morris et al., 1998; Rotshtein et al., 2010; Sah et al., 2003). On the contrary, very few studies have investigated the neural basis of gender discrimination and have reported that there was no gender-specific increases in mean levels of brain activity in any single area of the face network, and rather than localized to a single region, information about the gender of a face is represented in multiple face-responsive regions (Kaul et al., 2011).

Conclusions

In conclusion, our study demonstrates that ccPAS, aimed at strengthening the synaptic efficacy of STS-to-V1 connections, selectively enhances visual functions tapping into STS-V1 networks. Plastic enhancement critically depended on the repeated pairing of pre-and post-synaptic nodes of the STS-to-V1 pathway – meeting the physiological constraint of the temporo-visual hierarchy. Our findings provide the first causal evidence that STS-to-V1 connections are functionally malleable and sensitive to exogenous manipulations of cortico-cortical connectivity. Our study provides proof-of-principle evidence that ccPAS can be used to improve visual functions in healthy humans. These findings have important theoretical and methodological implications, as they suggest that ccPAS might be a useful tool for targeting specific cortico-cortical pathways and they demonstrate a causal effect of directional connectivity on behaviour (Romei et al., 2016; Romei, Thut, et al., 2016). Moreover, these findings add to the growing literature showing the potential utility of non-invasive brain stimulation for improving cortical functions in humans (Avenanti et al., 2017; Fregni et al., 2005; Krause & Cohen Kadosh, 2014; Romei et al., 2016; Vallar & Bolognini, 2011). By showing that increasing the synaptic efficacy of cortico-cortical pathways can lead to behavioural gains, our study suggests potential applications to neuroenhancement and clinical uses (e.g., in conditions where recovery of a function depends on establishing new activity patterns across cortico-cortical pathways or reestablishing old ones). In particular, our findings may have implications for designing novel therapeutic strategies based on associative brain stimulation of cortico-cortical pathways for the recovery of abilities that have been lost due to brain injury or neurodegenerative disease. Therefore, future studies should carefully assess the clinical and applied potentialities of ccPAS.

CHAPTER II

Plasticity and functional relevance of temporo-occipital connections in gaze-cueing

Introduction

The eyes represent one of the most powerful vehicles of social information on the human face. Perceiving where people look causes a preferential recruitment of attention, since another's eye-gaze can enable the observer to detect that person's focus of attention and to align their own attention accordingly (Calder et al., 2002; Emery, 2000). The tendency to direct attention to an external stimulus targeted by other people's gaze is a phenomenon called "Joint Attention" and it is thought to occur in a relatively automatic way (Kingstone et al., 2000). Attentional effects triggered by seeing eye-gaze are mainly studied with tasks based on Posner's spatial cueing paradigms (Posner et al., 1980). In these studies, an attentional cue depicting a human face looking towards the subject is visually presented on a centrally display position and, typically, its gaze shifts away to a specific spatial location. After a certain stimulus-onset asynchrony (SOA), a target appears to either one or the other position signalled by the gaze, which the participant has to detect or recognize (Bayliss et al., 2011; Lachat et al., 2012; Pecchinenda & Petrucci, 2016). The behavioural effect typically found in this prototypical paradigm is named "gaze-cuing effect", characterized by shorter response times

(RTs) to targets appearing in the gazed-at-location (congruent trials) compared to RTs to targets appearing in the opposite location (incongruent trials) (Driver et al., 1999; Friesen & Kingstone, 1998). This effect appears rapidly and automatically, even if the cue is not predictive of the actual appearance of the target and it is not abolished by the explicit instruction to ignore the cue stimulus (Jonides & Irwin, 1981; Remington et al., 1992). For this reason, this type of cueing is considered to be involuntary and reflexive (for a review, Frischen et al., 2007), also due to its rapid onset, typically emerging within 100 to 400 ms SOAs (Deaner & Platt, 2003; Driver et al., 1999; Friesen et al., 2004; Jones et al., 2010; Langton & Bruce, 1999). Moreover, despite these characteristics, gaze-cueing is not an encapsulated effect, but it is permeable to contextual influences carried by the face, such as facial expression (Mathews et al., 2003; Pecchinenda & Petrucci, 2016; Tipples, 2006) or gender related traits (Ohlsen et al., 2013). Research to date has identified a distributed cortical network lateralized mostly to the right hemisphere which seems particularly susceptible to gaze stimuli (Nummenmaa et al., 2010), with a core area located to the superior temporal sulcus (STS) (Engell & Haxby, 2007). In particular, the posterior branch of STS (pSTS) has been majorly implicated in gaze processing (Akiyama, Kato, Muramatsu, Saito, Nakachi, et al., 2006; Akiyama, Kato, Muramatsu, Saito, Umeda, et al., 2006; Dasgupta et al., 2017; Roy et al., 2014) and recruited during gaze-cueing paradigms (Callejas et al., 2014; Grosbras et al., 2005; Lockhofen et al., 2014; Materna et al., 2008; Pelphrey et al., 2003). It has been proposed that the gaze could be processed via a cortical occipitotemporal pathway starting from early visual cortices V1/V2 and projecting indirectly into pSTS via V5/MT motion complex, bypassing ventral face-region like fusiform face area (FFA) and occipital face area (OFA) (Boussaoud et al., 1990; Gschwind et al., 2012; Pitcher et al., 2017; Pyles et al., 2013; Dalrymple et al., 2011; Steeves et al., 2006). A limited number of human studies used non-invasive modulation to target pSTS to affect processing of gaze (Pitcher et al., 2014; Pourtois et al., 2004; Saitovitch et al., 2016). A fundamental and yet unanswered question is how neural interactions between early visual areas

V1/V2 and pSTS give rise to effective processing of gaze information and to what extent occipito-temporal networks are malleable to exogenous manipulations.

This network is mediated by feedforward and feedback projections, some unidirectional and others of these bypassing transitions areas, permitting direct communication across early and late stages of processing (Kravitz et al., 2013). Anatomical evidence in non-human primates returned the possibility of direct and indirect feedback projections from STS to area V1 (Montero, 1980; Rockland & Van Hoesen, 1994; Zeki, 1971) but the functional relevance of this re-entrant stream needs to be addressed. In humans, the critical role of back-projections to visual cortices has been related to visual awareness (Pascual-Leone and Walsh, 2001; Silvanto et al., 2005), amplification of neural activity in lower-order areas (Bullier, 2001; Hupé et al., 2001, 1998), and improvement of stimulus processing (Koivisto et al., 2010; Silvanto et al., 2005; Vetter et al., 2015; Wyatte et al., 2014). Recent evidence has been provided for a functional role of V5/MT to V1/V2 back-projections for motion processing, by exploiting the plasticity of the targeted network (Chiappini et al., 2018; Romei et al., 2016) through a novel paradigm named cortico-cortical paired associative stimulation (ccPAS, Suppa et al., 2017).

In light of these late findings, we aimed at investigating how specific neuromodulation of pSTS-V1 connectivity, by means of the ccPAS protocol, could modulate the gaze-cueing effect in expected directions. To date no experimental attempt was made for humans to demonstrate a causal role of the pSTS-toV1 network in covert gaze orienting. Specifically, in the present study we tested the hypothesis that by enhancing pSTS-toV1 connectivity by means of ccPAS we can boost the gaze-cueing effect, i.e., favor the implicit orientation in a gaze-cueing task (Friesen and Kingstone, 1998).

Methods

Participants

Sixty participants aged between 20 and 28 years (27 males, mean age 23.08 +- 2.02 years) were recruited for the study. They were all right-handed, according to the Edinburgh Handedness Inventory (Oldfield, 1971) and all had normal or corrected vision. None of them reported personal history of mental or neurological illness and no contraindication to the TMS procedure (Rossi et al., 2009; Wassermann, 1998). Participants gave their written informed consent. The procedures were approved by the Bioethics committee at the University of Bologna and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. No discomfort or adverse effects during TMS were reported or noticed.

Experimental design and Procedure

The experimental procedure was designed to test the modulatory effects of ccPAS administered over the right pSTS-V1/V2 re-entrant pathway on a gaze-cueing task. Participants were randomly assigned to 1 of 4 different groups of 15 participant each (each group balanced for gender and age of subjects), corresponding to 1 experimental and 3 control ccPAS protocols (see ccPAS paragraph). After an initial training session aimed at familiarizing with the gaze-cueing task (see Task paragraph), participants underwent 5 test sessions (Fig.1) performed before any ccPAS administration (baseline, BSL), immediately after the ccPAS administration (Post-0) and at regular intervals spaced out by 20 minutes (Post-20, Post-40, Post-60). For each session, participants performed 3 blocks of 80 trials each separated by ~ 20 seconds, for a total of 240 trials per session (and a total time per session of about 9 min). The entire experiment, including neuronavigation procedure (~30 min), lasted approximately 2.30 h.

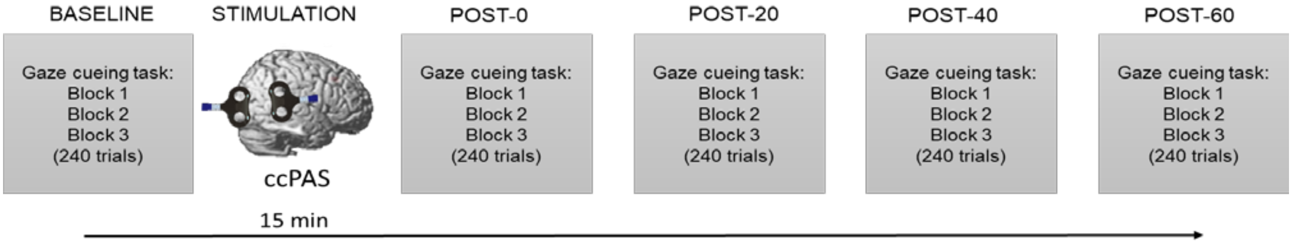


***Fig. 1**. Schematic representation of the experimental procedure*

Stimuli and task

The stimuli were selected from the NimStim set of facial expressions (Tottenham et al., 2009) and included faces belonging to 10 different actors, five males (codes:4M, 7M, 10M, 11M, 12M) and five females (codes:2F, 5F, 6F, 8F, 9F). For each actor, an emotionally neutral facial expression was selected. The background and model's hair were excluded as a result of cropping the image into an elliptical shape (Goshen-Gottstein and Ganel, 2000). Using Adobe Photoshop 6.0, copies of each stimulus were created in which the ocular regions were manipulated (moving the pupil position on the horizontal axis) to obtain a direction of the deviated gaze to the right, then inverting these versions on the vertical axis to create the mirror images with the opposite direction of the gaze. The dimensions of the stimuli were 3.7 x 5.2 cm, subtended to a visual angle of 3.5 ° x 5 °. The targets to be discriminated in the task used were letters with dimensions 1.3 x 1.6 cm, which respectively represented a "T" and a "L" subtended to a visual angle of 1.2 ° x 1.5 °.

The stimuli were presented on a Samsung Syncmaster 920n 19" monitor with a screen resolution of 1280 x 1024 and 75 Hz refresh rate. Each participant sat with his head aligned on the central axis of the screen at a distance of 60 cm from it. All pictures projected on the monitor were included in a 346x496 pixels' box, in which male and female faces were presented in a totally randomized order. In the gaze-cueing task (Dalmaso, Edwards, et al., 2015; Langton & Bruce, 1999) each trial started with the appearance of a white background screen with a black central cross presented for 680 ms; then, the cross was replaced by a neutral facial stimulus gazing straight towards the observer (for 900 ms), followed by the same face with the gaze oriented either on the left or on the right. Following the presentation of the left/right oriented gaze, an alphabetic target (i.e., T / L) appeared, with equal probability, both on the right and left side of the screen (symmetrically at 5.43 ° from the centre), with a constant Stimulus Onset Asyncrony (SOA) of 200 ms: an optimal latency to elicit the cueing effect (Bobak & Langton, 2015; Law et al., 2010; Pecchinenda et al., 2008). In this way the trials could be either valid (congruence between gaze direction and target position) or invalid (inconsistency between gaze and target). Participants were instructed to maintain fixation at the centre of the screen throughout the duration of the trial. Their task was to discriminate which target appeared on the screen by pressing 2 keys (counterbalanced), one for each target letter, through two fingers of the dominant hand (the keys were vertically aligned to avoid spatial bias); this had to be performed by the participant as quickly and accurately as possible (Fig. 2). In addition, participants were informed that the direction of the stimulus gaze was not predictive of the target's position (50% valid trials). Thus, each observer performed 1200 trials distributed across 5 sessions of 240 trials each. Gender of the model in the picture (male or female), position of the target (right or left), congruence of the gaze (congruent or incongruent) and type of target (T or L) were all equally probable and presented with a random sequence. At the end of the first session (BSL), the ccPAS stimulation was administered (15 min).

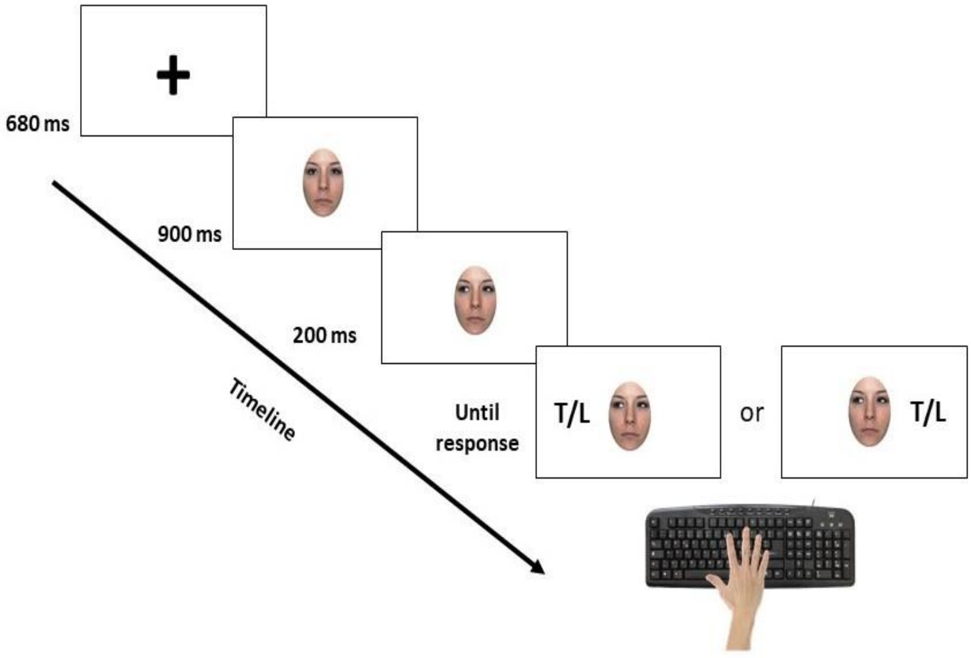
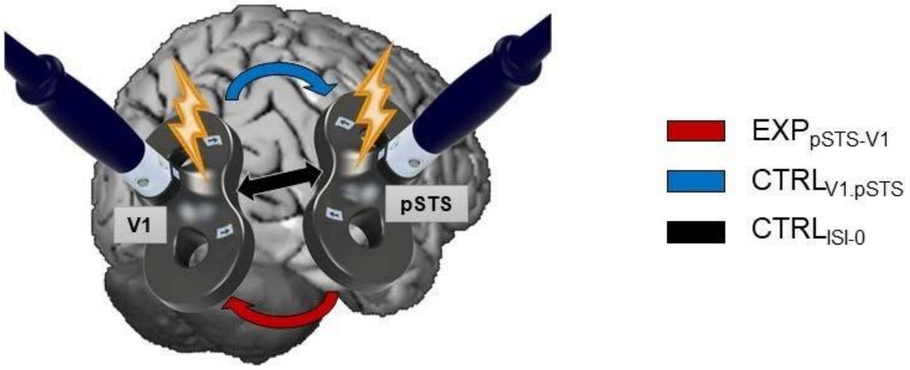


Fig.2 *Illustration of the gaze cueing task used in this study. Participants had to maintain fixation on a central cross where subsequently appeared a face gazing straight and then towards a lateral direction, which could be congruent or not with the position of a target stimulus represented by a letter (T/L). Task request was the identification of the target letter by pressing specific key, maintaining fixation on the face cue.*

Transcranial Magnetic Stimulation: ccPAS protocol ccPAS was delivered by means of a Magstim BiStim2 machine (Magstim Company, UK) via two 50 mm figure-of-eight coils. 90 pairs of stimuli were continuously delivered at a rate of 0.1 Hz for ~15 min (Chiappini et al., 2018; Romei et al., 2016; Veniero et al., 2013); each pair of stimuli consisted of two monophasic transcranial magnetic pulses. The pulses were triggered remotely using MATLAB software (Mathworks, Natick, USA) that controlled both stimulators. The coils were positioned tangentially to the scalp with the handle perpendicular to the surface target. The experimental group ($\text{Exp}_{\text{pSTS-V1}}$) received the first TMS pulse to pSTS followed by a second pulse over V1/V2 with an ISI of 200 ms. This interstimulus interval (ISI) was selected according to the average peak time of STS-to-V1/V2 interactions found in chapter I. Thus, such ISI was chosen to repeatedly activate presynaptic and postsynaptic neurons in re-entrant pSTS-to-V1/V2 connections in a way that is consistent with spike timing dependent plasticity (STDP), i.e., a form of synaptic plasticity meeting the Hebbian principle (Hebb, 1949) and predicting that synapses are potentiated if the presynaptic neuron fires repeatedly before the postsynaptic neuron (Markram et al., 1997). In the first control group ($\text{Ctrl}_{\text{V1-pSTS}}$) we reversed the order of the pulses, with the first pulse given to V1/V2 and the second pulse to STS at the same ISI as the experimental condition (200 ms). This group controlled for direction dependent effects, i.e., we verified that any effect as found in the experimental group was the result of enforced feedback connections and not feedforward. The second control group ($\text{Ctrl}_{\text{ISI-0}}$) received both pulses simultaneously (ISI = 0 ms). According to the Hebbian principle (Koganemaru et al., 2009), although neural interactions may occur during simultaneous TMS pairing, no STDP-like was expected. This ccPAS condition therefore controlled for timing dependent effects (Fig. 3). Lastly, for the third and last control group ($\mathrm{Ctrl}_{\mathrm{Sham}}$), stimulation parameters were identical to the experimental group, except for the fact that the coils' surface were held perpendicular to the scalp, ensuring that no current was induced in the brain. The coil positions for targeting both areas were determined by means of a neuronavigation system (see next paragraph). For the right pSTS the coil was placed tangentially to the scalp inducing an anterior-to-posterior current flow in the brain. The right V1 was stimulated with the coil placed tangentially to the scalp and parallel to the midline, inducing a medial-to-lateral current. The intensity of TMS was set at 60% of the maximum stimulator output for both areas, a magnitude consistent with previous studies involving STS or V1/V2 stimulation (Koivisto et al., 2014; Pitcher et al., 2014, 2008).



90 pulses at 0.1 Hz, ISI 200 ms

Fig.3 ccPAS paradigm*. Graphical representation of ccPAS administration protocols. For* CTRL_{Sham} *condition (not shown) the coils were settled perpendicularly to brain surface in order to avoid delivery of magnetic pulses.*

Neuronavigation

Coil position were identified on each participant scalp with the SofTaxic Navigator system (Electro Medical Systems, Bologna, Italy) as in previous studies (Avenanti et al., 2007; Bertini et al., 2010; Bolognini et al., 2009; Bolognini & Maravita, 2007). Skull landmarks (nasion, inion, and two preauricular points) and about 80 craniometric points providing a uniform representation of the scalp, were digitized by means of a Polaris Vicra digitizer (Northern Digital, Inc., Ontario, Canada). An individual estimated magnetic resonance image (MRI) was obtained for each participant through a 3D warping procedure fitting a high-resolution MRI template to the participant's scalp model. This procedure has been proven to ensure a global localization accuracy of roughly 5mm (Carducci and Brusco, 2012). Coordinates in Talairach space were automatically estimated by the SofTaxic Navigator from an MRI-constructed stereotaxic template. To target right pSTS a recent fMRI study was considered that traced how the gaze-cueing task recruits specific portions of pSTS compared to non-biological directional stimuli (Lockhofen et al., 2014), with the highest activation volume in the posterior portion of the STS of the right hemisphere, at the MNI stereotaxic coordinates: $x = 57$, $y = -46$, $z = 7$, consistent with hotspots found by metanalysis studies (Grosbras et al., 2005; Nummenmaa et al., 2010). Our mean coordinates and standard deviation for all group corresponded to Brodmann area 21 in the posterior part of the right STS ($x = 58.58 \pm 1.75$, $y = -47.08 \pm 1.47$, $z = 6.96 \pm 1.6$). To target V1, it was identified the scalp location that corresponded best to the visual cortex ($x = 19$, $y = –98$, $z = 1$; Serino et al., 2011). The mean coordinates ± standard deviation obtained with our neuronavigation procedure corresponded to Brodmann's area 17, in the middle of the occipital gyrus ($x = 18.24 \pm 0.76$, $y = -96.05 \pm 0.84$, $z = -0.07 \pm 0.95$).

Data analysis

The entire dataset was analyzed using STATISTICA 11 software (StatSoft, Dell) and IBM SPSS Statistics version 25. RTs correspondent to incorrect responses (3% of all) and greater than 800 ms or smaller than 100 ms (4% of correct responses) were removed prior to RTs analysis (Al-Janabi & Finkbeiner, 2014; Pletti et al., 2015). We calculated the mean response time and error rates for gaze-congruent and gaze-incongruent trials for each participant, respectively for male and female cue stimuli (Table 1). For each observer, we then calculated the gaze-cueing index by subtracting the mean response time for gaze-incongruent trials from the mean response time for gaze-congruent trials, in line with previous literature (Deaner et al., 2007; Ponari et al., 2013). As for the response time data, for each observer, we calculated the gaze-cueing index on error rates by subtracting the mean error rate for gaze-incongruent trials from the mean error rate for gaze-congruent trials. In order to compare performance across the 4 groups ($\text{Exp}_{\text{pSTS-V1;}}$ $\text{Ctrl}_{\text{Sham;}}$ $\text{Ctrl}_{\text{V1-pSTS;}}$ $\text{Ctrl}_{\text{ISI-0}}$) as a function of time session (Post-0, Post-20, Post-40, Post60), changes in the gaze-cueing effect were baseline corrected such that the values obtained in the performance at baseline were subtracted from the value obtained in the performance for each session time after stimulation. After baseline correction, any resulting positive value reflected enhancement in the gaze-cueing effect, while negative values returned a reduction of the effect, compared to baseline values (Table 2). First, an ANOVA was performed to compare baseline values across the 4 groups to check whether they started from comparable mean values or not. Secondly, ANOVAs were used to evaluate differences in behavioural performance means as a function of group, time session, participants gender and stimuli's gender; gender was included as a factor because of precedent results attesting its influence in gaze-cueing effect (Deaner et al., 2007; Frischen et al., 2007). Finally, post-hoc analyses were performed using the Duncan's multiple range test to correct for multiple comparisons. In addition, partial η2 () was computed as a measure of effect size for significant main effects and interactions. Analyses were performed both for RTs and accuracy.

