

Split-brain patients: Visual biases for faces

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Abstract

Split-brain patients constitute a small subpopulation of epileptic patients who have received the surgical resection of the callosal fibers in an attempt to reduce the spread of epileptic foci between the cerebral hemispheres. The study of callosotomy patients allowed neuropsychologists to investigate the effects of the hemispheric disconnection, shedding more light on the perceptual and cognitive abilities of each hemisphere in isolation. This view that callosotomy completely isolates the hemispheres has now been revised, in favor of the idea of a dynamic functional reorganization of the two sides of the brain; however, the evidence collected from split-brain patients is still a milestone in the neurosciences. The right-hemispheric superiority found in the healthy population concerning face perception has been further supported with split-brains, and it has been shown that the right disconnected hemisphere appears superior to the left hemisphere in recognizing and processing faces with similar characteristics as the observers' (e.g., gender, identity, etc.). Even more controversial is the field of hemispheric asymmetries for processing facial emotion, some evidence suggesting a right-hemispheric superiority for all emotions, some others showing a complementary hemispheric asymmetry depending on the positive or negative emotional valence. Although the practice of callosotomy is mostly abandoned today in favor of pharmacological alternatives, further studies on the remaining split-brain patients could help advance our understanding of hemispheric specialization for social stimuli.

Keywords

Split-brain patients, Face perception, Hemispheric asymmetry, Social cognition, Visual processing

1 SPLIT-BRAIN PATIENTS

The expression “split-brain patient” typically refers to individuals suffering from epilepsy, who underwent the surgical resection of the *corpus callosum* (CC), in an attempt to reduce the spread of epileptic *foci* between the cerebral hemispheres (Zaidel and Iacoboni, 2003). This invasive treatment has been mostly abandoned today (Prete and Tommasi, 2017), due to the introduction of pharmacological therapies that are more efficient than those available some decades ago. Nevertheless, it is still used in the most drug-resistant forms of epilepsy (Englot et al., 2017). The surgery has been shown to effectively reduce the spread of epileptic activity between the hemispheres and improve the quality of life of patients (Unterberger et al., 2016).

The CC is the largest bundle of white matter connecting the left and right hemispheres, and it is composed of different functional portions (Fabri and Polonara, 2013). As shown in Fig. 1, the most posterior portions of the CC are the *splenium* and the *isthmus*, and they connect occipital, parietal, and temporal areas across the two hemispheres. Frontal and temporal cortices are connected via the *trunk*, whereas prefrontal areas are connected through the *genu* and the *rostrum* (Fabri and Polonara, 2013). The surgical section of the CC can either be complete (complete callosotomy), or it can involve only one or more specific portions of the fiber bundle (partial callosotomy). In some cases, additional interhemispheric commissures (i.e., anterior, hippocampal, posterior, and collicular commissures) are sectioned (commissurotomy; e.g., Uddin, 2011).

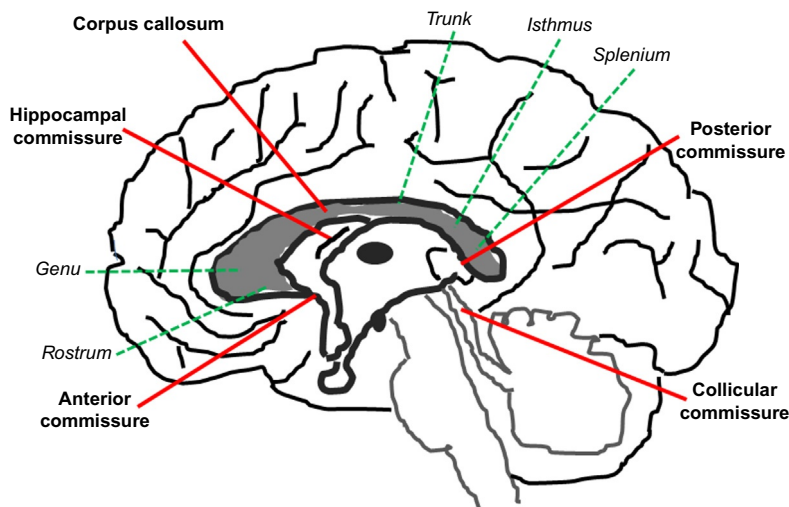


FIG. 1

Schematic representation of the interhemispheric commissures (the corpus callosum is represented in *gray*; portions of the corpus callosum are labeled in *italics*).