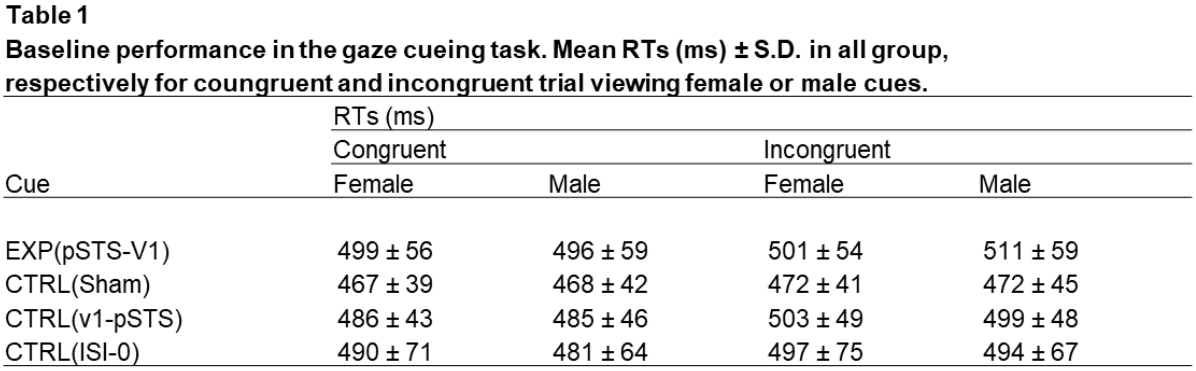


Table 1
Baseline performance in the gaze cueing task. Mean RTs (ms) ± S.D. in all group, respectively for coungruent and incongruent trial viewing female or male cues.

	RTs (ms)			
	Congruent		Incongruent	
Cue	Female	Male	Female	Male
EXP(pSTS-V1)	499 ± 56	496 ± 59	501 ± 54	511 ± 59
CTRL(Sham)	467 ± 39	468 ± 42	472 ± 41	472 ± 45
CTRL(v1-pSTS)	486 ± 43	485 ± 46	503 ± 49	499 ± 48
CTRL(ISI-0)	490 ± 71	481 ± 64	497 ± 75	494 ± 67

Results

RTs.

Firstly, to assess a comparable baseline performance between the different groups, RTs were included into a 4 x 2 x 2 x 2 mixed ANOVA with Group (Exp$_{\text{pSTS-V1,}}$ Ctrl$_{\text{Sham,}}$ Ctrl$_{\text{V1-pSTS,}}$ Ctrl$_{\text{ISI-0)}}$ and Gender of participant (male, female) as between subject factors, and Gaze direction (congruent, incongruent), Gender of stimulus (male, female) as within subject factors. Consistently with the literature, a highly significant main effect of Gaze direction was found ($F_{1,52}$ = 21.24, $p < 0.001$, = 0.28) with faster RTs on congruent compared to incongruent trials (Fig.4). In addition, a significant Gender of participant x Gender of stimulus interaction was found ($F_{1,52}$ = 7.01, $p = 0.01$, = 0.19), showing that male observers responded faster to male stimuli than female stimuli ($p = 0.01$). This effect was irrelevant to the purpose of our study and will not be further discussed. No other effects or interactions were found to be significant (Fs < 1.81, ps > 0.14), demonstrating that all the performances between experimental groups were comparable across baseline measurements. In order to best evaluate the presence of some differences at baseline, we performed a mixed ANOVA on gaze-cueing index with Group (Exp$_{\text{pSTS-V1,}}$ Ctrl$_{\text{Sham,}}$ Ctrl$_{\text{V1-pSTS,}}$ Ctrl$_{\text{ISI-0) as}}$), Gender of stimulus (male, female), and gender of participant (male, female) as between and within factors, respectively. No main effects or interaction were noticed as significant (Fs < 1.88, ps > 0.14), confirming that performance from all groups was comparable, only denoting a tendency (although not significant) of higher gaze-cueing values for male stimuli.

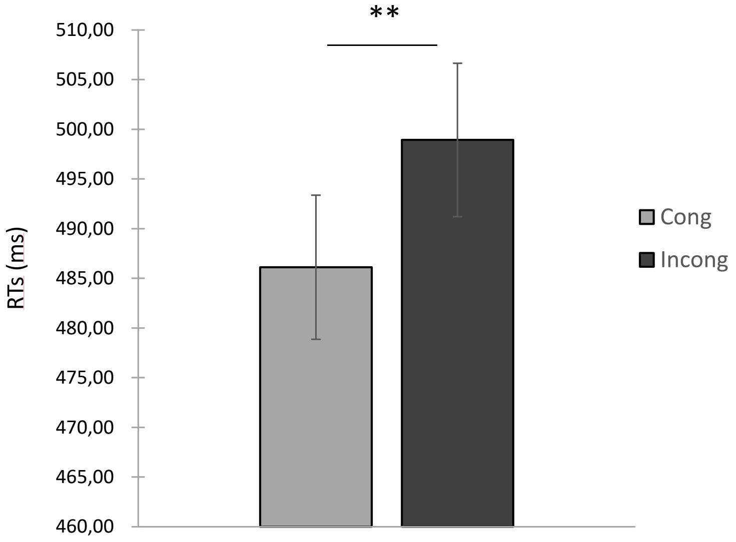


Figure 4*. Main effect of Gaze direction, between congruent (light grey) and incongruent (dark grey) trials. Asterisks denote significant main effect and errors bars represent s.e.m.*

In order to quantify the impact of ccPAS on the gaze-cueing effect, baseline-corrected values were entered into a 4 x 2 x 2 x 4 mixed-design ANOVA with Group ($Exp_{pSTS-V1}$; $Ctrl_{Sham}$; $Ctrl_{V1-pSTS}$; $Ctrl_{ISI-0}$) and Gender of participant (male, female) as the between-subjects factors, and Gender of stimulus (male, female) and Time Session (Post-0, Post-20, Post-40, Post-60) as the within-subjects factors. A significant Stimuli x Group interaction emerged ($F_{3,52} = 2.96$, p = 0.041, = 0.15), showing that, irrespective of Time session and gender of participant, ccPAS had an impact on the gaze-cueing effect specifically for the experimental condition ($Exp_{pSTS-V1}$ group) and selectively so in response to female stimuli (Fig.5) which were significantly different from male stimuli (p = 0.004) as well as from the responses observed in the $Ctrl_{Sham}$ group both to female (p = 0.027) and male (p= 0.025) stimuli; from the responses observed in the $Ctrl_{V1-pSTS}$ group both to female (p = 0.002) and male (p= 0.007) stimuli; and from the responses observed in the $\text{Ctrl}_{\text{ISI-0}}$ group both to female (p = 0.017) and male (p= 0.005) stimuli. No other contrast was found to be significant (ps > 0.308). The remaining main effects or interactions were not significant (Fs < 1.95, ps > 0.13). In order to validate whether the gaze cueing gain was specifically effective for stimuli's gender in the $\text{Exp}_{\text{pSTS-V1}}$ group, we computed a series of one-sample t-tests to compare the gaze-cueing mean changes (all time sessions after BSL collapsed) in each condition against what would be expected if there were no gaze-cuing effects (i.e. the chance value of 0 ms). Only in the $\text{Exp}_{\text{pSTS-V1}}$ group condition with female stimuli (t(14) = 2.548, p = 0.023, *Cohen's d* = 0,66) and in the $\text{Ctrl}_{\text{ISI-0}}$ with male stimuli (t(14) = - 2.284, p = 0.038, *Cohen's d* = -0,59) the results were found to be significant (t(14) = 2.548, p = 0.023), while no significance was traced for other comparisons.(t(14) = - 1.78, ps >= 0.096).

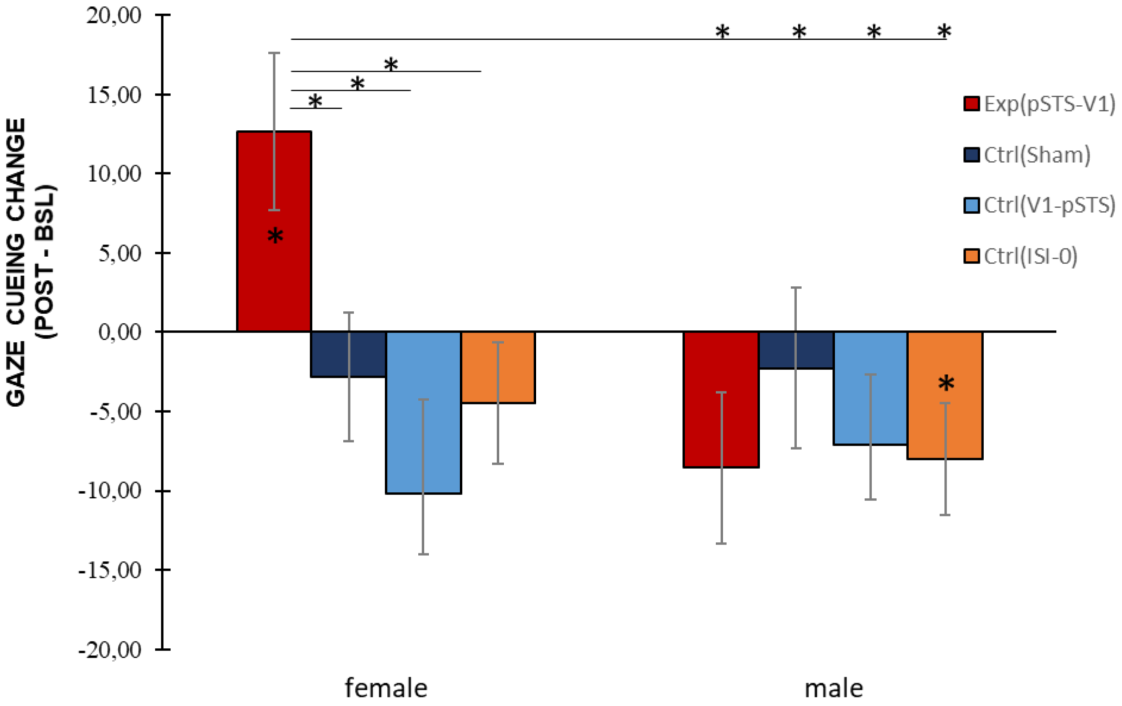


Figure 5. *Gaze cueing changes after ccPAS. Group (line pattern) x Gender of stimulus (X axis) interaction. Values represent collapsed means of baseline-corrected indices (Post ccPAS session – baseline performance; in milliseconds) for gaze cueing index in all groups. Positive values indicate a major gaze cueing effect compared to baseline. Error bars denote s.e.m. Asterisks indicate significant post-hoc comparisons and one sample t-test.*

Accuracy.

In line with the RTs analysis, for the baseline accuracy values we initially performed a 4 x 2 x 2 x 2 mixed ANOVA with Group (Exp$_{\text{pSTS-V1,}}$ Ctrl$_{\text{Sham,}}$ Ctrl$_{\text{V1-pSTS,}}$ Ctrl$_{\text{ISI-0)}}$ and Gender of participant (male, female) as between subject factors, and Gaze direction (congruent, incongruent), gender of stimulus (male, female) as within subject factors. The analysis did not reveal any significant effect or interaction (Fs < 2.28; all p > 0.13). Similarly, the analysis conducted on accuracy index at BSL, with Group (Exp$_{\text{pSTS-V1,}}$ Ctrl$_{\text{Sham,}}$ Ctrl$_{\text{V1pSTS,}}$ Ctrl$_{\text{ISI-0}}$) Gender of participant (male, female) as between subject factors, and Gender of stimulus (male, female) did not show any significant result (Fs < 0.87; all p > 0.41). The absence of differences in performance with respect to congruency, could be explained by the high proportion of correct responses (TAB). The mixed ANOVA 4 x 2 x 2 x 4 conducted on accuracy changes with Group (Exp$_{\text{pSTS-V1;}}$ Ctrl$_{\text{Sham;}}$ Ctrl$_{\text{V1-pSTS;}}$ Ctrl$_{\text{ISI-0)}}$ and Gender of participant (male, female) as the between factor, and Gender of stimulus (male, female) and Time session (Post-0, Post-20, Post-40, Post-60) as the within subject factors, did not shown any significant main effect or interaction (Fs> 1.73; ps> 0.16).

Table 2
Task performance changes. Mean baseline-corrected values of gaze cueing index (in ms) ± S.D.
In all groups across sessions after ccPAS, both for female and male cues.

	Female				Male			
	Post-0	Post-20	Post-40	Post-60	Post-0	Post-20	Post-40	Post-60
EXP(pSTS-V1)	16 ± 6	15 ± 4	6 ± 7	11 ± 5	-7 ± 4	-8 ± 6	-5 ± 5	-12 ± 6
CTRL(Sham)	-0,8 ± 5	0,5 ± 5	-4 ± 3	-6 ± 4	1 ± 6	-7 ± 6	-6 ± 5	3 ± 7
CTRL(V1-pSTS)	-5 ± 7	-11 ± 8	-8 ± 6	-15 ± 6	-10 ± 6	-5 ± 5	-9 ± 6	-3 ± 4
CTRL(ISI-0)	-0,2 ± 5	-8 ± 5	-6 ± 5	-2 ± 5	-12 ± 6	-6 ± 4	-7 ± 6	-5 ± 4

Discussion

The study we have conducted shows how, through a cortical associative stimulation paradigm, it was possible to provide behavioural evidence to support the existence, and a potential functional role, of feedback connections transiting from right pSTS to V1/V2, involved in the gaze-cueing phenomenon. Specifically, assuming that pSTS is a crucial region for gaze movement elaboration (Dasgupta et al., 2017; Lockhofen et al., 2014) through its interconnection with early occipital areas (Pitcher et al., 2014; Ungerleider and Desimone, 1986), we hypothesized an increase of visual saliency of perceived eyes regions after ccPAS administration over pSTS-V1 feedback stream, verifiable on the magnitude of the gaze-cueing effect. Our results demonstrate that only the main experimental group (i.e., feedback network stimulation) showed a behavioural change after stimulation, with an increase in the gaze-cueing effect (i.e., differential time responses between gaze congruent and incongruent in respect of target position) selectively for the vision of female gazes, compared to male ones. An absence of modulation in the other groups allowed us to deduce that the mean gain in the cueing effect was due to the functional improvement of the feedback projection and not caused by another type of connection in the occipito-temporal circuit, such as feedforward stream ($Ctrl_{V1}pSTS$ group). We also found that the causal sequence of stimulation was necessary to induce LTP-like phenomena, if we consider that pulses on the same areas with different timing have not established behavioural effects changes ($Ctrl_{ISI-0}$ group). Consistent with a series of recent studies that have revealed the effects of ccPAS in inducing cortical plasticity between two interconnected visual areas (Chiappini et al., 2018; Romei et al., 2016) here we reported behavioural results that suggest how it is possible to alter the process of gaze-cueing by modifying the synaptic efficiency of the temporo-occipital stream.

The modulation of the connections that bind pSTS to early visual areas appears, therefore, to take shape in an effective transitory increase in the tendency to follow preferentially, and covertly, the female gaze. It has to be considered that orientation in response to a gaze is not a phenomenon encapsulated from contextual influences, but is susceptible and can interact with other factors that characterize the facial stimulus: such as sexual dimorphism, status, dominance, familiarity, and gender (Frischen et al., 2007). In fact, some studies showed a greater effect of cueing in relation to gender, specifically during the vision of masculine dominant faces (Jones et al., 2010; Ohlsen et al., 2013). From data available in our study, it can be noted, on baseline measures, that participants report a general tendency (even if not significant) to manifest a superior cueing effect towards male stimuli when compared with the female faces, consistent with the abovementioned literature. It is plausible to hypothesize that the stimulation protocol we carried out allowed a levelling of the presumed attentional bias related to the category of the stimulus. In other words, the ccPAS of feedback stream may have been able to enhance the gaze-cueing selectively for the female cues since there was a greater modulation margin (probably due to a lower salience of the female cues, at least in our set of stimuli). Consequently, selective improvement was most likely caused by this baseline difference intensity, which, as already discussed, appears to be in line with the literature suggesting a greater impact of the male and dominant gaze. This would suggest a potential mechanism of re-entrant connections in increasing the perceptual impact of visual stimuli with limited salience (here, gaze of women), confirming their amplification role of lower region activity (Bullier, 2001; Hupé et al., 1998; Klink et al., 2017). At the same time, these emerging results could imply a ceiling effect of ccPAS, such that our protocol would have not been able to increase the effect of gaze-cueing on visual stimuli with greater baseline salience (in our case, gaze for men stimuli). Analysing possible neurofunctional mechanisms, right pSTS itself is a crucial area for eye processing (Dasgupta et al., 2017), and thanks to the increased functional connectivity obtained with ccPAS, we may have been able to broaden the receptivity of V1/V2 to process such stimuli. An effect similar to the strengthening seen in the perception of movement after application of the ccPAS protocol on V5 and V1 (Chiappini et al., 2018; Romei et al., 2016).

The theoretical assumption of our study originates from evidence proving the recursive structure of occipito-temporal network with the presence of both feedforward and feedback connections (Kravitz et al., 2013), and that early visual areas are exposed to extensive modulations by hierarchically superior regions (Thiele et al., 2009) which also include projections from STS (Rockland and Van Hoesen, 1994); together with the fact that V1 shows involvement in tasks that also imply visual-spatial attention (Watanabe et al., 2011). The re-entrant connections that generate from temporal areas could orchestrate the activity of selective occipital areas in order to extract highly defined characteristics, a mechanism coherent with feedback signal functions in visual areas (Bullier, 2001; Galuske et al., 2002) and supposed to mediate the processing in face-selective areas (Ayzenshtat et al., 2012; Gauthier et al., 2000; Kok et al., 2012; Rossion et al., 2003). An idea also justified by evidence from non-human primates that have suggested the influence of cortical feedback to the visual areas during facial perception (Ayzenshtat et al., 2012), in addition to the fact that early visual regions are able to code specific facial patterns (associated with gender or expressions) by receiving representations elaborated from other higher areas that then project back to V1 (Petro et al., 2014). Hence, through our experimental paradigm, we have provided a possible functional role of the network of connections that from hierarchically higher temporal areas projects to the first occipital processing stations. As widely reported, pSTS is a crucial region for the processing of eye movements that have biological significance in indicating spatial positions or intentionality in general (Baseler et al., 2014; Carlin & Calder, 2013; Hietanen et al., 2006) and its causal implication in processing this stimulus was also demonstrated by other TMS studies that generated virtual lesions in this temporal area (Pourtois et al., 2004; Saitovitch et al., 2016). In addition, the area is also recruited for the gaze-cueing (Lockhofen et al., 2014) and alters his connectivity when perceiving eyes movement (Dasgupta et al., 2017; Ethofer et al., 2011; Nummenmaa et al., 2010).

In the last years, cumulative proofs have highlighted the effectivity of cortico-cortical associative stimulation for the induction of neuroplasticity (Buch et al., 2011; Rizzo et al., 2009; Veniero et al., 2013). Based on Hebbian's principles of synaptic association (Hebb, 1949; Markram et al., 1997) these protocols resemble STDP phenomena, in which interconnected neurons that fires repeatedly in a causal order are able to modulate their transmission (Caporale and Dan, 2008; Müller-Dahlhaus et al., 2010). Most paradigms using ccPAS have focused on frontal and parietal motor cortices and their modulation, mainly reporting changes in physiological variables (Arai et al., 2011; Chao et al., 2015; Koch et al., 2013; Koganemaru et al., 2009). Recently, interest has also moved on the applicability of this novel protocol also on the visual network, demonstrating a perceptual enhancement induced by paired stimulation of interconnected occipital areas implicated in motion elaboration (Chiappini et al., 2018; Romei et al., 2016). This novel line of research has opened up to several possibilities for the investigation of other brain circuits' malleability by means of ccPAS, and to evaluate the behavioural effect induced. Indeed, here we have considered whether it was possible to act on the elaboration of more relevant biologically stimuli, as are the eye movements. Considering that gaze has an evolutionary value for shared attention, danger signalling as many social functions (Emery, 2000). The induction protocol was developed in such a way that STDP-type long-term potentiation effects were emulated (Wolters et al., 2003) with pre-and-post synaptic discharging in a temporally consecutive way; actually, the ISI we have used (i.e., 200ms) is a temporal interval not common for synaptic strengthening parameters, which usually occurs with near-contemporary stimulations (Dan and Poo, 2004; Suppa et al., 2017). The reason for using this latency, as mentioned before, derives from the results of a TMS-EEG study we conducted targeting right STS, which has shown a positive peak of TMS evoked potential (TEPs) around 200ms over occipital electrodes following STS stimulation (Chapter I). We have therefore used this timing as a marker of the functional timing of connection between STS and early visual areas.

However, the specific latency between the two stimulations of pSTS and V1 that we applied, having a wide temporal profile (200ms) is likely to have induced activity into various neural relays part of the eye-processing network before influencing V1/V2. It follows that the stimulation protocol has acted plausibly on the indirect pSTS-V1 connections, through a conditioning interval compatible with the recruitment of large populations of neurons, i.e., modulating the temporo-occipital network responsible for eye-processing, perhaps recruiting MT/V5 region (Nummenmaa et al., 2010). Overall, our findings confirmed the possibility of intervening on the neural plasticity of the visual network through ccPAS and paves the way for the development of further paradigms using this technique on this brain circuit. For instance, it would be logical to adopt a state-dependent approach (Chiappini et al., 2018; Silvanto and Pascual-Leone, 2008) to investigate whether online stimulation during exposure to a specific gender of stimuli could generate a selective perceptual aftereffect. Moreover, the research should be expanded in order to provide other neurophysiological measures of those behavioural modulations we found. Through TMS-EEG coupling it would be conceivably possible to assess and trace alterations of rhythm coherence between stimulated areas following ccPAS administration (Veniero et al., 2013; Romei et al., 2016).

CONCLUSIONS

The study we conducted offers original experimental evidence showing that it is possible to increase the processing of the gaze through an associative TMS protocol. We have practically shown that pSTS, through feedback connections, can modulate V1 response. Having reported that gaze-cueing phenomenon is increased by the ccPAS protocol, implies that the stimulation of the right temporo-occipital network, interposed between pSTS and the primary visual areas, induces an amplification of the receptivity for the gaze in V1. These data have repercussions for the implementation of theoretical models about visual elaboration and suggest plausible implications for the rehabilitation of deficits associated with the maintenance of eye contact or gaze perception in general, a distinctive tract in autistic spectrum syndromes (Tanaka & Sung, 2016). Concluding, future clinical trials could take advantage of this evidence for the development of neurostimulation treatments using ccPAS.

CHAPTER III

Driving plasticity in cortico-cortical visual reentrant networks to affect perceptual decisions

Introduction

The ability to exploit available sensory information in order to select the most adaptive option from a set of alternatives represents a fundamental decisional skill. Once a perceptual judgement about a stimulus is made, the resulting subjective belief that the perceptual decision is correct is referred to as confidence. Evaluation of confidence can be intended as a metacognitive process, since it represents a post-decisional outcome regarding the accuracy of first-order choice (Fleming & Daw, 2017; Yeung & Summerfield, 2012). These choice features may appear intrinsically intertwined and yet, recent behavioural and neural findings hint at a possible functional dissociations between performance accuracy and confidence (Maniscalco et al., 2016; Rahnev et al., 2012).

From a behavioural perspective, accuracy and confidence in perceptual decision have been frequently dissociated in non-human primates (Ferrigno et al., 2017) and humans (Boldt et al., 2017; Samaha et al., 2016; Vlassova et al., 2014; Zylberberg et al., 2012). Importantly, there is further empirical evidence of simple dissociations between perceptual sensitivity and confidence in the form of selective metacognitive perturbations without alterations of discriminative performances (Fleming et al., 2015; Rounis et al., 2010); supported by the existence of specific neural correlates which suggest distinct computations underlying perceptual decisions and metacognitive abilities (Peters, Thesen, et al., 2017; Samaha et al., 2017). Given these findings, it still seems unclear whether it is possible to actively induce a targeted modulation between objective and subjective measures of visual perception, for example by intervening on the efficiency of the cortical networks that process these functions.

Perceptual decision-making studies have classically focused on visual motion processes (Hanks & Summerfield, 2017). These studies have suggested that neurons in the middle temporal area (V5/MT+), which are tuned to the direction of motion stimuli, are essential for perceptual sensitivity, ultimately leading to accurate motion discrimination (Britten et al., 1992).

Moreover, electrical micro-stimulation in animals (Ditterich et al., 2003) has confirmed the causal role of V5/MT+ in representing sensory evidence, showing that enhanced perceptual discrimination is possibly driven by signal amplification mechanisms which may in turn influence confidence generation (Fetsch et al., 2014). Conversely, other animal studies pointed to the fundamental role of the lateral intraparietal cortex (LIP) in shaping the decision process per se (Hanks et al., 2006). Decision certainty modulations have been found during LIP stimulation in monkeys (Kiani & Shadlen, 2009), in line with the notion that this area and the corresponding Intraparietal Sulcus (IPS) in humans (Gould et al., 2012; Hauke R. Heekeren et al., 2008) are implicated in choice formation (Gold & Shadlen, 2007; Zhou & Freedman, 2019).

Visual awareness for global coherent motion (i.e., evidence of movement) has been shown to require the recruitment of feedback pathways from V5/MT+-to-V1//V2 (Silvanto, Lavie, et al., 2005; Vetter et al., 2015). Such connections can be transiently strengthen by means of a novel TMS protocol, based on Hebbian principle, namely cortico-cortical paired associative stimulation (ccPAS) (Guidali et al., 2021; Pitcher et al., 2021; Rizzo et al., 2009; Romei, Thut, et al., 2016; Suppa et al., 2017). This non-invasive stimulation implies a repetitive activation of connected cortical sites at specific inter-stimulus intervals, based on their physiological and functional communication, so to mimic patterns of neuronal stimulation shown to induce spike-timing-dependent plasticity (STDP) – a form of synaptic plasticity meeting the Hebbian principle that synapses are potentiated if the presynaptic neuron fires immediately before the postsynaptic neuron in a coherent and repeated manner (Caporale & Dan, 2008; Jackson et al., 2006; Markram et al., 2012). This technique has proved capable of modifying neurophysiological responses (Arai et al., 2012; Buch et al., 2011; Chiappini et al., 2020; Veniero et al., 2013) and recently opened the possibility of testing its behavioural consequences (Fiori et al., 2018; Rizzo et al., 2011), ultimately leading to enhanced visual awareness for global coherent motion (Chiappini et al., 2018; Romei, Chiappini, Hibbard, & Avenanti, 2016).

Yet, the relevance of IPS/LIP in decision construction and the degree of certainty about choice, in association with evidence of back-projections from parietal to early visual areas (Greenberg et al., 2012; Parks et al., 2015; Silvanto et al., 2009), raises the question about the functional role of these latter parieto-occipital connections in visual awareness processes. However, a key question to be addressed is whether and how do IPS/LIP-to-V1/V2 back-projections functionally contribute to decision-making process, including its confidence.

Here we specifically aim to dissociate the functional role of V5/MT+-to-V1/V2 and IPS/LIP-to-V1/V2 back-projections in motion perception decisions by means of ccPAS. In line with previous findings (Chiappini et al., 2018; Romei, Chiappini, Hibbard, & Avenanti, 2016), strengthening V5/MT+-to-V1/V2 connectivity is expected to enhance coherent motion perception. Crucially, assuming IPS/LIP major involvement in decision processes, IPS/LIP-to-V1/V2 ccPAS is expected to drive changes in response certainty, without impacting sensory discrimination per se. The specificity of the role of the parieto-occipital reentrant connections has also been disambiguated by including a control modulation of the IPS-V1 network, alongside the experimental stimulations.

Methods

Experimental design.

Participants. Fifty-one healthy individuals were recruited for the study. Seventeen participants (8 males) were submitted to the V5/MT+-to-V1/V2 ccPAS condition (Exp$_{V5\text{-}V1}$), seventeen participants (9 males) participated in the IPS/LIP-to-V1/V2 condition (Exp$_{IPS\text{-}V1}$) and the remainder seventeen (7 males) were assigned to the control IPS/LIP-V1/V2 condition (Ctlr$_{IPS\text{-}V1}$). Participants' ages varied between 20 and 28 years. All studies were approved by the University of Bologna Research Ethics Committee. All participants had normal or corrected-to-normal vision. Informed consent was obtained from all participants before the experiment. Participants were all volunteers and received no payment or compensation. All investigators were blinded to any group, participant or sequence allocation during data collection and analyses.

Visual stimuli. Stimuli were presented on a gray background and consisted of 400 white dots (6 pixels each) moving within a square region subtending 12.8 x 12.8 degrees of visual angle, which appears on the right side of a white fixation cross (20 x 20 pixels) located in the centre of the screen on a grey background. In each trial, dots moved with a different level of motion coherence (0, 4, 8, 12, 16, 20, 25, 35, 50 or 80%) leftward or rightward. Motion coherence was expressed as the percentage of dots that were moving in the signal direction. In the 0%

coherence trials, all the dots moved randomly; in the 80% coherence trials, 320 dots (80%) moved coherently towards leftwards or rightwards while the remaining 80 dots (20%) were each given a randomly selected direction of motion. Each dot moved at a speed of 4.5°/sec. The stimuli were presented in an 18-inch screen with a resolution of 1280 x 1024 pixels and a refresh rate of 85 Hz. In all tests, stimulus presentation was implemented by MATLAB (R2016b, MathWorks) using the Psychophysics Toolbox (Brainard, 1997).

Coherent Motion direction discrimination paradigm. The task was a random dot motion discrimination task (Fig.1b). Each trial began with a fixation cross appearing in the middle of the screen for 500 ms, followed by the stimulus, the duration of which was 400 ms. After each trial participants were asked to respond by pressing the left arrow or the right arrow key to indicate the perceived global direction of motion. After collecting this response, participants were asked to select the confidence level associated with the direction of motion decision using a discrete scale (1: totally uncertain, 2: uncertain, 3: quite certain, 4: totally certain). Participants had to press keyboard button corresponding to their confidence judgment (Fig.1a). A task block consisted of 200 trials: 10 trials x 2 directions (left/right-ward coherent direction of motion) x 10 coherence levels. Each session consisted of 3 blocks, for a total of 600 trials and it lasted approximately 18 minutes.

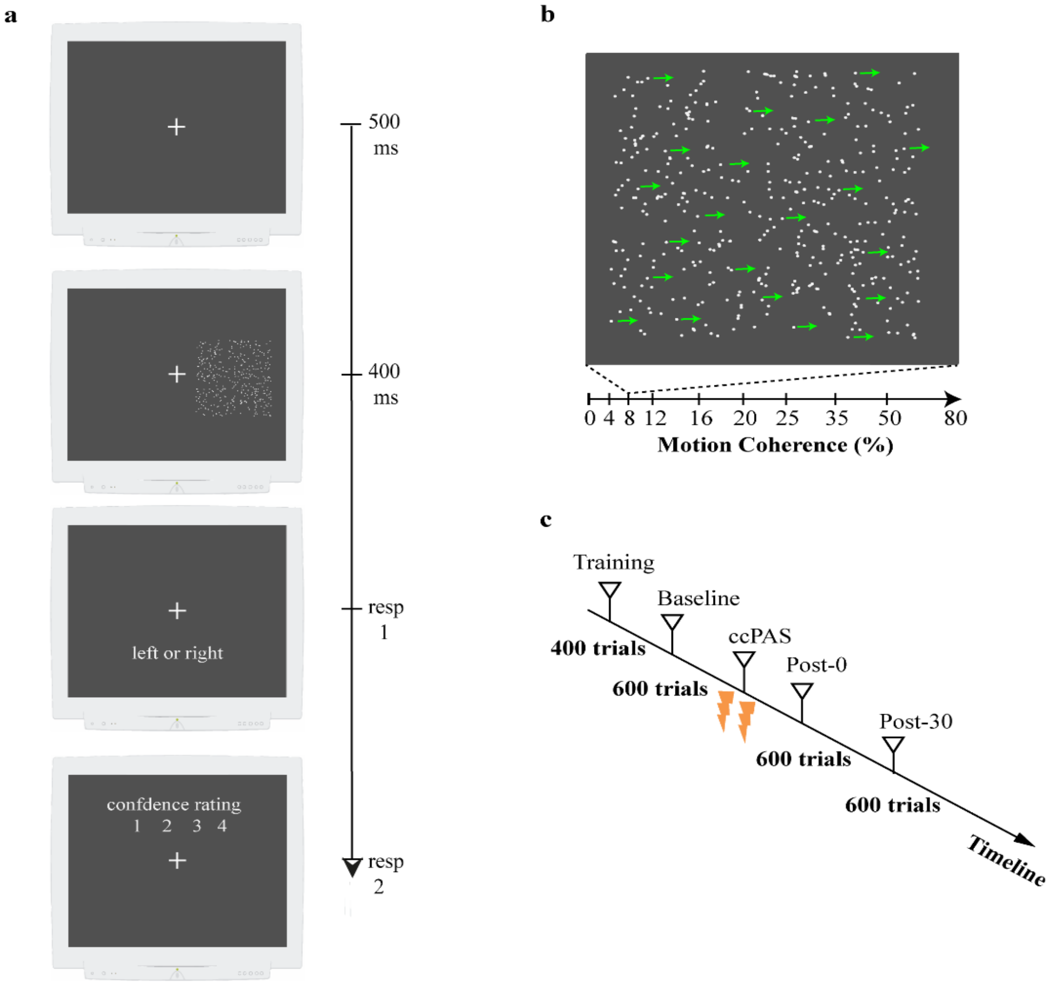


Figure 1. (a). *Task sequence. Each trial started with a fixation cross displayed for 500 ms followed by a dot motion stimulus displayed for 400 ms, presented on the right side of the cross. Participants were requested to press a response key immediately after the offset of the stimulus, by selecting the coherent motion perceived (e.g., leftward or rightward) and subsequently to report their confidence by pressing the respective numeric keys (e.g. 1,2,3,4). No time-out was present for both responses.* ***(b).*** *Stimuli. The motion coherence of the stimulus varied across trials (ranging from 0% up to 80%, across ten levels); here a schematic representation of a stimulus with 8% of dots moving rightward.* ***(c)****. Experiment timeline. For each participant, the experiment began with a training session of 2 blocks, performed to allows the participant to reach a stable performance level before the actual experiment. This preliminary phase was followed by a baseline session (BSL). After the BSL measurement, participants were randomly assigned to one of two ccPAS conditions. Participants had to perform the same task immediately (T0), and 30 (T30) minutes following the ccPAS protocol. One session consisted of three blocks of 200 trials each.*

General procedure.

The experiment was a between-subject design carried out in separate sessions. Participants were randomly assigned to two different groups according to the Transcranial Magnetic Stimulation (TMS) protocol they would undergo. After having familiarized themselves with the task and achieving a stable performance on the motion task in a training session, participants performed their baseline session (BSL) before undergoing their assigned TMS protocol. Participants performed the motion direction discrimination task again, immediately (T0) and 30 (T30) minutes after the stimulation (Fig.1c).

ccPAS protocol

Cortico-cortical Paired Associative Stimulation (ccPAS) was delivered by means of two 50 mm figure-of-eight coils, connected to a Magstim dual pulse monophasic stimulator (Magstim Company, Whitland). 90 pairs of stimuli were continuously delivered at a rate of 0.1 Hz for ~15 min, each pair of stimuli consisted of two monophasic transcranial magnetic pulses (Stefan et al., 2000). The pulses were triggered remotely using a Matlab interface that controlled both stimulators. In every condition, intensity of TMS was set at 60% of the maximum stimulator output (Pitcher et al., 2007; Silvanto et al., 2007; Silvanto, Lavie, et al., 2005). A neuronavigation software (SofTaxic, E.M.S., Bologna, Italy) combined with a 3D optical digitizer (Polaris Vicra, NDI, Waterloo, Canada) was used to control the consistency of EEG scalp position with the mean MNI coordinates of the involved cortical site. The SofTaxic software estimated the volume of magnetic resonance images of the participant's head by means of a warping procedure, on the basis of the participant's skull landmarks (nasion, inion, and two preauricular points) and a set of 65 points providing a uniform representation of the scalp. The ccPAS protocol was manipulated in the 3 different groups of participants, stimulating the V5/MT+-V1/V2 and the IPS-V1/V2 network respectively (Fig.2).

ccPAS condition V5/MT+-to-V1/V2 (Exp$_{V5\text{-}V1}$).

Left V5/MT+ and central V1/V2 were stimulated using established procedures (Chiappini et al., 2018; Romei, Chiappini, Hibbard, & Avenanti, 2016). To target left V5/MT+, the coil was centred 3 cm dorsal and 5 cm lateral to the inion, corresponding to the average functionally localized scalp position where perception of moving phosphenes and disruption of motion perception can be elicited by TMS (Silvanto & Muggleton, 2008). The coil was held tangentially to the scalp with the handle pointing upwards and laterally at 45° angle to the sagittal plane. To target V1/V2, the coil was centred 2 cm dorsal to the inion, corresponding to the scalp position where phosphenes in the centre of the visual field are typically elicited. The handle was held tangentially to the scalp and pointed downwards at an angle of 120° clockwise. On each pair, the first TMS pulse was delivered to left V5/MT+ followed by another pulse, delivered over V1/V2 with an ISI of 20 ms. This ISI was selected in accordance with the average timing of V5/MT+-V1/V2 interactions reported by Pascual-Leone & Walsh (2001) and Silvanto and colleagues (2005) and corresponds to the optimal timing at which V5/MT+ exerts a physiological effect on V1/V2 (Pascual-Leone & Walsh, 2001; Silvanto, Lavie, et al., 2005). This ISI was critical to repeatedly activate presynaptic and postsynaptic neurons in re-entrant V5/MT+-V1/V2 connections in a way that is consistent with spike timing-dependent plasticity (STDP), i.e., a form of synaptic plasticity meeting the Hebbian principle and predicting that synapses are potentiated if the presynaptic neuron fires repeatedly before the postsynaptic neuron. Thus, ccPAS in the Exp$_{V5\text{-}V1}$ was aimed at strengthening re-entrant connections from V5/MT+ to V1/V2 in order to affect accuracy.

ccPAS condition IPS/LIP-to-V1/V2 (Exp$_{IPS\text{-}V1}$).

The first pulse was delivered to the left IPS/LIP area followed by another pulse, delivered over V1/V2. Considering that we want to stimulate the human homolog of the LIP area, anatomical and functional studies suggest that IPS is the critical area for this purpose (Connolly et al., 2002; Schluppeck et al., 2005; Sereno et al., 2001). For this reason, we selected as a proxy for the stimulation site the P3 EEG coordinate (International system 10-20), because it was coincident with the spatial positioning of IPS/LIP according to previous studies (Bagattini et al., 2015; Mazzi et al., 2014; Tapia & Beck, 2014). V1/V2 was targeted as in the other experimental group. Temporal sequence of stimulation was set to 30ms, in accordance with the average timing of interaction at which IPS/LIP exerts a physiological effect on V1/V2 (Parks et al., 2015; Silvanto et al., 2009). This ISI adopted in Exp$_{IPS\text{-}V1}$ was thus critical to enhance re-entrant IPS/LIP-to-V1/V2 connections according to STDP (Hebb, 1949).

ccPAS control condition IPS/LIP--V1/V2 (Ctrl$_{IPS\text{-}V1}$).

In this stimulation group, the target areas were the same as in the IPS V1 group, with the difference that the pulses were released on both areas simultaneously (ISI = 0). In accordance with Hebbian principles (1949), synapses require temporally causal activation, so in the circumstance in which two neurons are activated at the same time, the precondition for establishing a connection is not satisfied. According to our hypothesis, the modulation of connectivity should have manifested itself selectively through a temporal order of interaction between the areas, simulating STDP phenomena (Caporale & Dan, 2008). Consequently, this protocol was found to be necessary to assess whether any changes obtained at the behavioural level were nonspecifically generated by the perturbation of activity in the parieto-occipital system.

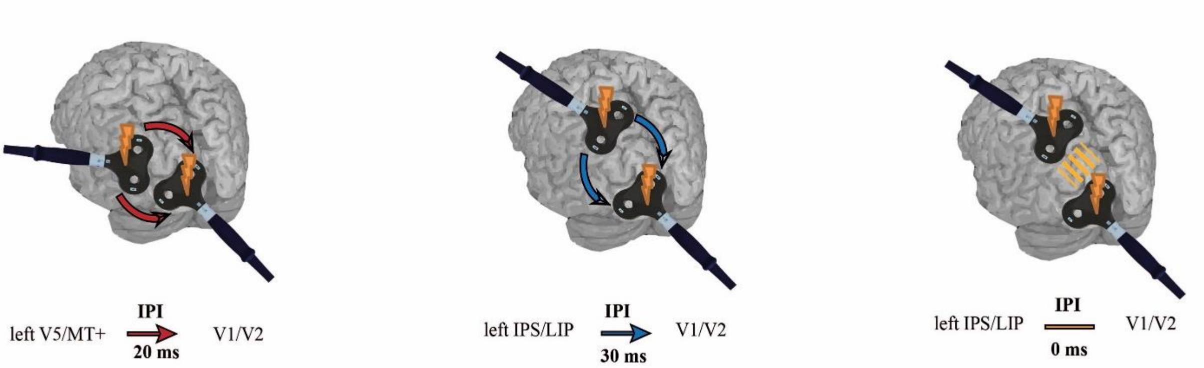


Figure 2. *ccPAS protocols. The stimulation lasted 15 minutes, and consisted of 90 paired pulses at fixed intensity (60% of TMS max output). The parameters and cortical target varied relative to the pathway involved. In particular, the Inter-Pulse Interval (IPI) between stimulated areas was set to 20ms for Exp$_{V5\text{-}V1}$,; 30ms for Exp$_{IPS\text{-}V1}$ and 0ms for Ctrl$_{IPS\text{-}V1}$.*

Data Analysis

Motion sensitivity threshold. Discrimination performances collected through the task were plotted on a cartesian plane with the X axis representing the motion coherence and the Y axis the percentage of accuracy (Fig.3). Data distribution described a psychophysical curve having a sigmoidal shape roughly ranging between 50 (at 0% of motion coherence; guessing rate) and 100% (at 80% of motion coherence) of accuracy. Therefore, data were well fitted by a nonlinear function modelled on the logistic curve:

$$y = \frac{1}{2}\left(1 + \frac{a}{1 + e^{-\frac{x-b}{c}}}\right)$$

where “a” determines the value of the upper horizontal asymptote; “b” represents the value of the point of critical change in the function behaviour at half the way between the lower and the upper asymptotes, named the inflection point of the curve; “c” defines the slope. For each participant, all parameters of the curve for each block were calculated using MATLAB (version 2019b, the MathWorks, Natick, MA), applying the Levenberg-Marquardt algorithm. By solving the equation, we defined the exact value representing the motion sensitivity threshold as the coherence level at which the direction was correctly perceived 75% of the times. This was intended as the percentage of coherent motion that mathematically described the change in the global motion perception. Shifts in motion sensitivity threshold were baseline-corrected such that the values obtained in the performance at each time after the stimulation were subtracted from the value obtained in the performance at baseline. In this way, any negative value reflected enhancement in performance, while positive values reflected reduction in performance, compared to baseline values. The value of the R^2 was calculated to verify the goodness of fit of individual’s data-points to the logistic curve (Tab1).

Metacognition. As a measure of the relative perceptual awareness about the response on the direction of the stimulus we estimated the metacognitive efficiency, which represents the optimality with which confidence ratings discriminate between ‘correct’ and ‘incorrect’ trials, while controlling for differences in perceptual sensitivity (Fleming & Daw, 2017; Maniscalco & Lau, 2012). It was adopted a single-subject Bayesian estimation approach, which is more robust to low trial numbers and does not use correction for missing cases relatively to previous implementation of meta-d’ (Fleming, 2017). We considered the metacognitive efficiency scores (i.e., meta-d’- d’) a reliable measure of second-order performance since they are not biased by differences in perceptual sensitivity between condition as meta-d’ per se (Beck et al., 2019). After obtaining these estimates, performance change was obtained by subtracting the baseline values from the post-stimulation sessions, resulting in positive values for metacognitive gain and negative ones for metacognition reduction. Eventually we analyzed metacognitive performance at threshold level by considering, for each participant in each session, the mean values of metacognitive efficiency of the two coherence levels containing the actual motion sensitivity threshold (e.g., for a motion threshold of ~9%, the resulting metacognition was averaged from the 8 and 12% coherence levels).

Statistical tests. To assess the effect of the ccPAS condition on discrimination performance at the coherent motion task, a repeated measure ANOVA with Targeted Network ($\mathrm{Exp}_{V5\text{-}V1}$; $\mathrm{Exp}_{IPS\text{-}V1}$) as between subject factor, and Time (T0, T30) as within subject factor was performed on baseline-corrected motion threshold. To evaluate the effect of the ccPAS on metacognition, a repeated-measure ANOVA including the Targeted Network ($\mathrm{Exp}_{V5\text{-}V1}$; $\mathrm{Exp}_{IPS\text{-}V1}$) as a between subject factor, and Time (T0, T30) as within subject factors was performed on baseline-corrected metacognitive efficiency (i.e., dependent variable). Bonferroni-Holm corrected T-test were performed to compare condition of main interests.