The absence of callosal fibers can also result from a congenital condition, and in this case it is defined as *callosal agenesis* (e.g., [D'Antonio et al., 2016](#)). Even if callosal agenesis was previously considered to be “asymptomatic” (thanks to an interhemispheric reorganization due to cerebral plasticity), it has been found that patients with callosal agenesis show a syndrome similar to that of split-brain patients, both in the perceptual and in the motor domains ([Lassonde et al., 1995](#)).

In the 1940s, Akelaitis described the positive clinical outcome of the first surgical resections of the CC carried out on epileptic patients by van Wagenen ([Akelaitis, 1941a,b](#); [Akelaitis et al., 1942](#); [Mathews et al., 2008](#)). [Akelaitis \(1941a,b\)](#) and [Akelaitis et al. \(1942\)](#) described the medical improvement in seizure control after complete or partial callosotomy: according to these pioneering observations, the intervention did not affect the patient’s perceptual ([Akelaitis, 1941a](#)) and motor abilities ([Akelaitis et al., 1942](#)), nor their psychiatric condition ([Akelaitis, 1941b](#)). Possibly the first paper describing the cognitive outcome of an epileptic patient who underwent the surgical resection of the CC was that published about two decades later, in 1962, by [Gazzaniga, Bogen, and Sperry](#) (previous cases were described for instance by [Sperry in 1961](#), but no cognitive effects had been noticed). The authors confirmed that the surgical intervention improved the clinical condition of the patients, by decreasing the frequency of seizures, but they presented the so-called classical disconnection syndrome (see [Section 2](#)).

Conducting research with split-brain patients constitutes a milestone for the neurosciences, but it is a hard and provides limited opportunities, due to the patients’ difficulties in maintaining a high level of attention, the effect of patient medications, and often an unfamiliarity with the use of computers used for presenting experimental paradigms (see [Corballis and Häberling, 2017](#)). Nevertheless, the research carried out with split-brain patients over the last decades has continued to help clarify hemispheric competences in disparate domains, such as language ([Bogen, 1997](#); [Levy, 1983](#)), music perception ([Prete et al., 2015c](#)), spatial abilities ([Corballis et al., 2010](#); [Hausmann et al., 2003](#); [Prete et al., 2017a, 2018b](#)), memory ([Zaidel, 1995](#)), attention ([Berlucchi et al., 1997](#); [Luck et al., 1994](#); [Ptito et al., 2009](#)), and moral reasoning ([Miller et al., 2010](#)), among others.

Because the CC is the main connection between the left and right hemispheres, the first observations of split-brain patients were centered on the evaluation of the specific skills of each hemisphere, based on the idea that the functional separation was so sharp and strong to give rise to two “minds” or two “consciousnesses”: [LeDoux et al. \(1977\)](#) described the case of a split-brain patient who showed preserved linguistic skills in both of his disconnected hemispheres, so that the authors concluded that “*human conscious processes can be doubled by cerebral commissurotomy*” ([LeDoux et al., 1977](#), p. 420). When detailing the clinical case, the authors reported that “On a day that this boy’s left and right hemispheres equally valued himself, his friends, and other matters, he was calm, tractable, and appealing. On a day when testing indicated that the right and left sides disagreed on these evaluations, the boy became difficult to manage behaviorally. It is as if each mental system could read the emotional differences harbored by the other. When they were

discordant, a feeling of anxiety, which appeared to be read out by hyperactivity and general aggression, was engendered. This clear example of surgically produced psychological dynamism, seen for the first time in P. S., raises the question whether such processes are active in the normal brain, where different mental systems, using different neural codes, coexist within and between the cerebral hemispheres” (LeDoux et al., 1977, p. 420).