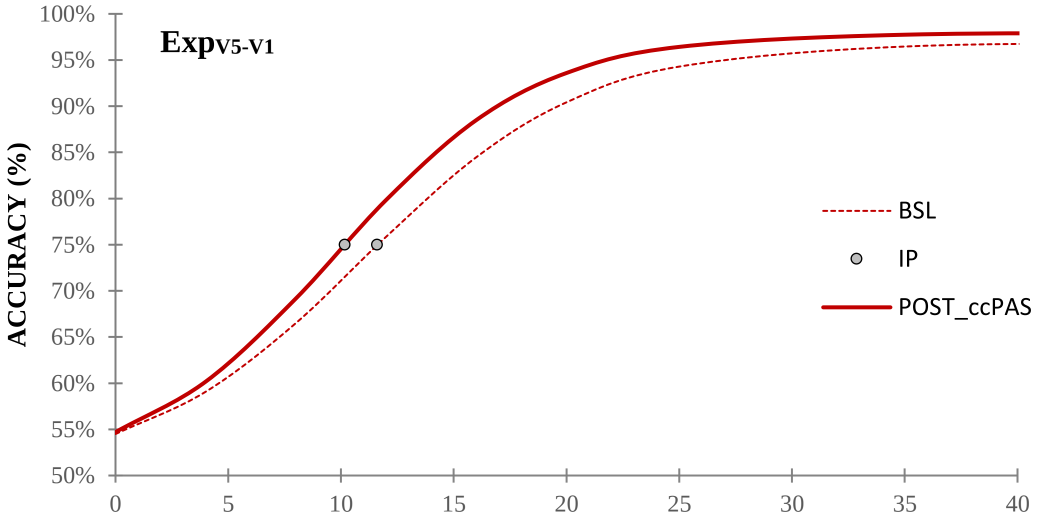
In all analyses, effect sizes were estimated by Cohen's d or ηp2. All data distributions were subjected to visual inspection to assess normality. All frequentist analyses were implemented using STATISTICA v.12.

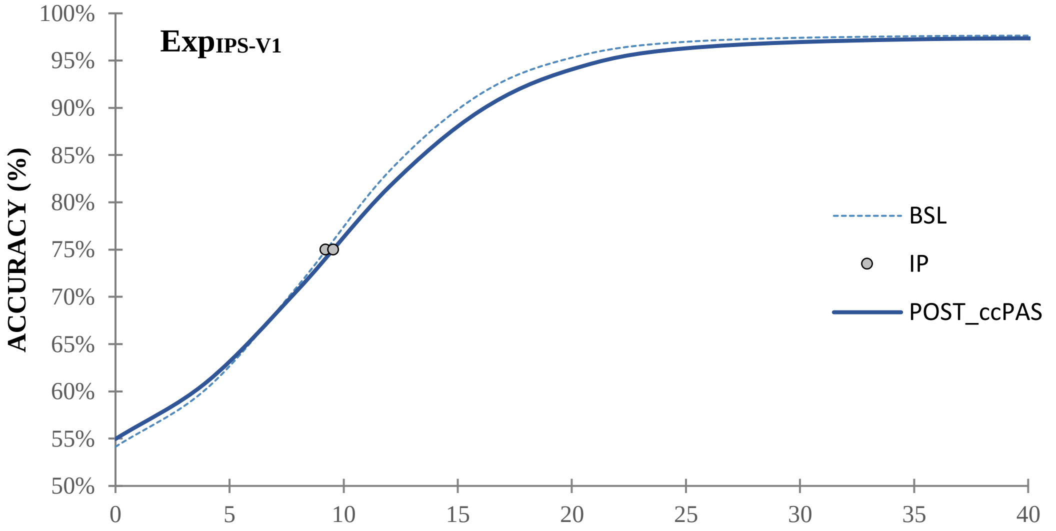
Bayesian repeated measure ANOVAs were implemented in the main analyses for sensitivity and metacognition, to evaluate the strengths of evidence for the null and alternative hypothesis by computing the model-averaged results. The inclusion Bayes factor (i.e., $BF_{inclusion)}$ for matched models was estimated. This quantifies the change from prior inclusion odds to posterior inclusion odds and can be interpreted as the evidence in the data for including a predictor in a model (Van Den Bergh et al., 2020). Bayesian one-sample T-test were additionally performed on averaged baseline-corrected values for sensitivity and confidence, comparing the null model H0, which posits that the effect size δ is zero, to the alternative hypothesis H1 (Wagenmakers et al., 2018). The Bayes factor was obtained by setting default t-prior (van Doorn et al., 2020). All Bayesian analysis were implemented by the JASP software (JASP Team, 2020).

Results

Motion Sensitivity

The ANOVA on bsl-corrected motion sensitivity values including all stimulation groups (Exp $_{V5\text{-}V1}$;Exp $_{IPS\text{-}V1}$;Ctrl$_{IPS\text{-}V1}$) and sessions (T0; T30) returned a Main effect of Targeted Network (F1,48=6.51; p= .003; np2= .21). Post-hoc tests showed that only Exp $_{V5\text{-}V1}$ differed in performance from Exp $_{IPS\text{-}V1}$ (p = .001) and from Ctrl$_{IPS\text{-}V1}$ (p = .02). Bonferroni-Holm corrected t-test on post ccPAS changes confirmed the significant motion threshold reduction following Exp$_{V5\text{-}V1}$ (AVG T0+T30: Mean= -1.85; SEM=.58; p = .02; cohen's d = -.77), without any modulation for Exp $_{IPS\text{-}V1}$ (AVG T0+T30: Mean= .88; SEM=.57; p = .28; cohen's d = .38) and Ctrl$_{IPS\text{-}V1}$ (AVG T0+T30: Mean= -.01; SEM=.48; p = .97; cohen's d = -.008) (Fig.4).


Exp$_{V5-V1}$
ACCURACY (%)
100%
95%
90%
85%
80%
75%
70%
65%
60%
55%
50%
0
5
10
15
20
25
30
35
40
BSL
IP
POST_ccPAS


Exp$_{IPS-V1}$
ACCURACY (%)
100%
95%
90%
85%
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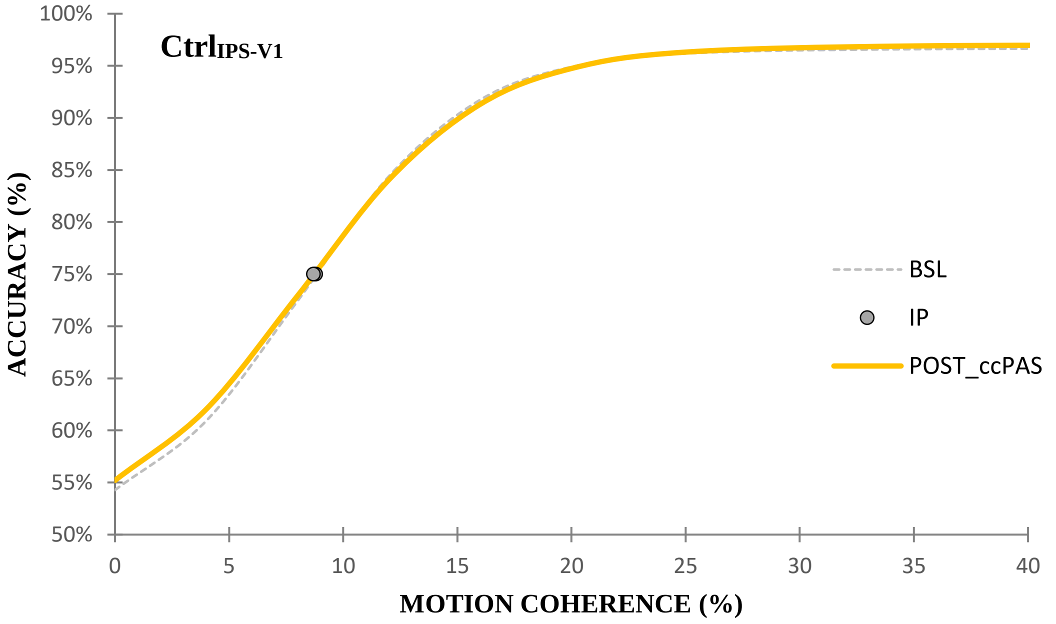

Ctrl$_{IPS-V1}$
ACCURACY (%)
100%
95%
90%
85%
80%
75%
70%
65%
60%
55%
50%
0
5
10
15
20
25
30
35
40
MOTION COHERENCE (%)
BSL
IP
POST_ccPAS

Figure 3. *Psychometric Curves. Fitted data modeled on the logistic function to obtain the perceptual thresholds of motion discrimination. The group performance are separately plotted depending on the type of stimulation (top panel, in red Exp*$_{V5\text{-}V1}$*; middle panel, in blue Exp*$_{IPS\text{-}V1}$ *;bottom panel, in yellow Ctrl*$_{IPS\text{-}V1}$*) and as a function of the session. The dotted lines represent the baseline session (BSL), while the solid lines represent the sessions following the ccPAS (e.g., POST_ccPAS, collapsing T0 and T30 sessions). Grey dots depict the inflection points (IP) coincident with the percentage of coherent motion where the logistic function had a value of 75% of correct responses.*

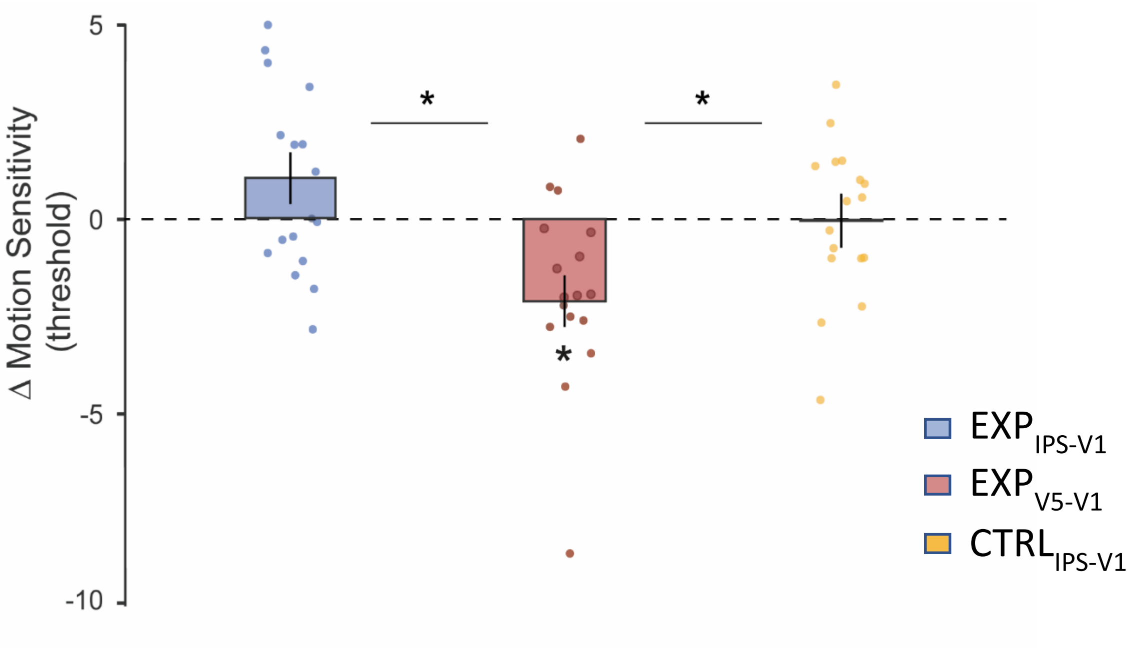


Figure 4. *Motion threshold following stimulation. Filled bars represent the mean change Δ in sensitivity threshold (e.g., differences between Post ccPAS and BSL) and error bars represent the s.e.m. Individual data points are plotted by scattered dots. Asterisks point out significance (*p < .05) for Exp*$_{V5\text{-}V1}$ *mean and between group means.*

Metacognitive Efficiency

On the other hand, the corresponding ANOVA 3x2 (Targeted Network x Time) considering the bsl-corrected metacognitive efficiency score, showed a Main effect of targeted network (F(1,48)= 3.32; p= .04; np2= .12). Post-hoc tests evidenced that Exp $_{IPS\text{-}V1}$ significantly differed from Exp $_{V5\text{-}V1}$ (p=.03) and from Ctrl$_{IPS\text{-}V1}$ (p=.04). Bonferroni-Holm corrected t-test on post ccPAS changes confirmed that a significant improvement in metacognitive efficiency was caused by the stimulation in Exp $_{IPS\text{-}V1}$ (AVG T0+T30: Mean= .46; SEM=.14; p = .01; cohen's d = .79), and was absent for Exp $_{V5\text{-}V1}$ (AVG T0+T30: Mean= -.02; SEM=.14; p = .89; cohen's d = -.03), and for Ctrl$_{IPS\text{-}V1}$ (AVG T0+T30: Mean= .02 ; SEM= .16; p = 1; cohen's d = .04)(Fig.5).

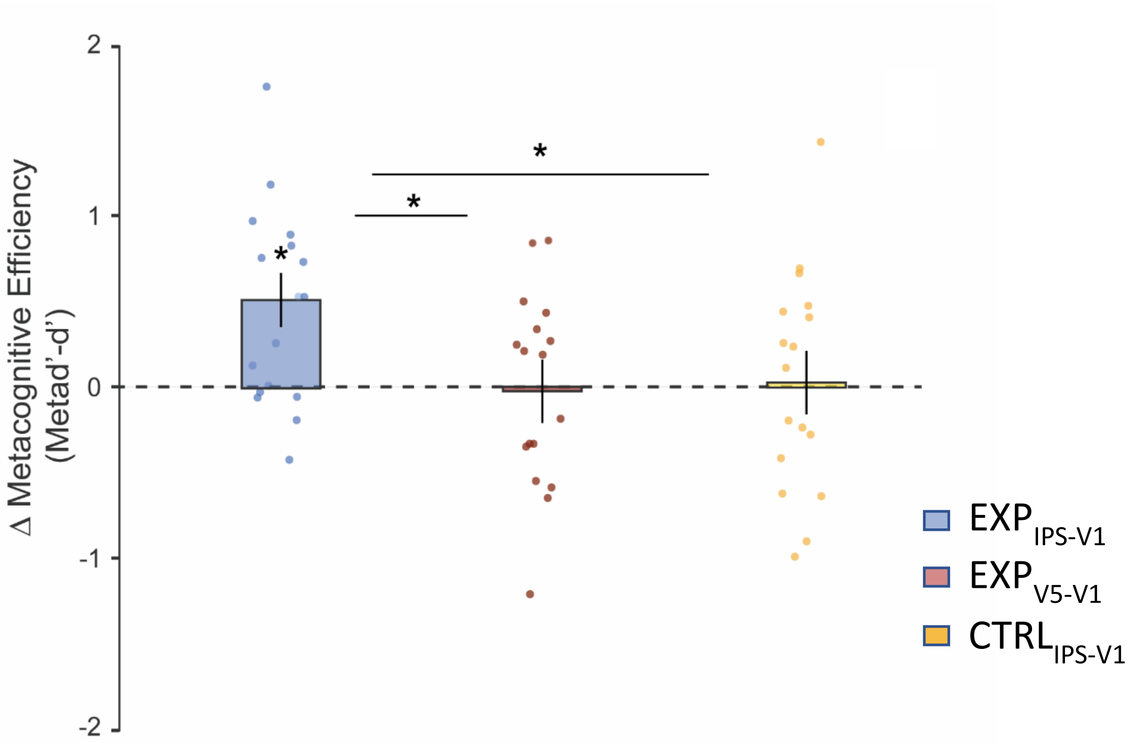


Figure 5. *Metacognitive efficiency following stimulation. Filled bars represent the mean change Δ in metacognition with error bars representing s.e.m. Individual performances are plotted by scattered data points. Asterisks point out significance (*p < .05) for Exp$_{IPS-V1}$ mean and between group means.*

Metacognitive Sensitivity and Bias

The ANOVA 3x2 (Targeted Network x Time) considering the bsl-corrected metacognitive sensitivity showed no significant effect and interactions (Fs < 1.44; ps > .24). Similarly, the Anova 3x2 (Targeted Network x Time) performed on bsl-corrected metacognitive bias (i.e., average confidence levels) did not highlighted any significant effect or interaction (Fs < 1.67; ps > .19). At this point, complementarily to motion sensitivity results, we showed that distinct visual networks can be functionally dissociated when investigating metacognitive functions, in addition to perceptual discrimination performance. These effects cannot be alternatively explained by simple time passing – which in principle might have made participants more confident over time – or any unspecific effect of TMS. Indeed, in a control experiment, a non-specific stimulation of the parieto-occipital stream showed an absence of modulatory effects both in terms of motion sensitivity and metacognitive functions.

Discussion

Our findings provide the first causal evidence of a double dissociation of functional networks orchestrating perceptual decision-making in humans, namely V5/MT+-to-V1/V2, accounting for visual motion discrimination sensitivity, and IPS/LIP-to-V1/V2, accounting for accurate confidence judgments. In line with current opinions (Limbach & Corballis, 2016; Maniscalco et al., 2016) that sensitivity and confidence could be served by partially distinct processes, we reported for the first time that the enhancement of IPS/LIP-to-V1/V2 pathway connectivity selectively affects metacognitive capacity in a functional way, with participants becoming effectively more optimal in rating the quality of their choices. Crucially, we found evidence of a functional segregation of targeted networks. The enhanced metacognitive capacity did not lead to simultaneous increase of motion sensitivity, being this a function subserved by another network. Indeed, V5/MT+-to-V1/V2 ccPAS was critical in increasing motion sensitivity and accuracy, as expected (Chiappini et al., 2018; Romei, Chiappini, Hibbard, & Avenanti, 2016). Moreover, in previous studies we showed the selectivity of this effect (Chiappini et al., 2018; Romei, Chiappini, Hibbard, & Avenanti, 2016) as we found no improvement in perceptual discrimination when the order of stimulation pairs was reversed in a control protocol (i.e., V1-to-V5 ccPAS).

These findings challenge the view that higher perceptual accuracy, as the one induced by V5/MT+-to-V1/V2 ccPAS, may produce a modulation of metacognitive functions due to a finer discrimination of the stimuli, as assumed by a model where perceptual decision and confidence are based on a common underlying sensory information (Fetsch et al., 2014; Ratcliff & Starns, 2013). This interpretation would not explain why V5/MT+-to-V1/V2 ccPAS does not lead to enhanced metacognitive efficiency. Instead, it supports the notion that confidence generation and perceptual sensitivity are supported by independent mechanisms (De Martino et al., 2012; Jang et al., 2012; Rahnev et al., 2016).

In fact, increasing connectivity of IPS/LIP-to-V1/V2 improves metacognitive ability without impacting motion sensitivity. Consistently to what had already been demonstrated for the V5/MT+-to-V1/V2 network, here the effect was conditional to the causal order of the pulses, since no outcome could be observed when controlling for timing. This result, taken together with previous findings reporting the selective manipulations of confidence without affecting accuracy (Bang et al., 2019; Boldt et al., 2017; Peters, Thesen, et al., 2017; Wokke et al., 2017), is in line with the proposal which considers metacognition as a distinct functional process (Bang et al., 2019; Fleming & Daw, 2017; Maniscalco & Lau, 2012). This implies a system where the actual computations that underlie these two processes may be sustained by distinct neural circuits (Yeon et al., 2020). By taking into account the evidence that early visual areas and higher-order regions constitute a recurrent feedback system (Gilbert & Li, 2013), we hypothesize the existence of a hierarchical Bayesian architecture in which looping iterations perform near-optimal computations (Bach & Dolan, 2012; Summerfield & de Lange, 2014). The parietal node may serve a higher order supervisory function feeding back lower-level areas and thus integrating recursive information across the hierarchy. For example, comparing the expected sensory signal as computed in V5/MT+ (motion direction) with the effective signal update recorded in early visual areas (actual stimulus position) may provide a near-optimal mechanism modulating confidence levels depending on the match between expected and actual sensory signal in V1/V2 (Murphy et al., 2021; Wimmer et al., 2015). Perfect match computation prompts maximum confidence and vice-versa. Recursive feedback connections between IPS/LIP and V1/V2 would then promote the metacognitive awareness associated with the task.

It should be noted that a previous attempt of active manipulation in posterior parietal cortices by means of TMS failed to trace any effect on metacognitive functionality (Bor et al., 2017). This outcome was presumably due to a different cortical site location and a distinct stimulation paradigm employed relative to ours. Nevertheless, the potential of TMS at dissociating choice component of accuracy and confidence has been proven extensively in other works, mainly involving the causal manipulation of the prefrontal cortex (Fleming et al., 2015; D. Rahnev et al., 2013) and early visual areas (Hurme et al., 2017; D. A. Rahnev et al., 2012). Here, we provide for the first time evidence for the causal involvement of the functional pathway from parietal to early visual areas in metacognitive processes.

In conclusion, we functionally dissociate the role of V5/MT+-to-V1/V2 and IPS/LIP-to-V1/V2 back-projections in perceptual decision processes by showing selective modulation of perceptual sensitivity through signal amplification by V5/MT+-to-V1/V2 back-projections and metacognitive efficiency through signal supervision by IPS/LIP-to-V1/V2 back-projections speaking in favor of distinct but integrated systems subserving near-optimal perceptual decision processes in humans.

GENERAL DISCUSSION

The optimal communication between the hubs of a brain network is crucial for transmitting relevant data to be processed as well as for convey modulatory signals for fine-tuning cortical operations. The purpose of the investigation outlined above sought to bring a detailed understanding of the neural pathways that subserve ordinary cognitive mechanisms that are important for human behavioural functioning. This was achieved primarily by means of non-invasive brain stimulation (NIBS) specific protocol named cortico-cortical paired associative stimulation (ccPAS), an approach built on the plastic properties of the brain. Significantly, ccPAS is an innovative TMS technique useful in establishing associative plasticity phenomena over the targeted cortical areas, which has been implemented throughout the course of the experiments proposed in this dissertation. The brain, like other sophisticated architectures, features an extensive set of dynamic activity and communication patterns which are considered to be critical for facilitating the integration and analysis of information during behaviour and cognition. Whenever humans observe visual events, the activation of parallel counterstreams of computation take place, resulting in a percept capturing the ensemble of functional states of all regions in the visual system network. Within the visual system, perception emerges through a complex integration that implies a bidirectional exchange of information between the areas considered "low level" and those located upwards, according to a caudal-a-rostral order, defined as "high level". According to a growing body of theories, the early visual cortex (EVC) would not uniquely represent a gateway for visual input, but might be necessary and actively involved in the construction of the percept and its awareness (Ahissar & Hochstein, 2004; Froudarakis et al., 2019; Juan & Walsh, 2003). This seem to be allowed by a reciprocal wiring with the most advanced areas, which are more specialized on particular stimuli and processes, through re-entrant connectivity (Markov et al., 2014; Muckli & Petro, 2013). Specifically, there would exist distinct visual processing pathways, consisting of feedforward and feedback channels, functionally segregated according to the domain of processed stimuli. Indeed, EVC gathers several fibers from several areas (Felleman & Van Essen, 1991; Pan et al., 2021; Pascual-Leone & Walsh, 2001); findings supported by further evidence of neural activations of early visual areas due to top-down feedback mechanisms (Koivisto et al., 2017; Kok et al., 2013; Wyatte et al., 2014), suggesting the importance of these connections in perceptual processes. In the present thesis were investigated reentrant networks of the extended visual system that is distributed on the lateral surface of the brain, and the *fil rouge* of the studies regarded the characterization of the potential behavioural outcomes arising from the causative modulation of these reentrant networks, through ccPAS protocols.

In the first two chapters, the topic of investigation concerned the study of the long-range network that is believed to reflect the social pathway of the brain, which extends from the occipital cortex to the posterior region of the superior temporal sulcus (pSTS) (Pitcher & Ungerleider, 2021). This processing route is primarily involved in the perception of the dynamic aspects of the face (Pitcher, Dilks, et al., 2011; Sliwinska, Bearpark, et al., 2020), and recently has emerged that there might be a computation pattern that does not follow a strict hierarchy with rigid order, but rather a reciprocal interactive process with nodes that work in parallel and iteratively (Duchaine & Yovel, 2015; Grimaldi et al., 2016). As a first experimental step (Chapter I), the communication profile between the pSTS area and the early visual cortex was explored, through the combination of TMS-EEG. This neurophysiological evidence allowed to causally trace the activity induced in the V1 / V2 areas by the activation of pSTS, highlighting the specific temporal dynamics critical for establishing the plasticity induction protocol through ccPAS. Through experiments 2-4, it was possible to demonstrate that the temporal profile obtained from the physiological correlates was functionally crucial for establishing behavioural modifications in the perception of emotional expression. Starting from the specific implication of this network in the elaboration of these expressive aspects of the face (Schobert et al., 2018), it has been proved that the increase in temporal-occipital backward connectivity, according to a precise causal order of stimulation of the sites involved, is fundamental in favoring the perception of these stimuli. Moreover, this effect was selective, considering that by reversing the order, using other timings or adopting different stimuli, no behavioural changes occurred. This supports the view that reentrant connectivity from higher-order to early visual areas subserves integrative visual functions (Koivisto & Revonsuo, 2010; Lamme et al., 1998; Silvanto, Cowey, et al., 2005; Silvanto, Lavie, et al., 2005; Wyatte et al., 2014).

In the subsequent study (Chapter II), the investigation of the temporo-occipital pathway between pSTS and EVC was pursued. Bearing in mind that the class of stimuli that are primarily encoded in this network are those with dynamic and variable properties (Foley et al., 2012; Pitcher, Dilks, et al., 2011); once having reported and confirmed the involvement of the pSTS-V1/V2 route in defining the perception of emotionally expressive faces, it was explored whether the modulation of the aforementioned connectivity had an impact on the processing of the human gaze. Previously, considerable research has adequately shown that the pSTS area plays an important role as a neural substrate for the processing of gaze and orientation mechanisms in response to its movements (Dasgupta et al., 2017; Ethofer et al., 2011; Lockhofen et al., 2014). For this reason, in this experiment we took advantage of the communication parameters of the previous study to set up a further ccPAS paradigm and investigate the effects on the elaboration of the ocular region, in particular the phenomenon of gaze cueing (Bayliss & Tipper, 2005; Greene et al., 2009). Similar to findings on the previous report, the facilitation of the functionality of the temporo-occipital network has generated a specific modulation of the perceptive processes related to the observation of the gaze, even if in a particular way according to the type of stimuli (see Chapter II). What should be highlighted, however, is that the effect on gaze cueing behaviour was evident only in the case of causal stimulation of the reentering network and not in the conditions in which the pathway was stimulated in reverse order, simultaneously, or in a fictitious way.

In the third chapter of the thesis, the research focus has shifted to another distributed network that can be partially overlapped with the canonical dorsal occipito-parietal visual processing pathway, and which is involved in the most low-level perceptual decision-making processes. As far as this system is concerned, the main areas that have emerged as fundamental and most important are the V5 / MT+, IPS / LIP regions (Ding & Gold, 2012; Gold & Shadlen, 2007; Hanks & Summerfield, 2017). The experimental evidence regarding the reciprocal connectivity between these nodes is extensive, in fact there is evidence of the existence of feedback influences on the EVC deriving from the V5 (Rockland & Knutson, 2000; Silvanto, Cowey, et al., 2005) and IPS (Kanai et al., 2008; Parks et al., 2015) regions, and how they have a possible role in perceptual and fine-tuning mechanisms (Koivisto et al., 2014; Pascual-Leone & Walsh, 2001). A crucial proof about the functionality of these connections was recently reported by Romei and colleagues through the ccPAS protocol (Romei, Chiappini, Hibbard, & Avenanti, 2016), in which the stimulation of the reentrant pathway V5-V1 allowed to increase the perceptual sensitivity to motion during the observation of kinematograms; supported by a subsequent follow-up in which the potential of the protocol on this network was also seen through state-dependent (Chiappini et al., 2018) mechanisms. These latter studies provided the solid starting point on which to set the study in Chapter III, in which the reentrant connectivity originating from V5 and IPS and targeting EVC were investigated. Following a dissociative strategy, we examined different aspects of perceptual decision-making processes and how they could be modulated according to the specific pathway stimulated via ccPAS. Overall, the induction of plasticity on both networks caused behavioural consequences attributable to the strengthening of the connections, confirming the efficacy of this stimulatory protocol. importantly, it has been shown that such networks can be causally and functionally dissociated depending on the role they play in the perceptual decision process, given that the increase in the effectiveness of V5-V1 influences objective and sensory aspects of the decision while for IPS-V1 the subjective and metacognitive components of the choice are influenced. Therefore, on the one hand the V5-V1 feedback fibers are confirmed as crucial in the fine processing mechanisms of the global motion, increasing the awareness of the percept. While, an innovative aspect suggests the involvement of the reentering IPS-V1 fibers in second order decision-making processes related to metacognition, without specific involvement in the sensory processing of stimuli in motion.

In addition to the main studies exposed in the discussion, in the appendix there are supplementary experiments involving NIBS in which some aspects investigated during the thesis have been further explored. In particular, an exploratory study has been reported in Appendix A in which the involvement of the reentrant connectivity pSTS-V1 in the phenomenon of gaze cueing has been expanded. Given that the detection of the gaze elicits both cover and overt (Friesen & Kingstone, 2003) automatic orientation mechanisms, and given that the stimulation of the temporal-occipital pathway causes alterations on the perceptual salience of that stimulus, thus altering gaze cueing in covert conditions (chapter II); we have further explored the possible influence of ccPAS on overt gaze behaviour. Although not conclusive, the study demonstrates that the increase in temporal-occipital functionality via ccPAS alters saccadic behaviour in response to gazes, confirming the possible role of this feedback network in favoring the fine processing of dynamic social stimuli such as gaze. With regard to Appendix B, the respective roles of the visual decision-making networks including V5 and IPS have been explored in further depth. Through a paradigm that involved the concurrent use of distinct NIBS protocols useful for establishing transient plasticity phenomena in the targeted substrates (Guidali et al., 2021; Suppa et al., 2016), it was possible to causally test the function of the aforementioned areas and related networks interactively. In this study, the functional dissociation between V5 to V1 and IPS to V1 was confirmed, demonstrating different behavioural consequences depending on the type of stimulation and the neural stream involved. This result corroborates the existing beliefs on the presence of modular cortical systems, that are not strictly hierarchical, that mediate distinct perceptual (V5 to V1) and decisional (IPS to V1) aspects (Desender et al., 2019; Peters, Thesen, et al., 2017).

The research reported in this thesis considerably advances existing prior understanding on cortical connectivity, which is essential for the functional interchange of information among the circuits engaged in visual social stimuli perception and sensory decision-making. These findings provide evidence to the assumption that V1 might express two languages (Muckli and Petro, 2013). It not merely acts as a primary stage of sensory visual input computation, responding to low-level properties, but it also collects feedback from several regions of the cortex. These signals may be used to complement local processing by furnishing contextual and predictive information. The findings are relevant to the existing literature in the topic and provide a wide range of behavioural data to validate conceptual framework (Kravitz et al., 2013; Lamme et al., 1998; Lee et al., 1998; Vezoli et al., 2021). Furthermore, advances and development on the ccPAS protocols has also been achieved to bring concrete evidence about the implementation and feasibility of this technique.

Prior to the investigations carried out throughout this doctorate research, the effectiveness of this compelling instrument had been mostly assessed on motor-related domains (e.g., Arai et al., 2012; Chao et al., 2015; Johnen et al., 2015), with inconsistent evidence on behavioural outcomes. Conversely, we demonstrated the potential to affect perceptual performance on low-level visual attributes, as well as the processing of complex social stimuli. Importantly, ccPAS was efficiently handed on feedback circuits with functional and anatomical specificity.

Although these reports are intriguing, additional information about the underlying neurophysiological processes of the ccPAS are required to properly characterize the manifestations induced. Nonetheless, proof of functional enhancements on critical visuo-cognitive capacities in humans may result promising for the progress of future neurorehabilitation therapies manipulating network connectivity (Koch, 2020; Rajji, 2019).

APPENDIX A

TEMPORO-OCCIPITAL NEUROSTIMULATION AFFECTS OVERT ORIENTATION IN GAZE CUEING

Introduction

The perception of the eyes, and the associated movements, underlie a set of socio-cognitive abilities that go well beyond mere visual detection (Frischen et al., 2007). In particular, paying attention to the gaze of conspecifics allows us to obtain information that exceeds a purely attentive connotation, thus relating to directional orientation, and so providing useful clues about the mental states of the others (Klein et al., 2009). This modulatory effect that the perception of direct eye contact has on cognitive processing and the immediately subsequent behavioural responses is called the "eye-contact effect" (Senju & Johnson, 2009). In social and natural situations, the ability to infer the attentional focus of other conspecifics from the dynamics of the gaze movements is essential to be adaptive (Capozzi & Ristic, 2018), indeed it was found that gaze stimuli specifically influence various cognitive domains (e.g., Burra et al., 2019; Conty et al., 2016; Hamilton, 2016; Senju & Johnson, 2009). Nonetheless, one of the most well-known effects regards attentional shifting. A typical case is represented by the "gaze-cueing effect" (GCE), which is the predisposition to shift attention towards the spatial position signaled by a task irrelevant face with averted gaze presented at fixation (Friesen & Kingstone, 1998) and stands at the basis of more complex social behaviours, which require the conscious participation of the actors involved. In its classic setting, the gaze-cueing task requires participants to keep their gaze in constant fixation for the entire trial, and so has been largely explored through manual response paradigms which allows to characterize the covert orienting. (Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999; Langton & Bruce, 1999). However, the potential of the gaze has also been studied in relation to overt orienting. Accordingly, the perception of the movement of someone else's gaze signals a shift in the attentional focus and can in turn be used by the observer to redirect their attention to the same position, through a saccade. This reflexive orientation may also occur when the signal mediated by the gaze is counter-predictive with respect to the appearance of the cue (Pfeiffer et al., 2013) and therefore seems not to be fully under the voluntary control of the individual. Among the first to study overt gaze orienting, Ricciardelli and colleagues (2002) introduced a paradigm that required from the participants the execution of saccades following instructive cues, placed in spatial congruence with distracting stimuli representing averted gaze. The tendency to make a saccade in the direction indicated by the observed gaze, can be stronger than that elicited by the instruction of the task (Friesen & Kingstone, 2003), so in situations of incongruity, and, moreover, the cueing effect linked to the eyes is stronger than that due to symbolic cues such as arrows (Ricciardelli, Bricolo, et al., 2002). Usually, more accurate and faster saccades emerge when the gaze and the direction cue indicate the same spatial location as compared with the condition in which the two cues indicate different spatial locations (see also, Kuhn & Benson, 2007). This suggests a spontaneous, overt gaze following behaviour, even when eye-gaze stimuli are task-irrelevant. Our ordinary social interactions, on the other hand, are marked by a heavy usage of eye movements, which we use to keep track of the many stimuli offered by our conspecifics (Pfeiffer et al., 2013). As a consequence, compared to standard manual response tasks, an experimental technique built on overt oculomotor tasks provides a superior ecological validity. Furthermore, compared to manual response time used in covert attention investigations, which reflect the final outcome of several processing steps, oculomotor measures are a more straightforward index of attentional allocation over space. The manipulation of the presentation interval between the distractor cue and the instruction also made it possible to evaluate which is the critical interval in which this cueing effect linked to the gaze is greatest. Studies have highlighted a time window, i.e. SOAs between -150ms and 150ms, in which it is possible to detect strong gaze-related cueing effects, which denote a tendency in the subject to involuntarily prepare the motor program of the saccade in response to the distractor (Crostella et al., 2009; Ricciardelli et al., 2013). In line with the effects of task-irrelevant social variables on social orienting, which tend to be early-rising and short-lasting (Dalmaso et al., 2014, 2017; Dalmaso, Galfano, et al., 2015; Jones et al., 2010).

Although oculomotor control is believed to play a different role in overt and covert orienting, they both rely on similar brain networks (e.g., Corbetta et al., 1998). Further studies have confirmed that observing a shift in the gaze of others automatically evokes a similar motor response in the observer (Farroni et al., 2003) and, moreover, a strong overlap of neural activity during the execution and observation of eye movements (Grosbras et al., 2005), denoting the presence of a motor mirroring system similar to that previously observed for grasping and reaching actions (Di Pellegrino et al., 1992). It has been previously reported by several fMRI investigations that an essential circuitry accountable for gaze-following exists (Puce et al., 1998; Allison et al., 2000; Hoffman and Haxby, 2000; Pelphrey et al., 2003, 2004; Materna et al., 2008) which relies on a circumscribed region in the posterior superior temporal sulcus (pSTS), adjacent to the middle and superior temporal gyri. This region of pSTS has been found to play a role in encoding dynamic features of faces such facial expression and face orientation, the latter of which is crucial for gaze-following (Puce et al., 1998; Wicker et al., 1998). Importantly, the system appears to be lateralized, since functional activation has been traced mainly in the right hemisphere (Pelphrey et al. 2004; Pitcher, 2011; Burra et al., 2017); this is confirmed by neuropsychological studies adopting facial cuing, which reported that gaze direction was dominantly processed in the right hemisphere (Akiyama, Kato, Muramatsu, Saito, Nakachi, et al., 2006; Okada et al., 2006; Ricciardelli, Ro, et al., 2002). Moreover, inhibitory TMS delivered to the right pSTS is capable of reducing visual orienting to eye regions (Saitovitch et al., 2016), in a manner that led participants to focus less on the eyes of the stimuli presented, relative to baseline levels or in respect to stimulation of the left pSTS counterpart. This indicates that the right pSTS plays a causal role in eye gaze overt mechanisms, consistently with related neuroimaging evidence (Marquardt et al., 2017).

We also recall that, at the anatomical level, the superior temporal area is widely connected to the early visual regions for the visual processing of stimuli. In particular, there is evidence of how the visual pathway that runs from the striate cortices to the temporal lobe is arranged by a complex network of both reciprocal and non-reciprocal feedback and feedforward connections (Markov et al., 2011; Markov et al., 2014), with the occurrence of projections that bypass the intermediate areas, facilitating a rapid and direct communication between distant areas (Kravitz et al., 2013). Indeed, the primary visual cortex (V1) and STS exhibit bidirectional connections highlighted in studies on non-human primates (Rockland & Van Hoesen, 1994). In line with the idea of a third visual pathway that can allow a processing flow between V1 and STS (Pitcher and Ungerleider 2021).

At this point, considering the information reported and in the light of the previous attempt (Chapter II), the present study aims to explore the involvement of the already investigated temporo-occipital pathway (pSTS-V1) during overt orienting of gaze cueing. For this purpose, we want to examine the behavioural effect of the increased connectivity between pSTS and V1 in the right hemisphere, obtained through cortico-cortical paired associative stimulation (ccPAS). Specifically, this follow-up represents a continuation of the previous experiment (Chapter II), in which the covert mechanisms of gaze cueing were explored. Such attempt highlighted the impact that the ccPAS protocol, targeting reentrant connections between pSTS and V1, had on covert orienting in response to eye movements; demonstrating the role of this circuit in reflexive attentional processes in response to gaze perception. To further investigate the involvement of that reentrant pathway in gaze elaboration, and also question the possible dissociation between covert and overt responses in gaze cueing, a novel paradigm was therefore developed. In an overt cueing task, through the mapping of saccadic movement by means of an eye-tracker device, we were able to evaluate how the increase in connectivity between pSTS and V1, obtained following the ccPAS protocol, influenced the perception and attentional orientation of the participants in response to gaze cues.

Methods

Participants

20 participants voluntarily participated in this study (F = 10, M = 10, mean age ± standard deviation = 25.55 ± 2.19). All participants included in the data analysis have a normal view and no previous experience with the experimental task. Before the start of the test phase, informed consent was collected for participation in the study and for stimulation with TMS,

after explaining the experimental paradigm and remembering the possibility of withdrawing from the study at any time. None of the participants presented exclusion criteria for TMS (Rossi et al., 2009) and no negative effects were detected during and after stimulation. Each step of the process was approved by the local ethics committee.

Stimuli and apparatus

All the experimental tests took place in an isolated room, in semi-dark conditions. The task and the stimuli were viewed on an LCD screen, with a resolution of 1280x1024, at 60Hz. During the carrying out of the task, participants sat on a chair, at a distance of 57cm from the screen, with the head placing on a chin rest and aligned with the centre of the screen, in order to minimize any unintentional movement and maintain the head position throughout the task.

The stimuli used were created ad hoc for the experimental paradigm. In particular, the faces used as distractors were selected from the NimStim database (Tottenham et al, 2009), in order to obtain a set of ten faces (5 men and 5 women) with neutral expression. Subsequently, the photographs of the faces were inscribed in an oval of constant size in order to make them more similar to each other, eliminating hair, neck and ears (Goshen-Gottstein & Ganel, 2000). The resulting images were 8x8.5cm (8 ° x 11 °) in size. In order to recreate the movement of the gaze, the aforementioned faces have been modified using the Photoshop graphic software (version cc 2016, Adobe), generating copies of the same with the eyes diverted to the left and to the right. The other stimuli used are a central fixation point, represented by a circle of size equal to 0.30 ° x0.30 °, and two squares (0.50 ° x0.50 °) of black color, placed on the sides of the dot of fixation at a distance of 10 ° from it, in the right and left visual fields. The preparation and presentation of the task were carried out using the Matlab software (version r2017b, Mathworks).

Eye tracking

The position of the eyes and related movements were binocularly measured on-line, using the three-dimensional CMOS eye-tracking device (Clarke et al., 2002), with a sampling rate of 200Hz, and the relative dedicated Windows software. The Purkinje-Pupil method was used for recording, with a spatial resolution lower than 0.1 °. At the end of each block (120 trials), the calibration of the eye position was repeated, which was useful for off-line analysis. The latter was conducted using the "Iris Pupil Tracker" software (version 2.1.7.1., Chronos vision GmbH).

Neuronavigation

The proper stimulation site was obtained by neuronavigation, using the SofTaxic Navigator System (Electro Medical System, Bologna, IT). This method involves the creation of an estimated magnetic resonance image of the subject. To this end, through the use of the digital sensor Polaris Vicra (Northern Digital), four reference points of the skull were defined (inion, nasion and the two preauricular points) and then approximately 80 points were taken on the subject's skull, creating a representation uniform. This model of the participant's scalp was processed by the software, which returned a 3D image of the subject's brain, adapted to a reference model based on a high-resolution MRI sample. Thanks to this reconstruction, it was possible to identify the estimated position of an area in the subject's cortex, with an overall accuracy of about 5mm (Carducci & Brusco, 2012). The specific localization of the areas was defined by Talairach coordinates, therefore for the present study the coordinates for pSTS ($x = 57$, $y = -46$, $z = 7$) (Fig.1), and for V1 ($x = 19$, $y = -98$, $z = 1$) have been used as reference (Serino, Canzoneri, & Avenanti, 2011). As for pSTS, the selection of these specific points was based on experimental evidence. In particular, we used as a source the study by Lockhofen and colleagues (2014) , in which it was highlighted that the greatest neural activation occurred at the coordinates previously exposed in response to gaze in spatial cueing tasks.

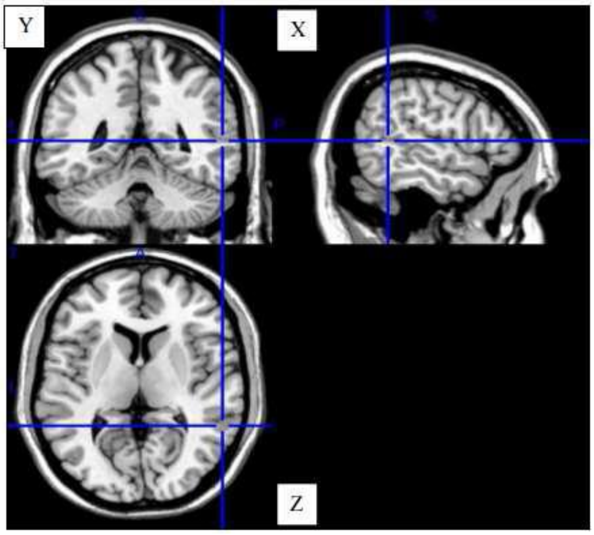


Figure 1. *STS stimulation coordinates on stereotaxic scheme (sagittal plane X = 57, coronal plane Y = -46, transverse plane Z = 7)*

Stimulation protocol (ccPAS)

For this stimulation protocol, two special eight-shaped coils were used, with the handle perpendicular to the plane of the coil, which facilitates the positioning of the coils close to each other, without interfering with the stimulation. One coil was placed on the right pSTS and connected to a monophasic Magstim 200 ^ 2 stimulator, while the other was positioned on the right V1 and connected to the Magstim Rapid ^ 2 biphasic stimulator (The Magstim Company, Carmarthenshire, Wales, UK). The protocol provided for the continuous administration of 90 pairs of TMS pulses at 0.1 Hz for 15 minutes (Buch et al., 2011; Chiappini et al., 2018; Rizzo et al., 2011, 2008). Each pair of pulses stimulated pSTS and V1 with an ISI of 200 ms, in order to activate the long-latency connections between the two areas, in line with what has been shown in the opening chapter. In this report, the data of two groups were considered, balanced by age and by gender of the participants: an experimental group that received an effective TMS stimulation (Active: 5 Female, mean age ± dev.std = 25.50 ± 2.27) and a control in which the stimulation was fictitious (Sham: 5 Female, mean age ± dev.std = 25.60 ± 2.22). In both groups, the direction of stimulation was STS-to-V1, so the first pulse of the pair was administered on pSTS and the second on V1. In the experimental group the coils were correctly positioned tangentially with respect to the scalp on the target point, while in the sham group, the coil plane was placed perpendicular to the scalp, so as to recreate the basic sensation of stimulation, in physical and sound terms, in the absence of actual perturbation of neural activity.