The idea of a split consciousness was also proposed by Dimond (1978) who pointed out that the *splenium* was the site in which a general consciousness circuit takes place. In the same vein, Zaidel and Iacoboni (2003) wrote “*Soon after surgery there are episodes of intermanual conflict, in which the hands act at cross-purposes. Patients sometimes complain that their left hand behaves in a ‘foreign’ or ‘alien’ manner, and they routinely express surprise at apparently purposeful left-hand actions (autocriticism)*” (p. 320). The issue of one integrated vs two separated conscious entities in the human brain remained a central core to the neurosciences, so much so that after 40 years of research, the “unity of consciousness” is still one of the most debated issues in the split-brain literature (e.g., Bayne, 2008; Colvin et al., 2017; Volz and Gazzaniga, 2017).

Over time the idea of callosal fibers as mere connection between two independent hemispheres has been replaced by the softer interpretation of two cooperating halves of the brain that continue to interact even in the absence of callosal connections, thanks to subcortical bilateral projections (e.g., Funnell et al., 2000). Similarly, also the idea of a “dominant” hemisphere has been replaced with that of a possible superiority of one hemisphere over the other, but with the possibility that the processing of information can occur in each half of the (disconnected) brain (see Corballis and Häberling, 2017). Support for this view can be found in some studies with split-brain patients. For instance, split-brain patients were able to make perceptual judgments, such as matching of nonsense shapes, across the vertical meridian (Zaidel, 1995), showing that unilateral information can reach the contralateral hemisphere in the absence of callosal fibers, even if spatial information is more efficiently processed by the right hemisphere (Funnell et al., 1999). In summary, the findings highlighted by testing split-brain patients add important evidence about the role of interhemispheric connections, as well as about the specific competences of the two halves of the brain and the mechanisms involved in neuroplasticity.

1.1 THE CALLOSAL DISCONNECTION SYNDROME

The so-called callosal disconnection syndrome manifests itself in a combination of several impairments, mainly concerning bimanual coordination (Berlucchi, 2012), spatial attention, and language impairment of the nonlinguistic hemisphere (e.g., Lausberg et al., 1999). The central core of this syndrome is rooted in the associationist theory proposed by Wernicke (1874), and then revised by Geschwind (1965a,b), according to which all cognitive functions emerge from white matter connections with different cerebral areas. In this view, cognitive, behavioral, and

psychological dysfunctions occur as the result of white matter lesions. In this frame, the expression “disconnection syndromes” is used to define all of the disorders due to an acquired lesion involving neuronal projections, which leads to specific high-level disorders, including language disability (aphasia), motor disorder (apraxia), sensory processing deficit (agnosia), reading disorder (alexia), and so on (Catani and ffytche, 2005). When referring to split-brain patients, the “callosal syndrome” is mainly defined as the linguistic inability of the right hemisphere, which is evident in higher order deficits in the left hemisphere, such as the inability in reading, moving, and recognizing objects in the left hemisphere (Zaidel, 1983).

In the past, the classic view posited that callosal fibers simply allow the exchange of information between the two hemispheres: “*a copy of the visual world as seen in one hemisphere is sent over to the other*” through the callosum (Gazzaniga, 1967, p. 29). Similarly, Geschwind and Kaplan (1962) asserted that the callosal disconnection syndrome was the exact result of the interrupted exchange of information between the two sides of the brain. However, besides being the largest group of fibers connecting the two halves of the brain, the CC also plays a role in functional asymmetries. Only recently it has been found that the CC is not solely constituted of white matter, but it contains active cells: a series of functional magnetic resonance imaging (fMRI) studies highlighted functional activation in different portions of the CC depending on the nature of stimuli presented (Fabri et al., 2014; Gawryluk et al., 2009). It is now considered that symptoms following callosal disconnection are attributable to the loss of a distributed balance mediated by the callosal fibers together with the other cortical and subcortical commissures. The notion of an equilibrating role of the callosum was initially put forward by Kinsbourne (2003), based on evidence that callosal fibers are both excitatory and inhibitory and that some excitatory fibers activate inhibitory interneurons. On these grounds, the callosal disconnection syndrome could be seen as the result of a lack of response of the “uninformed” hemisphere, assuming that information reaches it anyway by means of subcortical pathways. With regard to the subcortical interhemispheric connections, Doty (1989) previously proposed that the serotonergic raphe system in the pons and the mesencephalon could be responsible for bilateral subcortical activation.