Experimental procedure

The experimental paradigm consisted of a cueing task carried out over three sessions (Baseline, T20, T40). The task procedure of the three experimental sessions was the same: each of them consisted of two blocks and, for each of these, 120 trials were presented, followed by a calibration phase. The total duration of each block (task and calibration) was approximately eight minutes. At the end of the first session, neuronavigation was performed for each participant in order to identify the location of the target areas of stimulation. Subsequently, the stimulation phase was carried out using ccPAS, dividing the participants into two conditions, active and sham, with the participants been unaware of the group they were assigned to. The overall duration of the stimulation phase (Neuronavigation and cc-PAS) was approximately 30/40 minutes. After the first session (Baseline), there was therefore the stimulation phase, at the end of which there was an interval of 15/20 minutes, before proceeding to the second session (T20). Between the end of the second session and the beginning of the last (T40), there was another interval of the same duration as the first. The trials, the same for each session, presented an initial appearance of a central fixation dot and lateral squares, on a gray background. After 600ms, one of the faces of the stimulus set appeared in the centre of the screen, gazing toward the participant. The fixation point remained visible, positioned at the level of the nasion of the face stimuli, equidistant from the eyes. This frame had a duration of

1500ms, at the end of which the instruction appeared, represented by the color change of the fixation point. Specifically, the participants were instructed to direct their gaze towards the right square when the color of the fixation point turned orange and to made a saccade towards the left placeholder when it turned blue. The instruction cue, represented by the color change of the fixation dot, was superimposed to the gaze movement of the background face stimulus, which occurred at three possible SOAs (-75ms, 0ms, 75ms), defining situations of congruence or incongruence between instruction cues and gaze stimuli (Fig.2). Specifically, SOA-1 (-75ms) defined situations in which instruction appeared 75ms earlier than the eye movement; at SOA-2 (0ms), the presentation of the instruction and the lateral deviation of the eyes of the stimulus occurred simultaneously; while at SOA-3 (+ 75ms) gaze shift preceded the onset of instruction.

The participants were instructed to keep their gaze on the fixation point and, at the appearance of the instruction, to made a saccade towards the target indicated by the latter, ignoring the underlying deviation of the gaze of the stimulus. Completed the saccade, they had to return their gaze to the centre of the screen, at fixation. This procedure was repeated for 120 trials, at the end of which the calibration was carried out, in which the participants must follow with their eyes the movement of a point, graphically identical to the fixation point, which appeared alternately in four points (right, left, top, bottom) equidistant from the centre (10 °). For each trial, the probability of the occurrence of a specific instruction cue and a specific distracting stimulus, at a given SOA, was balanced according to a random sequence. The overall duration of the entire experimental session was approximately two hours.

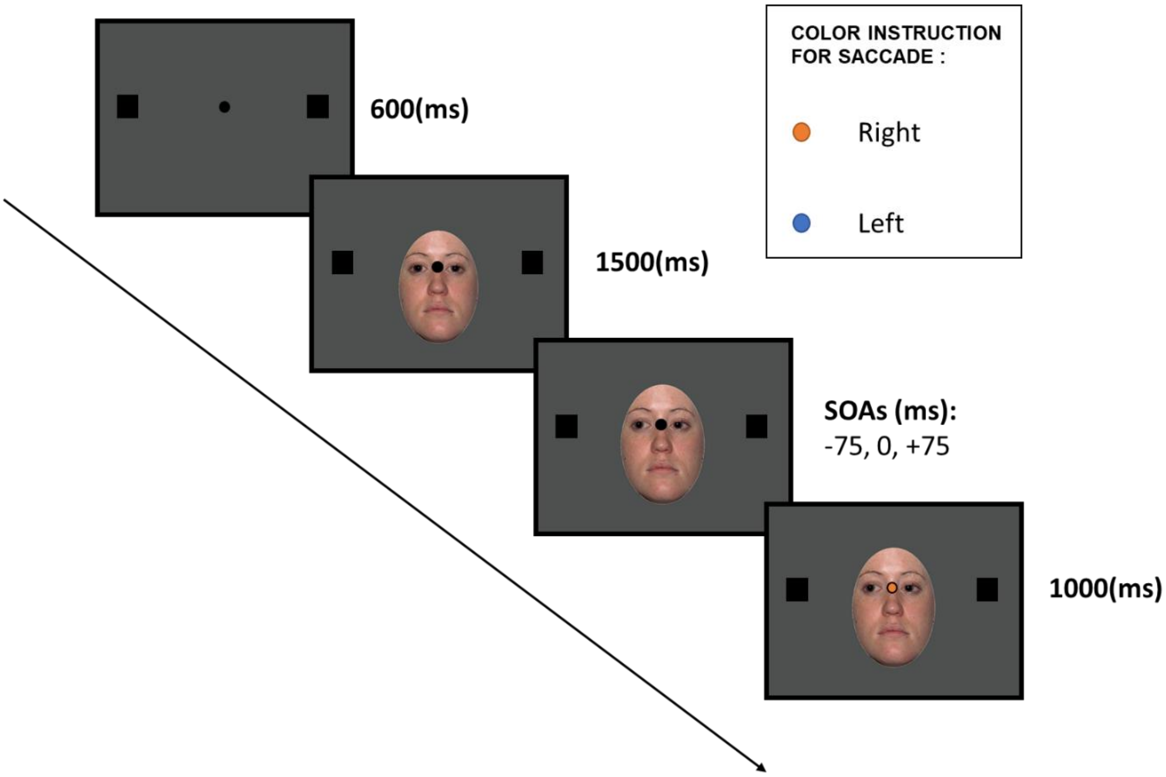


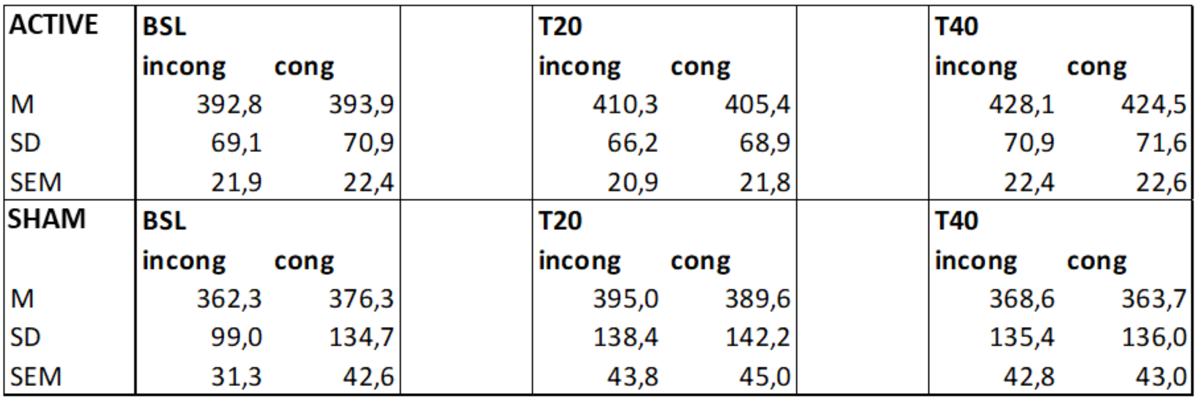
Figure 2. *Schematic example of the experimental task of overt gaze cueing, the face and eye movements served as a distracting cue. the instruction cue for the saccade was represented by the dot superimposed on the nasion (i.e., right saccade with orange color; left saccade with blue color).*

Data Analysis

The eye tracing was analyzed offline using the Iris Tracker software algorithm and Matlab (R2019b). The directional accuracy of the first horizontal saccade following the instruction cue with a visual amplitude> 2 ° was analyzed. The proportion of eye movements opposite to the instruction cue (saccadic errors) was then calculated. Trials in which the onset of the saccade occurred <500 ms and the speed reached a minimum of 35 ° / sec were selectively considered. Trials with eye-blinks (closing of the eyes) were also not considered in the analysis. In addition, the saccadic latencies were calculated, corresponding to the time necessary for the ocular movement to begin following the appearance of the instruction cue; and the arrival coordinates on the target (landing coordinates). For the statistical analyzes the software SPSS (version 23 IBM Spss Statistic) and STATISTICA (StatSoft, version 12) were used.

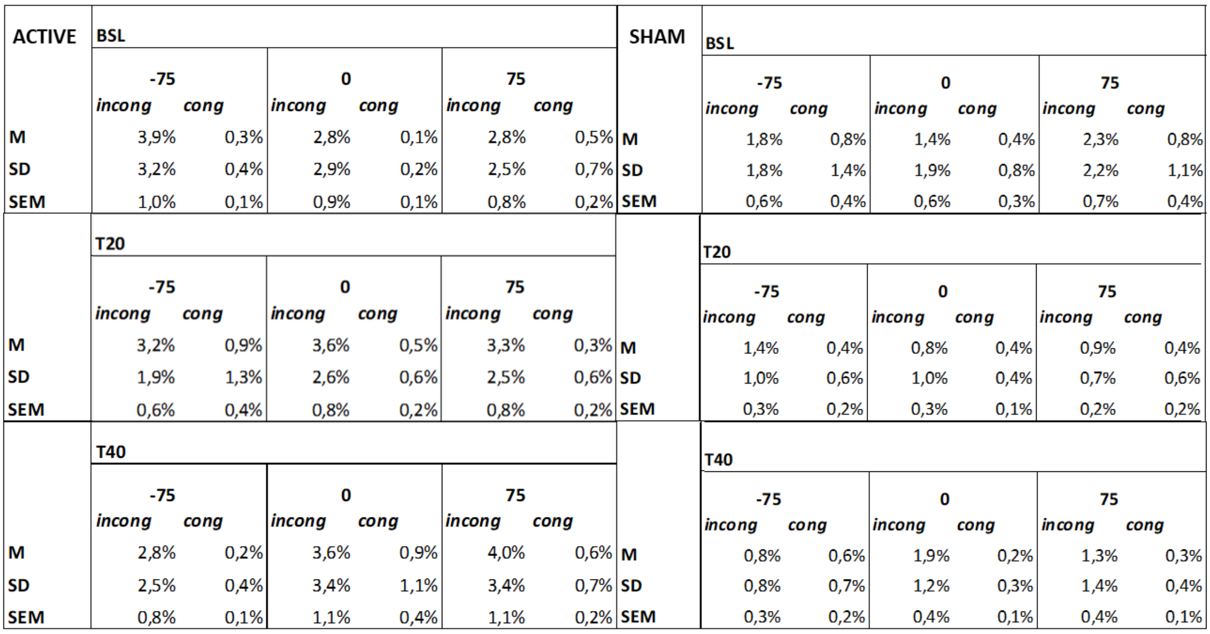
Results

Consistently with other studies in the literature (Crostella et al., 2009; Hermens & Walker, 2010; Ricciardelli et al., 2013), in order to analyze the performance of participants in the saccadic task, saccadic latencies (RTs; Tab.1), the proportion of errors made (i.e. percentage of saccades with direction contrary to the cue; Tab.2) and the landing coordinates (Tab.3) were considered as dependent variables and performed for each experimental session, calculating the values separately for the condition of congruence and for SOAs.



ACTIVE	BSL			T20			T40	
	incong	cong		incong	cong		incong	cong
M	392,8	393,9		410,3	405,4		428,1	424,5
SD	69,1	70,9		66,2	68,9		70,9	71,6
SEM	21,9	22,4		20,9	21,8		22,4	22,6
SHAM	**BSL**			**T20**			**T40**	
	incong	cong		incong	cong		incong	cong
M	362,3	376,3		395,0	389,6		368,6	363,7
SD	99,0	134,7		138,4	142,2		135,4	136,0
SEM	31,3	42,6		43,8	45,0		42,8	43,0

Table 1. *Saccadic Latencies (ms) with standard deviation and error mean.*



ACTIVE	BSL						SHAM	BSL					
	-75		0		75			-75		0		75	
	incong	*cong*	*incong*	*cong*	*incong*	*cong*		*incong*	*cong*	*incong*	*cong*	*incong*	*cong*
M	3,9%	0,3%	2,8%	0,1%	2,8%	0,5%	M	1,8%	0,8%	1,4%	0,4%	2,3%	0,8%
SD	3,2%	0,4%	2,9%	0,2%	2,5%	0,7%	SD	1,8%	1,4%	1,9%	0,8%	2,2%	1,1%
SEM	1,0%	0,1%	0,9%	0,1%	0,8%	0,2%	SEM	0,6%	0,4%	0,6%	0,3%	0,7%	0,4%
	T20							**T20**					
	-75		0		75			-75		0		75	
	incong	*cong*	*incong*	*cong*	*incong*	*cong*		*incong*	*cong*	*incong*	*cong*	*incong*	*cong*
M	3,2%	0,9%	3,6%	0,5%	3,3%	0,3%	M	1,4%	0,4%	0,8%	0,4%	0,9%	0,4%
SD	1,9%	1,3%	2,6%	0,6%	2,5%	0,6%	SD	1,0%	0,6%	1,0%	0,4%	0,7%	0,6%
SEM	0,6%	0,4%	0,8%	0,2%	0,8%	0,2%	SEM	0,3%	0,2%	0,3%	0,1%	0,2%	0,2%
	T40							**T40**					
	-75		0		75			-75		0		75	
	incong	*cong*	*incong*	*cong*	*incong*	*cong*		*incong*	*cong*	*incong*	*cong*	*incong*	*cong*
M	2,8%	0,2%	3,6%	0,9%	4,0%	0,6%	M	0,8%	0,6%	1,9%	0,2%	1,3%	0,3%
SD	2,5%	0,4%	3,4%	1,1%	3,4%	0,7%	SD	0,8%	0,7%	1,2%	0,3%	1,4%	0,4%
SEM	0,8%	0,1%	1,1%	0,4%	1,1%	0,2%	SEM	0,3%	0,2%	0,4%	0,1%	0,4%	0,1%

Table 2. *Percentage of Saccadic Errors reported with standard deviation and error means.*

ACTIVE	**BSL**			**T20**			**T40**	
	incong	**cong**		**incong**	**cong**		**incong**	**cong**
M	10,25	10,46		10,19	10,20		10,25	10,04
SD	0,68	0,92		0,63	0,63		0,92	0,81
SEM	0,21	0,29		0,20	0,20		0,29	0,26
SHAM	**BSL**			**T20**			**T40**	
	incong	**cong**		**incong**	**cong**		**incong**	**cong**
M	10,12	10,13		9,39	9,66		9,20	9,30
SD	1,21	0,95		1,57	2,03		1,64	1,65
SEM	0,38	0,30		0,50	0,64		0,52	0,52

Table 3. *Landing Coordinates (in visual degrees) with standard deviation and error mean.*

The ANOVA conducted on latencies did not report significant effects or interactions (Fs <0.88; ps> 0.42). With respect to the analysis of saccadic errors, a mixed-ANOVA was performed with TIME (BSL, T20, T40); SOA (-75, 0, +75 ms); CUE (congruent, incongruent) as the within factors and STIMULATION (ACTIVE, SHAM) as the between factor. The significant outcome that emerged were the main effect of the CUE (F1.18 = 35.85; p <0.001) (Fig.3), the CUE x STIMULATION (F1.18 = 9.32; p <0.01) and TIME x SOA (F4.72 = 4.03; p <0.01) interactions.

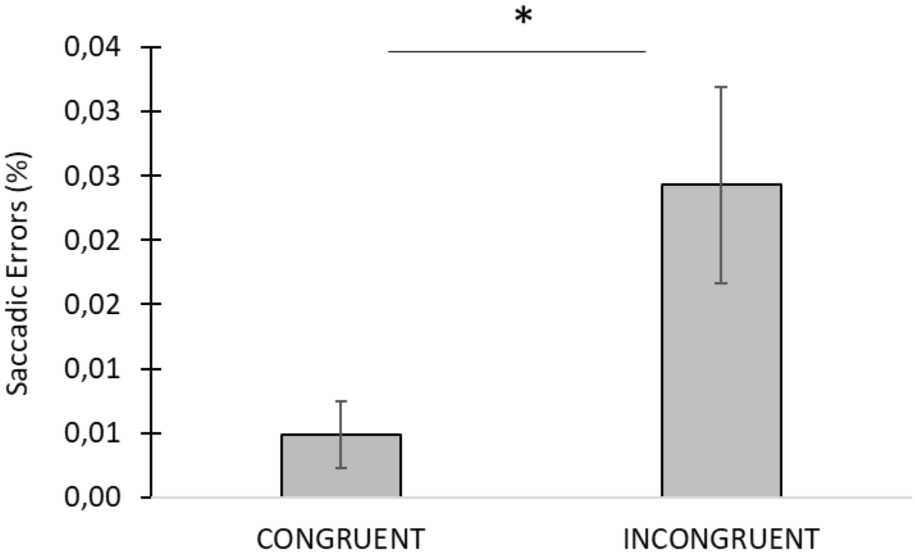


Figure 3. *Main effect of CUE in saccadic errors for both groups.*

The most relevant result was the emergence of a significant multiple interaction between the TIME x SOA x CUE x STIMULATION factors (F4.72 = 2.65; p <0.05). No other effects or interactions were found to be statistically significant (Fs <0.16; ps> 0.07). Finally, the ANOVA conducted on the landing coordinates did not return any significant effect or interaction (Fs <2.14; ps> 0.13).

To additionally characterize the effect found in the ANOVA on the saccadic errors, post-hoc tests were performed using the Duncan method in order to investigate the multiple interaction TIME x SOA x CUE x STIMULATION. The graphic representation of the interaction (Fig.4-6) allowed us to note how the stimulation protocol established different behavioural effects depending on the SOA, the session (TIME) and the CUE type (congruent / incongruent). The analysis showed that, by comparing the BSL sessions against the post-stimulation sessions, changes in performance were present for the incongruent trials. Regarding SOA_1 (-75ms), in the ACTIVE group, there was a significant reduction in errors associated with the incongruent cue (p = 0.02) in the T40 session. A similar reduction effect is observed in the SHAM group although it does not reach significance (p = 0.077; Fig.4), while in neither group a change is observed for congruent cues (all p> 0.18).

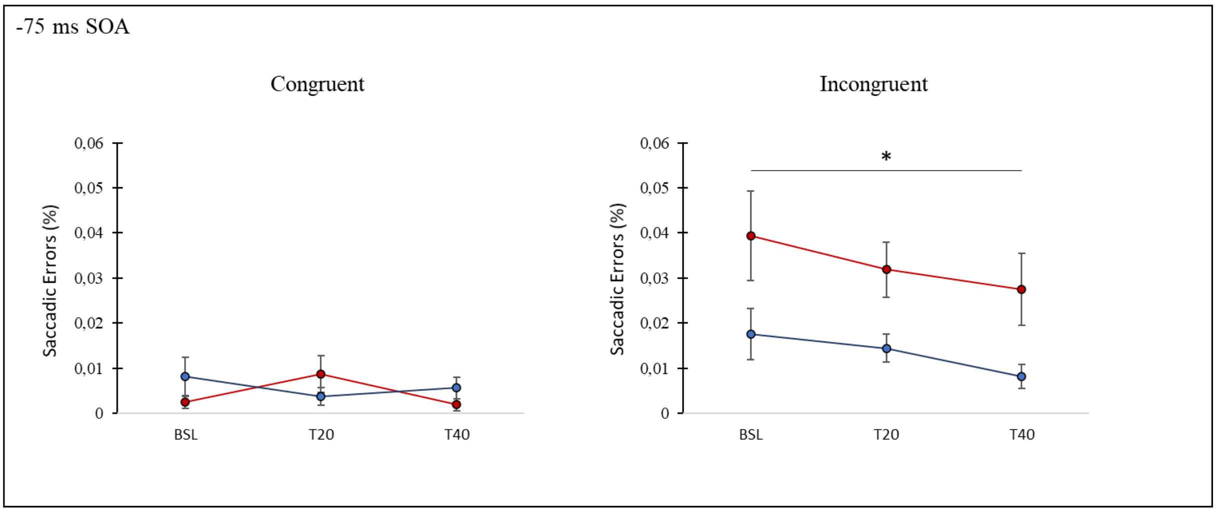


***Figure 4**. Graphs showing the percentage of errors for -75 SOA as a function of the CUE congruency and SESSION time for the ACTIVE (red) and SHAM (blue) conditions. Asterisks denote meaningful post-hoc comparisons and error bars represent SEM.*

For SOA_2 (0ms) in the incongruent trials there are trends towards the reduction of errors over time in both groups, however no comparison reaches significance (all p> 0.09; Fig. 5).

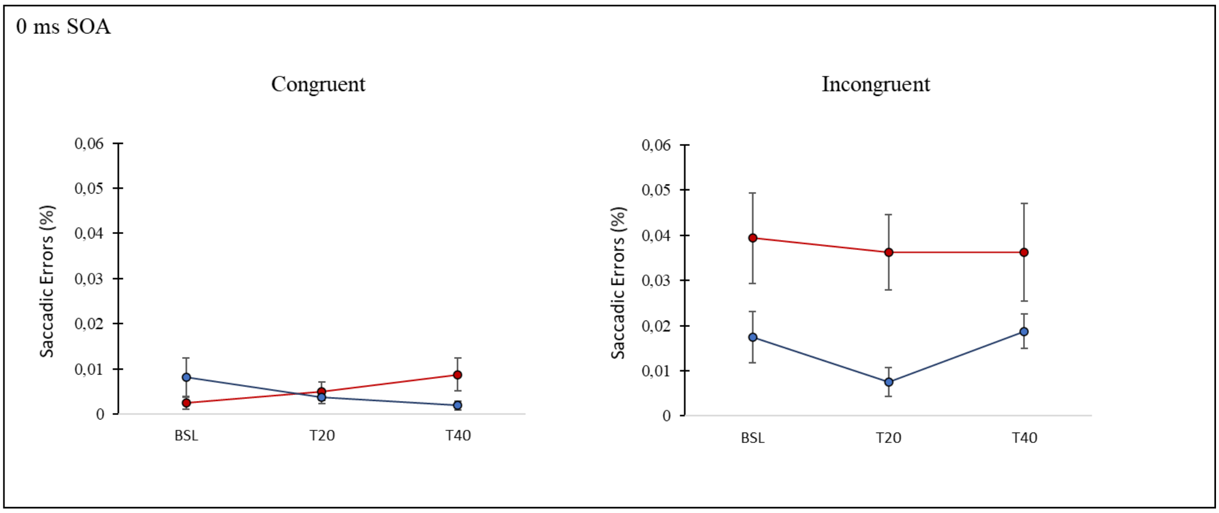


***Figure 5**. Graphs showing the percentage of errors for 0 SOA as a function of the CUE congruency and SESSION time for the ACTIVE (red) and SHAM (blue) conditions. Error bars represent SEM.*

Finally, for SOA_3 (+ 75ms) a dissociation is observed between the two groups: while the SHAM group shows a reduction of errors at T20 (p = 0.008) and marginally at T40 (p = 0.07), the group TMS, shows an increase in errors at T40 (p = 0.02; Fig. 6).

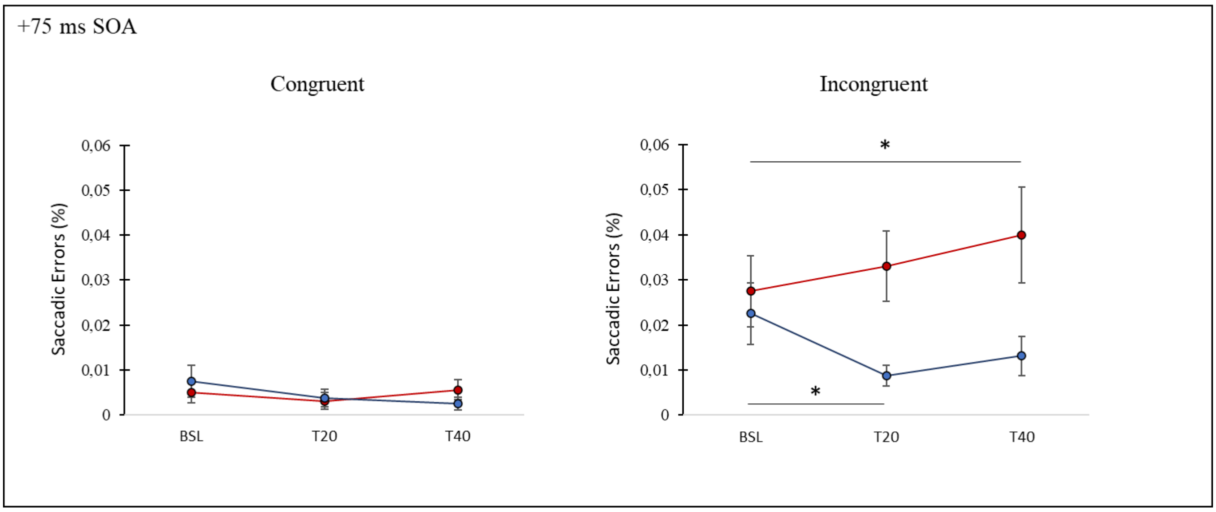


Figure 6. *Graphs showing the percentage of errors for +75 SOA as a function of the CUE congruency and SESSION time for the ACTIVE (red) and SHAM (blue) conditions. Asterisks denote meaningful post-hoc comparisons and error bars represent SEM.*

Summarizing, in the SOA-1 condition (-75ms) the participants show a trend towards improvement in performance for the incongruent trials over time and this improvement appears similar for the two groups (therefore not attributable to TMS). Also, in the SOA-2 (0 ms) a trend towards an improvement can be observed in both groups, although this does not reach significance. Finally, in the SOA-3 condition (+ 75ms) the sham group shows an improvement for incongruent trials while the TMS group shows a tendency to worsen over time.

Discussion

The present study investigated the role of the occipito-temporal pathway in the phenomenon of gaze cueing. Specifically, through cc-PAS, we wanted to deliver a stimulation that is supposed to be able to target the feedback connections between STS and V1 to increase the directional connectivity between these two areas. The impact of this modulation on the overt orientation in a gaze cueing paradigm was then evaluated, also in the light of a previous attempt (study 2) that had tested how the ccPAS STS-V1 modulated the covert responses related to the perception of the gaze, in in order to compare whether the modulation of connectivity from

STS to V1 can act differentially on the covert and overt orientation mechanisms in response to gaze.

In the present thesis, a gaze cueing paradigm was used in which participants were instructed to move their gaze towards one of two lateral placeholders, following the instruction represented by the color change of a centrally presented fixation point and ignoring the presentation of a face that turns its eyes to the right or left. The time difference between the movement of the eyes and the appearance of the instruction is differentiated into three SOAs (-75ms, 0ms, + 75ms). Therefore, the SOA-1 (-75ms) defines situations in which the instruction appears 75ms earlier than the movement of the gaze, while in the SOA-3 the instruction is presented 75ms after the ocular movement of the face stimulus. At SOA-2, the appearance of education and eye movement occur simultaneously. The direction indicated by the eyes and that indicated by the instruction may differ, configuring situations of congruence or inconsistency. Participants had to perform the task in three sessions (BSL, T20, T40). Between the first and the second experimental session, an off-line stimulation session of TMS with the ccPAS protocol conducted on all participants and divided into two groups: one experimental (TMS) and one control (SHAM). In both groups the stimulation protocol was identical, with 90 pulse pairs at a frequency of 0.1Hz. For each pair of pulses, the first was administered on STS and the second on V1, at a predetermined ISI of 200ms. However, while the experimental group received the stimulation, by correctly positioning the coils over the scalp, in the control group the coil was still positioned over the scalp but tilted at 90 degrees so as to deliver the magnetic field away from the cortex. This allowed reproducing the sound and the physical sensations associated with the stimulation without active stimulation being actually delivered over the brain. In order to evaluate the effects of stimulation on overt orientation, eye movements were recorded by eye tracker (ETD), thanks to which it was possible to analyze off-line the participants' saccadic latencies, saccadic errors and the coordinates of arrival of the saccades.

The analysis revealed a main effect linked to the congruence of the cues. The presence of this main effect of the CUE factor (Congruent vs Incongruent) highlights the influence of congruence between the stimuli presented on the attentional behaviour of the participants. Specifically, in line with the previous literature (Crostella et al., 2009; Friesen & Kingstone, 1998; Frischen et al., 2007), it emerged that in conditions of incongruity between the direction indicated by the gaze of the stimuli and that conveyed by the cue that serves as an instruction, the participants made a greater number of errors, compared to the congruent condition. This data confirms the presence of a gaze-induced cueing effect in our experimental protocol and therefore supports its validity.

The presence of a multiple interaction TIME x SOA x CUE x STIMULATION at the level of saccadic errors, required further analysis to evaluate the effect of the experimental manipulations on the behaviour of the participants. The post-hoc analysis of the interaction therefore revealed a different trend in the two experimental groups in the incongruent trials at different SOAs. Specifically, the effects of TMS stimulation emerge in the last experimental session (T40), manifesting themselves in the SOA-1 condition (-75ms) with a reduction of errors in incongruent trials; in the SOA-2 condition (0ms) with a similar reduction, although not significant; and in the SOA-3 condition (+ 75ms) with an increase in the percentage of erroneous saccades in the incongruent trials. It should be noted that in the SOA-1 and SOA-2 conditions the SHAM group shows a behaviour quite similar to the TMS group. Thus, the reductions observed in the TMS group (significant in SOA-1 and non-significant in SOA-2) cannot be attributable to ccPAS and appear to reflect rather an effect of practice as they are also observed in participants receiving sham stimulation. This effect of the practice is visible only in incongruent trials, and the lack of improvement in congruent trials is not surprising as the percentage of errors in these trials is already close to zero. The reduction of errors in incongruent trials suggests a better ability of participants to resist the gaze when it points in the opposite direction to that indicated by the imperative stimulus. It should be noted that in some cases the comparisons reach significance, an effect that could be attributed to the interindividual variability, which is known to be relevant in the gaze cueing paradigms (Bayliss et al., 2005; Hietanen et al., 2006) and to the low amplitude of the sample.

The most interesting data is the one observed with a SOA of + 75ms, that is when the movement of the eyes of the stimulus occurs earlier than the color change of the fixation point. In this condition, the TMS group and the SHAM group show a behavioural dissociation: the SHAM group shows a reduction of errors in incongruent trials (as observed with the other SOAs, an effect reasonably attributable to practice), while the TMS group shows a clear increased error rate in inconsistent trials.

This error rate increase indicates a greater ability of the gaze to interfere with the task of the participants and confirms the possibility of modulating the activity of the network involved in gaze processing and highlighting its impact on the overt component of attentional orientation. Specifically, the increase in connectivity between STS and V1 seems to lead to an increase in the normal tendency to automatically follow the direction of the observed gaze. In fact, the effect occurred despite this behaviour being counter-productive with respect to the demands of the task and the participants were explicitly requested to avoid it. A possible interpretation of these data is therefore that the occipito-temporal stream influences the attentional processing, implementing the coding of the salience of biological moving stimuli with social value. This role therefore becomes relevant in the gaze cueing paradigms, whereby the participant is captured by the observed gaze, making more mistakes when this precedes the onset of the instruction cue. The cc-PAS stimulation between STS and V1 would therefore have increased this attentional capture produced by the gaze, in particular at SOA of + 75ms, when there is a longer exposure time to the gaze. The increase in connectivity between STS and V1 would therefore seem to produce an increase in the signal of the occipito-temporal stream, increasing the salience linked to the biological stimulus and producing a greater distracting effect on the attention of the gaze. This effect becomes evident when the participant first processes the information related to the movement of the eyes and when the latter is inconsistent with that conveyed by the instruction. At the behavioural level, this phenomenon manifests as an error rate increase following ccPAS, precisely emerging at a SOA of + 75ms in the incongruent conditions and, in particular, in the last session, therefore despite the practice in the task, which is instead linked to a reduction in errors in the other conditions.

Another relevant data for the purpose of this study is the absence of an effect related to the stimuli, so the responses of the two stimulation groups do not differ in the different sessions and at the different SOAs on the basis of the gender of the faces presented. The important aspect of this result is related to the comparison with the previous effort study (Chapter II), which investigated the effects of the cc-PAS STS-V1 on covert orientation, highlighting a stimulation effect linked to the gender of faces used as a stimulus. A possible explanation for this difference is related to the dissociation between overt and covert mechanisms and to the characteristics of the task. In the study on which this attempt is focused, the paradigm required participants to remain focused on the ocular region of the stimuli and to respond quickly and accurately through a lateral shift of the gaze. Under these conditions, the participants use their eyes both for the detection of instruction and for the response, therefore it would be counterproductive to analyze the other regions of space, as it would lead to less reactivity and precision in the responses. These paradigmatic aspects could limit the coding of contextual elements such as the type of stimuli, reducing the impact of these aspects on attentional orientation. Otherwise, in the paradigm on covert orientation (Chapter II), the gaze of the participants was engaged only in detection, not in response, leaving the participants with the opportunity to focus exclusively on the central region, therefore on the stimulus. This could have increased the impact of facial features, including gender, on the perceived salience of movement. Despite these possible interpretations, it is however clear that further investigations are needed to analyze a possible dissociation between overt and covert orientation mechanisms in the phenomenon of gaze cueing.

The absence of significant effects regarding reaction times and saccadic coordinates denotes a lack of modulation of the experimental manipulation. This could be due to aspects related to the paradigm used or to the size of the sample. However, it would seem possible to discard the first hypothesis, as the analysis of the data has confirmed the effective ability of this paradigm to generate cueing effects related to the gaze. The most probable cause of the lack of these effects could be most likely the small sample size, which includes only 20 participants (10 for each experimental group). A third alternative, but currently only a suggestion, is that the absence of significant differences is due to the fact that the stimulation does not affect areas directly involved in the attention shift, but rather in the perceptual analysis and in the coding of the salience of the stimuli presented. In this regard, the evidence that it is still possible to obtain effects at the level of performance in the task linked to the increase in connectivity between STS and V1, indicates the possibility of investigating, with this stimulation protocol, portions of the network for gaze processing that include also areas directly implicated in attentional orientation, such as FEF (Awh et al., 2006; Corbetta et al., 2008; McDowell et al., 2008).

APPENDIX B

FUNCTIONAL NEUROMODULATION OF TARGETED PERCEPTUAL DECISION-MAKING NETWORKS CAUSALLY DISSOCIATES SENSORY DISCRIMINATION AND METACOGNITION

Introduction

The neural underpinnings of perceptual decision making have been investigated by systems and cognitive neuroscience. As a consequence, numerous studies in monkey's neurophysiology (Gold & Shadlen, 2007; Kim & Shadlen, 1999; Mazurek et al., 2003; Newsome et al., 1989; Shadlen et al., 1996; Shadlen & Newsome, 2001), human imaging (Cheadle et al., 2014; Heekeren et al., 2004, 2006, 2008; Ho et al., 2009; Ploran et al., 2007; Tosoni et al., 2008), and electrophysiology (De Lange et al., 2010; Donner et al., 2007; O'Connell et al., 2012; Philiastides et al., 2006; Philiastides & Sajda, 2006; Smith & Ratcliff, 2009; Wyart et al., 2012) have been conducted.

Confidence about a sensory choice is classically seen as a meta-cognitive process (i.e., an emergent property of the choice process) that is dependent on additional data accumulating beyond the stage of the selection process, in line with recent theoretical and empirical descriptions (Fleming et al., 2012; Pleskac & Busemeyer, 2010; Yeung & Summerfield, 2012). Beside this, from animal investigations (Kepecs et al., 2008; Kiani & Shadlen, 2009; Shadlen & Kiani, 2013) has also emerged an idea suggesting that decision confidence in perceptual judgements may be an intrinsic component of the decision process itself, and that the same cortical sources that store evidence also encode choice certainty.

Findings in human (Gherman & Philiastides, 2015) are consistent with a key study that found neurons in the primate brain, where lateral intraparietal cortex signal choice generation as well as the degree of confidence supporting that judgment (Kiani and Shadlen, 2009). In the aforementioned work, Gherman found that confidence signals appear as early as the evidence gathering the process itself, against a purely metacognitive (post-decisional) account of decision confidence, and are consistent with a recent report of pre-decisional self-reported confidence signals during perceptual choices (Graziano et al., 2015; Zizlsperger et al., 2014). Confidence may arises in concurrence with stimulus representations, and it may be distinguished from representations of sensory evidence, objective discrimination performance, and overt motor behaviour by its electroencephalographic parieto-occipital correlates (Zizlsperger et al., 2014).

Therefore, the brain's estimation of subjective choice confidence is still a matter of discussion (Charles et al., 2013; Fleming & Dolan, 2012; Ma et al., 2006; Orbán et al., 2016). Despite prevailing theories suggest that confidence is an appropriate representation of the likelihood that a decision is accurate (Fetsch et al., 2014; Kiani et al., 2014; Sanders et al., 2016; Zylberberg et al., 2016), it seems that such models have difficulty accounting for unexpected behaviours in which confidence and accuracy are decoupled (Koizumi et al., 2015; Rahnev et al., 2011; Rahnev, Bahdo, et al., 2012; Rahnev, Maniscalco, et al., 2012; Samaha et al., 2016).

The aspects of metacognitive ability, according to experimental investigation, are distinct from task performance and may have an independent neural and processing substrate (Bang & Fleming, 2018; Del Cul et al., 2009; Fleming et al., 2010; Fleming & Dolan, 2012; Lak et al., 2014). Several cases in literature reported the dissociation on task performance and metacognitive facets (Koizumi et al., 2015; Maniscalco et al., 2016; Peters, Fesi, et al., 2017; Rahnev et al., 2012; Samaha et al., 2016). Remarkably, alterations in metacognition have been associated to self-reported mental health symptoms, even when there are no variations in task performance (Hoven et al., 2019; Moses-Payne et al., 2019; Rouault et al., 2018; Seow & Gillan, 2020). Further recent investigation has focused on mimicking parallel neural populations engaged in perceptual decision-making, with the discovery that simulated neural network could account for cases where confidence is affected despite no differences in performance (Maniscalco et al., 2021). As a consequence, it seems necessary to figure out how confidence signals emerging from the decision-making process are integrated in the brain areas involved in metacognitive judgment (De Martino et al., 2012; Fleming et al., 2012; Hebart et al., 2012).

Experiments using stimulus manipulations (Zylberberg et al., 2016), as well as attention manipulations (Rahnev et al., 2011) and direct intervention on brain activity (Peters, Fesi, et al., 2017; Rahnev, Maniscalco, et al., 2012), can be modelled as affecting task performance or confidence by influencing the variability of sensory evidence. On this line, Hulme, Friston, and Zeki (2009) discovered a decoupling between stimulus features indicated by early visual cortex activation and a subsequent parieto/temporal cluster of activation, which is tied to conscious experience of decision-making.

Similarly, confidence-related activations were found in human prefrontal and parietal cortices (Filimon et al., 2013; Heekeren et al., 2006; Ploran et al., 2007; Tosoni et al., 2008). Indeed, in both primates (Freedman & Assad, 2006, 2011, 2016; Gold & Shadlen, 2007; Shadlen & Newsome, 2001; Yang & Shadlen, 2007) and rodents (Hanks et al., 2015; Harvey et al., 2012; Morcos & Harvey, 2016; Runyan et al., 2017), the posterior parietal cortex (PPC) is among the brain structures which exhibits considerable decision-related activity.

On the other hand, sensory features which lead choice accuracy appears to be mediated by a specifical temporo-occipital cluster. As seen in several single-cell recording investigations, neurons in area MT have been found to linearly increase firing rate with motion coherence (Newsome et al., 1989; Zeki, 1974), and the strength of visual motion is reflected in human area MT activity in fMRI, MEG, and EEG data (Becker et al., 2008, 2013; Händel et al., 2007; Helfrich et al., 2013).

Critically, interesting results in monkeys have questioned the causative involvement of the LIP area in choice computation as previously reported (Shadlen & Newsome, 2001). In fact, while inactivation of neurons in MT profoundly impaired psychophysical performance, inactivation in LIP had no measurable impact on perceptual decision performance (Chen et al., 2016; Katz et al., 2016). These dissociations seems in line with the idea that MT and LIP areas might build different behavioural aspects.

The main objective of this study is to dissociate, in a more targeted way than previously achieved (Chapter III), the neural activity responsible for objective accuracy and that underlying the metacognitive correlates of the decision-making process. In particular, it was intended to understand whether the IPS/LIP activity mediates exclusively the formation of the confidence judgment on the visual motion, or if it had a more general role of altering the perceptual improvement obtained due to the strengthening of the V5-V1 reentrant projections. In order to dissociate the activity of the two neural flows, it was implemented an experimental design that provided for the inhibition of IPS using the "continuous theta-burst stimulation" (cTBS) protocol, following the strengthening of the V5-V1 network obtained through ccPAS.

Methods

Participants

36 volunteers (17 men; mean age ± SD = 23.47 ± 5.21) participated in the study. None of them had previously reported mental or neurological pathologies or contraindications to the TMS administration procedure (Wassermann, 1998). Each participant provided their informed consent prior to the study and all procedures received the approval of the local bioethics committee of the Department of Psychology, University of Bologna.

Experimental task and stimuli

The experimental task, a version of the "motion direction discrimination task" previously used by Romei and colleagues (2016), was projected on a 18-inch CRT monitor (with a resolution of 1280 x 1024 pixels and a refresh rate equal to 85 Hz) distant ~57 cm from the participant. The stimuli were generated and presented using the MATLAB statistical analysis environment (version 2017a, The MathWorks Inc., Natick, MA) and the Psychophysics Toolbox (Brainard, 1997). At the beginning of each trial, the participant was shown, for a period of 500 ms, a fixation cross in the centre of the screen; later, within a square region of 12.8 x 12.8 visual degrees (°) to the right of the fixation point, a moving stimulus appeared for a duration of 400 ms. The stimulus was composed of 400 white dots (each 6 pixels in size) that could move left or right with 10 different percentages of movement coherence (0, 2, 4, 6, 12, 16, 20, 35 , 50, 80). By "coherence of motion" we mean the proportion of points moving in the direction of the signal; this measurement could fluctuate between 0 (totally random movement) and 80% (the majority of dots headed in the same direction).

During the stimulus presentation period, the participants were asked to keep their gaze on the fixation cross and, at the end of the presentation, they were asked to indicate the direction of movement as a whole perceived, choosing between two response alternatives (left-right) and selecting the corresponding arrow on a keyboard; this judgment was taken as a measure of objective performance accuracy. Participants were then asked to rate, on a discrete four-point scale, their level of confidence on the previously expressed judgment (1: absolutely unsure, 2: unsure, 3: quite sure, 4: totally sure) by selecting the corresponding number keys; this measure was considered a decision confidence indicator. Each block of tests included 20 repetitions for each of the 10 percentages of coherence in the two possible directions of movement (left-right), for a total of 400 trials over a period of approximately 12 minutes.

Experimental design

Two groups underwent the same protocol of ccPAS V5-V1 and then, dependently on the condition, were assigned to an active cTBS or a sham cTBS protocol. The crucial session was therefore the one following the administration of the inhibitory TBS. The participants were preliminarily subjected to a training session in order to gain familiarity with the task; subsequently, they were asked then to perform a baseline session (BSL) prior to the application of the ccPAS protocol aimed at strengthening V5-V1 reentrant connectivity. Participants performed again the task 30 minutes from the end of stimulation (T30). Subsequent to the T30 session, the participants underwent the cTBS protocol and then performed the task again in the last session (T60), 60 minutes from the ccPAS administration (Fig.1).

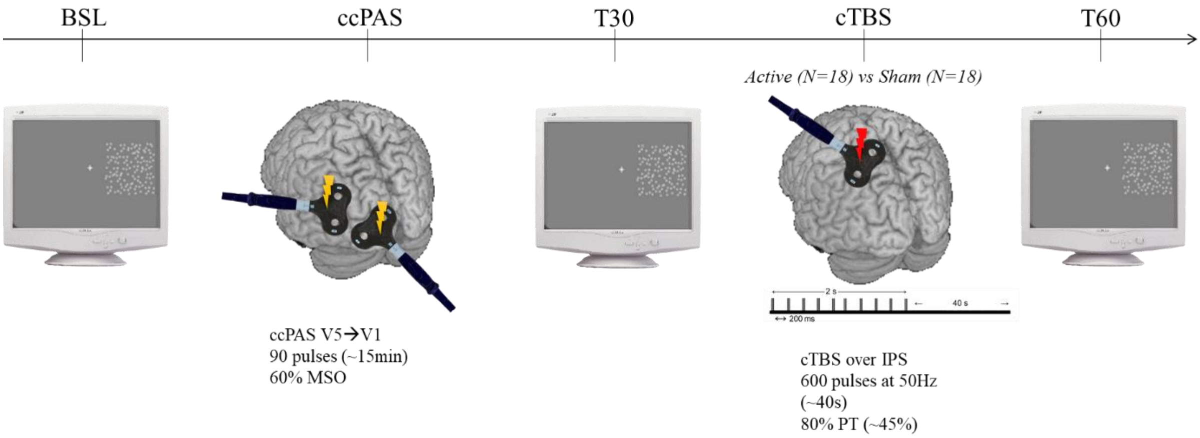


***Figure 1**. Representation of the experimental procedure: participants performed the motion discrimination task prior to(BSL) and 30 minutes after (T30) the V5-V1 ccPAS protocol. Half of the participants underwent a cTBS protocol and the remaining half a sham cTBS protocol, after which they were re-tested on the motion discrimination task 60 minutes after the ccPAS (T60).*

Cortico-cortical paired associative stimulation (ccPAS)

The ccPAS procedure required the use of a pair of coils (50 mm, figure-of-eights) connected to a Magstim BiStim2 stimulator assembled from two monophasic 200 modules. The application of the protocol took about 15 minutes. Ninety pairs of pulses were applied at a constant frequency of 0.1 Hz, in order to avoid any temporal summing effects (Stefan et al., 2000); each pair consisted of two monophasic transcranial magnetic stimulation (TMS) pulses, automatically activated remotely via a MATLAB interface. Both experimental groups underwent to the same ccPAS protocol.

The areas of interest in the stimulation paradigm were V5 / MT + of the left hemisphere and central V1 / V2. The coils were oriented tangentially to the scalp and a stimulation intensity equal to 65% of the stimulator's maximum output was used. In order to locate V5 / MT +, the coil was positioned 3 cm dorsally and 5 cm laterally with respect to the inion, coinciding with the localization on the scalp in which on average the TMS is able to modulate the perception of visual movement (Romei et al., 2016) and eliciting the vision of moving phosphenes (Pascual-Leone & Walsh, 2001). In order to stimulate V1 / V2, however, the coil was positioned 2 cm dorsal to the inion, in correspondence to the area of the scalp whose stimulation typically elicits phosphenes. The first TMS pulse of the pair was applied on V5. Since, as demonstrated by previously discussed studies, V5 takes a time interval of 20 ms to develop the reentrant projections towards V1 (Pascual-Leone & Walsh, 2001; Romei et al., 2016; Chiappini et al., 2018), an ISI of 20 ms between V5 and V1 stimulation was chosen in order to elicit the consequential pre- and post-synaptic activation of the cortical areas under examination.

Continuous theta-burst stimulation (cTBS)

Following the administration of the ccPAS protocol, the groups were then divided according to the continuous theta-burst stimulation (cTBS) protocol they would undergo. For the Active cTBS, stimulation was applied to modulate the activity of IPS in an inhibitory fashion, using a Magstim Rapid2 stimulator connected to a biphasic coil (70 mm, butterfly). The procedure, which lasted 40 seconds, consisted in the application of 600 pulses (cTBS-600). The bursts were repeated at 200 ms intervals and each of them consisted of three pulses administered at a frequency of 50 Hz. The stimulation intensity was subthreshold (80% of the phosphenes perception threshold) and corresponded on average to 45% of the maximum stimulator output. This inhibitory protocol has been shown to be able to exert a long-term depressive effect (LTD) of the cortical area subjected to stimulation for a period of more than 50 minutes (Wischnewski & Schutter, 2015). The targeted site, corresponding to the coordinates P3 (international system 10-20), coincided with the IPS/LIP areas of the left hemisphere with a variability of less than 2 cm (Herwig, Satrapi, & Schönfeldt-Lecuona, 2003; Okamoto et al., 2004), thus allowing to minimize the margin of error between subjects. For the Sham cTBS, all stimulation parameters were the same of the Active condition, with the critical difference that the coil was reversed in order to avoid a direct discharge on the cortical surface.

Statistical analysis

The collected data were plotted on a Cartesian plane in which the abscissa axis represented the coherence level of the movement (0–80%) and the ordinate axis represented the percentage of performance accuracy. The distribution of the variable simulated a psychophysical curve of sigmoid shape. Between the accuracy values of 50% (corresponding to a totally random coherence of motion) and 100% (corresponding to 80% coherence of motion) the curve tended to grow, as predicted based on the results of previous research (Romei et al., 2016). The data were adapted through a non-linear function modeled on the logistic curve:

$$y = \frac{1}{2}\left(1 + \frac{a}{1 + e^{-\frac{x-b}{c}}}\right)$$

In which:

- a represents the value of the upper horizontal asymptote;
- b represents the value at which the function changes its trend (inflection point), halfway between the lower and upper asymptotes;

- c represents the value that describes the direction and steepness of the curve (slope).

For each participant in each session, the value of the inflection point was calculated, corresponding to the intersection between the accuracy value of 75% and the relative level of coherence of the movement. As a result, the movement sensitivity threshold was determined, the value of which corresponded to the minimum percentage of coherent movement necessary to perform the movement discrimination task with an accuracy of 75%.

In order to investigate the modulation of visual metacognition throughout the experimental sessions, depending on the stimulation protocol, we evaluated different indices of metacognition. Specifically, by considering the level of performance in trials encompassing the mean motion threshold we obtained scores for metacognitive bias (average confidence ratings), metacognitive sensitivity (meta-d') and efficiency (meta-d'- d') (Fleming, 2017; Maniscalco & Lau, 2012). All the analyses were performed using SPSS 23 (IBM) statistical software and Matlab v2019b. Statistical analyses and comparisons were performed by ANOVA, Duncan Post-hoc test and Bonferroni-Holm corrected t-tests.

Results

Motion Sensitivity

In order to investigate the specific modulatory effects of the ccPAS protocol and the cTBS on visual motion sensitivity threshold, considered as a dependent variable, an ANOVA was performed on baseline corrected values (Post_ccPAS – BSL) by considering the session following the stimulation as within factor (Session: T30, T60) and the cTBS protocol (cTBS: Active, Sham) as between subject factor. We found no significant main effect or interaction (Fs<4.03; ps >0.053) (Fig.3), indicating that no differential outcome on motion sensitivity between groups were caused by the administration of the ccPAS and the cTBS. However, in order to ascertain whether the effect of ccPAS on V5-V1 connectivity was present in both groups in a similar way after stimulation, a further ANOVA was performed considering the raw pre- and post-stimulation performance levels (Session: BSL,T30,T60) for the two groups (cTBS: Active, Sham). This showed a significant effect of the Session ($F(2,68)=11.21$; $p < .001$) without any other significant outcome ($Fs<1.21$; $ps > .30$). Post-hoc tests revealed that both T30 ($p<.001$) and T60 ($p<.01$) motion thresholds were lowered relative to baseline (Fig.2), but these were not different between them ($p=.19$); proving that the stimulation of V5-V1 reentrant network was effective in improving motion sensitivity up to 60 minutes, in line with previous results (Romei, Chiappini, Hibbard, & Avenanti, 2016).

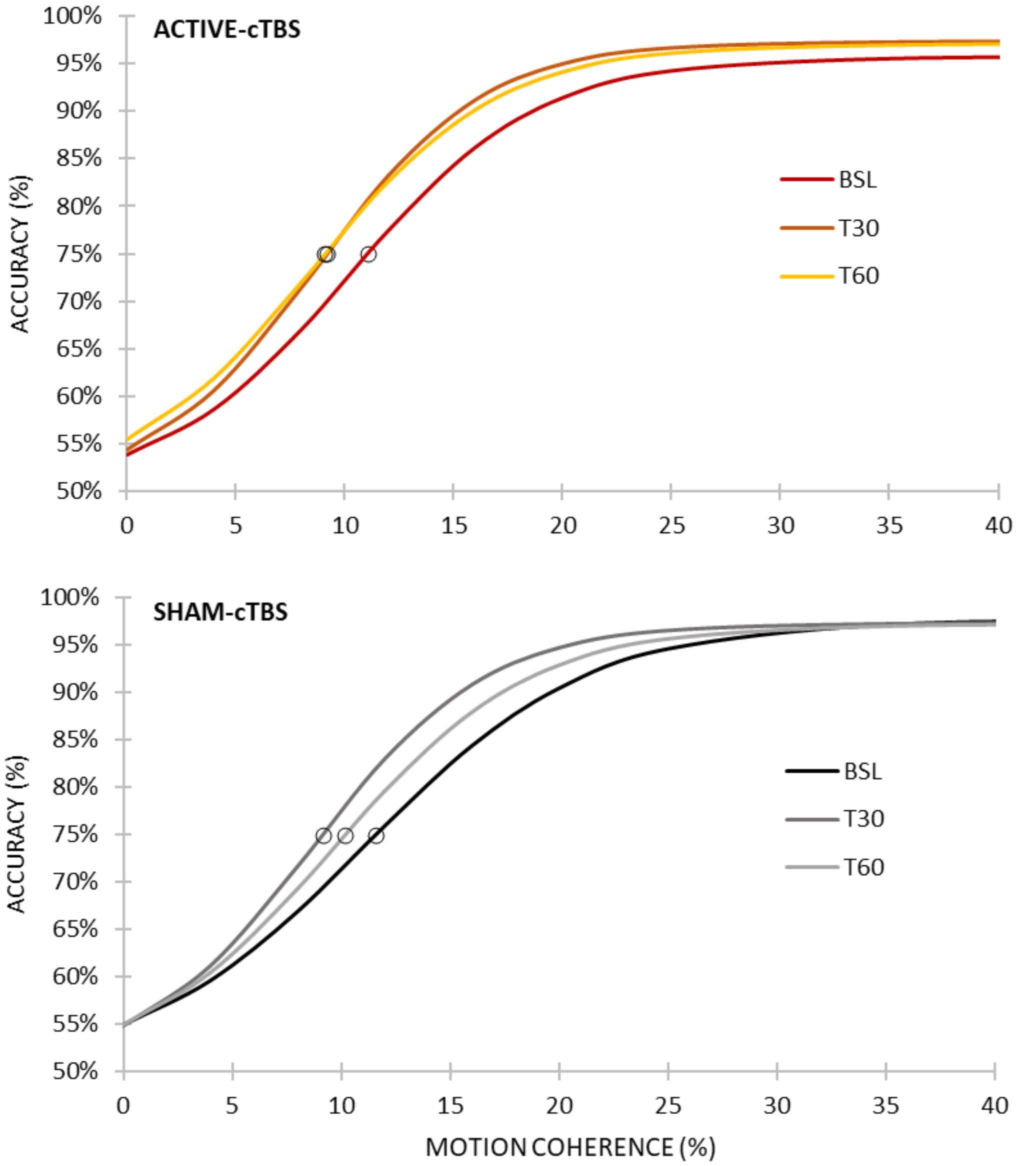


Figure 2. *Perceptual curves of motion discrimination. Fitted data modeled on the logistic function to obtain the perceptual thresholds. The groups' performance is separately plotted depending on the condition (top panel, in red shades ACTIVE_cTBS; bottom panel, in grey shades SHAM_cTBS) and as a function of the testing session (BSL, T30 and T60 sessions). Circle dots depict the inflection points (IP) coincident with the percentage of coherent motion where the logistic function had a value of 75% of correct responses.*

Additional corrected one-sample t-tests on post_ccPAS indices for each session and group were performed, confirming that motion sensitivity improved at T30 and T60 in both Active-cTBS (p=.049; p=.029) and Sham-cTBS (p=.004; p=.032). All these results clearly indicate that the specific neural substrate responsible for the changes in sensory discrimination performance is traceable in the network between the critical areas V5-V1, and that the inhibition of the IPS region (Active-cTBS) did not produce specific alterations in the accuracy of motion perception. This represents preliminary evidence in favor of IPS involvement in different mechanisms from mere sensory decision.

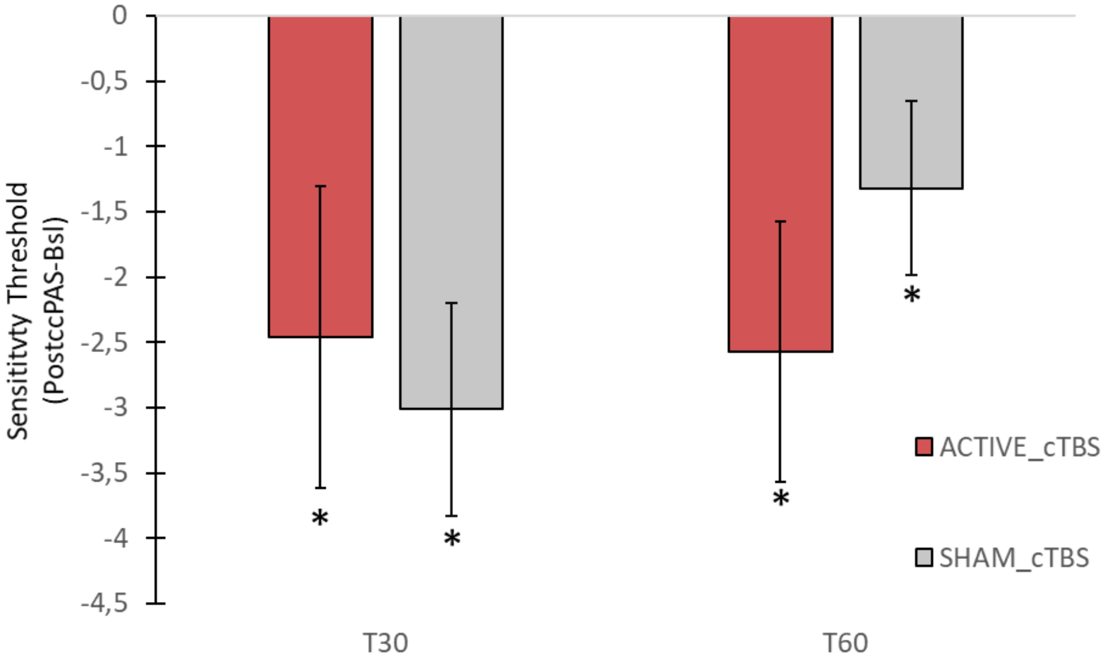


Figure 3. *Changes in motion sensitivity threshold following ccPAS and cTBS. Filled bars represent mean delta at T30 and T60 for active (red) and sham (grey) condition of cTBS; Asterisks show significant one-sample t-test and error bars are indicative of s.e.m.*

Metacognitive abilities

Once the impact of stimulation on sensory decisions was assessed, the performance on the metacognitive level was investigated. Firstly, taking into account the results of the previous study on decision making (Chapter III), an ANOVA was performed on the bsl-corrected values of metacognitive efficiency (meta-d'-d') considering again the factors of Session (T30, T60) and cTBS protocol (Active, Sham). The critical result that emerged was the significant interaction between Session x cTBS (F(1,34)=6.88; p=.01) (Fig.4), in absence of any other relevant outcome (Fs<1.79; Ps>.19). Post-hoc test showed a significant difference between Active and Sham-cTBS protocol at T60 (p=.041).

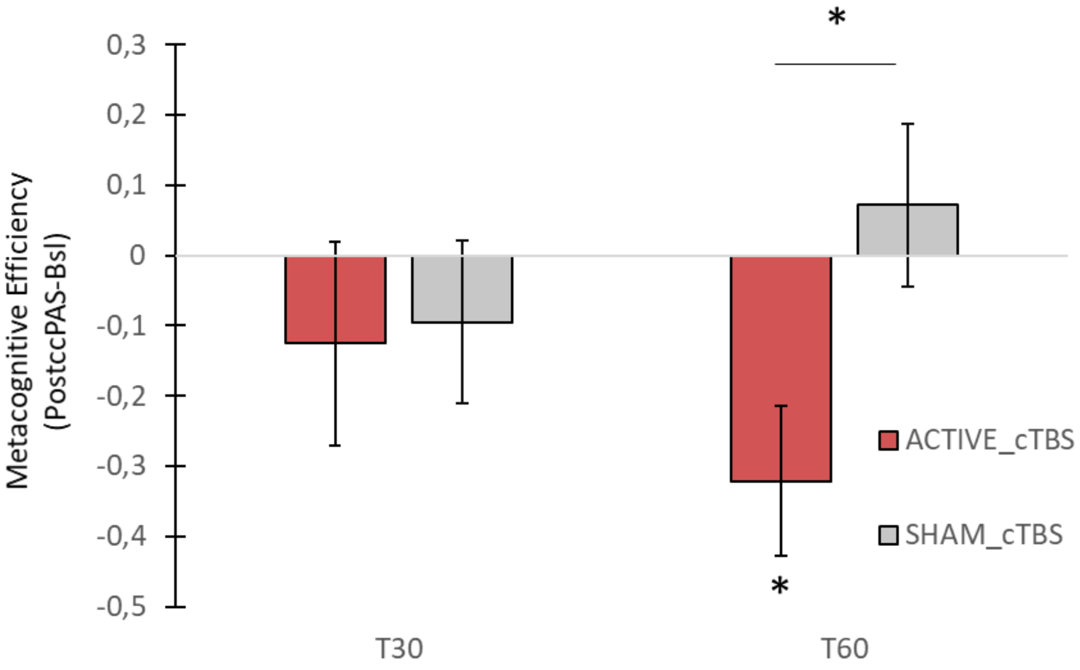


Figure 4.7 *Changes in metacognitive efficiency (metad-d) following ccPAS and cTBS. Filled bars represent mean delta at T30 and T60 for active (red) and sham (grey) condition of cTBS; Asterisks show significant one-sample t-test and post-hoc comparison and error bars are indicative of s.e.m.*

The related ANOVA on raw pre- and post-stimulation performance levels (Session: BSL,T30,T60) of the two groups (cTBS: Active, Sham), showed again a significant interaction of Session x cTBS (F(2,68)=3.65; p= .03). Post-hoc analyses showed only a significant difference between BSL and T60 for the Active cTBS condition (p=.012), suggesting a circumscribed effect on metacognitive efficiency provoked by the inhibition of IPS. Additional one-sample t-tests on post_ccPAS indices for each session and group were performed, confirming that the metacognitive alterations were not due to ccPAS administration, since at T30 sessions no significant effects were traced (Active, p=.59; Sham, p=.42). Indeed, the specific effect was only observable following the cTBS protocol at T60 sessions (Active, p=.017; Sham, p=.27). These results pointed out that IPS seems to be involved in a more complex role in perceptual decision-making, dissociable from the activity of sensory elaboration in V5/MT+.

Regarding the effects on metacognitive sensitivity (meta-d'), the ANOVA on baseline corrected values showed no relevant main effect or interactions (Fs<1.71; Ps>.19). This result further supports our previous findings (See previous report: Chapter III) showing an absence of modulation on this specific metacognitive component following the induction of plasticity on the IPS-V1 network.

Finally, we assessed the fluctuations on the metacognitive bias (average confidence). ANOVA on baseline-corrected values showed an interesting significant interaction of Session x cTBS (F(1,34)=4.81; p=.035). Post-hoc test indicated that a change in confidence was present only in cTBS active condition between T30 and T60 sessions (p=.016), without differences between groups at any Session. One sample t-test on post_ccPAS indices showed that metacognitive bias was generally higher than baseline levels in all sessions (Ps < .015) except the one following inhibitory cTBS (p=.12). This result is not clearly interpretable, but it seems to indicate that the inhibition of IPS influenced the building of perceptual confidence afterward the sensory decisions.

Discussion

In the current experiment, we attempted to understand through a manipulatory approach which neural substrates are responsible for building up sensory decisions and evaluating their accuracy. For this purpose, specific areas and networks involved in perceptual decision-making were targeted through offline stimulation protocols capable of modulating the functionality of cortical substrates in a plastic and reversible way (Suppa et al., 2017), allowing to evaluate the behavioural consequences (Guidali et al., 2021). Specifically, by involving two experimental groups, we preliminarily increased in all the participants the connectivity of the V5-V1 circuit, which is crucial for sensitivity to visual motion. Subsequently and within the temporal window of effectiveness of the ccPAS protocol, the activity of the IPS/LIP - which seems mainly involved in more complex aspects of integration of decision-making signals and on metacognitive aspects - was modulated in a dissociative way according to the group, by inhibiting its function (Active cTBS) and comparing it with a control condition (Sham cTBS).

Results showed a clear dissociation between the IPS/LIP and V5/MT influence on decision-making aspects. We found that motion sensitivity specifically relates to the activity of the V5-V1 recurrent network, since the improvements in motion elaboration (i.e., reduced perceptual threshold) were traced following the enhancement of the connectivity between the two areas in all subsequent sessions (T30 and T60) in both the tested groups, without any impact induced by the interference on the IPS functionality. This allows to exclude the involvement of the parietal area in the ability to accurately discriminate motion. Crucially, the latter region appears mainly involved in metacognitive aspects, as we found an evident modulation of metacognitive efficiency, or the extent to which a metacognitively optimal observer is aware of their performance, following the application of the cTBS over IPS. More in depth, in the specific session following the inhibition of the area (i.e., T60) the participants reported significantly lower levels of metacognitive efficiency relative to the control participants (Sham cTBS). This form of dissociation of behavioural effects in the T60 session would seem to imply a different cortical substrate for the aspects of perceptual accuracy and the rating of confidence, at least for the perception of movement.

A further metacognitive behavioural modification that has been traced concerns the modulation of the average confidence (i.e., metacognitive bias), considered as a less detailed index of metacognitive abilities than the measure of efficiency. However, the effect reflected a significant decrease in the overall confidence level after the administration of cTBS on IPS (T60), compared to the previous session (T30). Nevertheless, the experimental groups did not differ from each other in the T60 session, preventing us to speculate further on this effect.

To sum up, results suggest that sensory and metacognitive components of perceptual decisions emerge from dissociated neural substrates, which elaborate specific information and (or) express distinct computations.

Each decision is followed by a process of estimating the accuracy of our decisions, a process known as visual confidence that represents a judgment of a judgment, then taking the form of an element belonging to metacognition (Metcalfe and Shimamura 1994). Noting then, that although accuracy and trust are related, they can also be dissociated (Mamassian et al., 2016).

There is a close correlation between accuracy and perceived certainty, assuming that it has also been proposed previously (Kepecs et al., 2008), but subsequent studies have shown that although they emerge from a similar process, the measures of accuracy and decision-making confidence may not be related to each other, but dissociated (Mamassian, 2016).

The recurring network involving V5 / MT and the first visual areas appears to be closely related to signal movement processing and awareness. On the other hand, the network involving IPS/LIP and probably early visual areas appears to be crucial for orchestrating how subjective confidence in a choice regarding motion perception. In the previous related work (Chapter III), it was demonstrated the role of V5-V1 and IPS-V1 reentrant connections in perceptual decision-making, highlighting how the modulation of connectivity to feedback between IPS and V1 modulates the metacognitive efficiency, but not the sensory precision with which the decision is finalized. Strengthening the connections between V5-V1 through ccPAS with a simultaneous inhibition of the activity of IPS through the use of cTBS has allowed us to understand whether the activity of the latter is crucial only for what concerns the subjective component of decision making or whether it has a more generic role.

The study presented, thus proves the existence of a dissociation between an objective aspect of the decision, therefore of accuracy, and the certainty associated with the choice made. Confirming how close the relationship between parietal lobe and confidence is, as we have seen in previous chapters, and affirming the notion that decision confidence depends on the activity of the parietal cortices (Gherman & Philiastides, 2015; O'Connell et al., 2012; Van Den Berg et al., 2016). Moreover, based on neurophysiological evidence some authors proposed an 'uncertainty-monitoring' neuronal population (Fleming & Dolan, 2012; Kepecs et al., 2008). This ensemble, possibly the parietal node of LIP/IPS, could interacts with the other populations engaged in decision-making to continuously monitor uncertainty in the network via a feedback loop mechanism (Yeung et al., 2004).

Future research could shed light on the nature of IPS as a neural basis for a domain-general mechanism of perceptual security; specifically, the area in question could mediate the perceptual decision not only on movement, but also on other properties of visual stimuli.

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