The prevalent interpretation nowadays is that callosal connections are mainly involved in interhemispheric communication, but they also have a functional role and they are crucial in determining cerebral functional asymmetries. For instance, Barnett and Corballis (2005) found that the right-to-left information transfer time was faster than the opposite route (left-to-right), and they attributed this finding to the faster axonal speed arising in the right rather than in the left hemisphere, due to the greater number of fast-conducting, myelinated fibers in the right hemisphere. This idea had been previously proposed by Marzi et al. (1991, 1997) who argued that callosal projecting neurons are more numerous in the right hemisphere than in the left hemisphere. Based on this observation, the authors also proposed an explanation for a number of impairments following right-hemispheric damage that were possibly attributable to the callosal projections, as the deficit in attention to and awareness of the left visual field (LVF), namely, spatial hemineglect

(Berlucchi and Vallar, 2018), and the inability to consciously perceive stimuli presented in the LVF when they are presented together with stimuli in the right visual field (RVF), namely, visual extinction (Chen and Spence, 2017). According to the hypothesis proposed by Marzi et al. (1997), a right-lateralized brain injury should cause a greater loss of callosal fibers, resulting in a stronger impairment of interhemispheric transmission. Thus, the information reaching the left hemisphere can project to the right, but the information reaching the right hemisphere cannot be projected to the left: the result is the extinction (or neglect) of the stimuli presented in the LVF (Heilman et al., 1987). The model explained the case of right-damaged patients who did not show extinction as rare cases due to the preserved callosal projections despite the right hemisphere lesion.

The view of axonal fibers involved in functional asymmetries and lateralized attentional deficits (e.g., spatial hemineglect, extinction) has been widely referenced in a number of studies and neuropsychological models (Corbetta and Shulman, 2011; De Schotten et al., 2005; He et al., 2007; Gaffan and Hornak, 1997). Furthermore, Corballis et al. (2005) described a case of alternating hemineglect present in a split-brain patient with a complete callosal resection, further supporting the role of the callosal projections in attentional processes: the patient showed slower reaction times for stimuli flashed in the LVF, but he did not show attentional bias when stimulus location was defined by continuous markers presented in both visual fields.

It should be noted that when we refer to complex perceptual stimuli, the disconnection syndrome could be weakly evident, unless it is studied with specific methodologies. In the visual domain, for instance, the most exploited paradigm is that of the divided visual field presentation (Bourne, 2006). In this paradigm, a visual stimulus is presented in the left or in the RVF, for a duration shorter than that needed to make a saccadic movement (about 150 ms, computer-based, tachistoscopic presentation), and the observer is required to gaze ahead centrally, without moving their gaze directly to the location of the stimulus. When the stimulus is presented in a lateralized fashion, it is projected to the nasal portion of the retina, which is directly connected with the contralateral hemisphere (e.g., left eye/right hemisphere). This procedure allows researchers to be confident that a stimulus is directly processed by one hemisphere.

The computer-based presentation of lateralized stimuli has been widely exploited to investigate hemispheric skills in healthy observers. The performance of split-brain patients in this type of tasks gives researchers a unique opportunity to evaluate the ability of each hemisphere “in isolation.” Brown et al. (1999) recorded event-related potentials (ERPs) during a matching task in which letters and dots were presented unilaterally and bilaterally, in a group of six patients with either complete or partial (posterior) agenesis, in a commissurotomy patient, and in healthy controls. The authors found that none of the patients presented the early visual ERP components (P1/N1) related to visual perception without high-level cognitive processing, in the hemisphere ipsilateral to the stimulus presentation, showing that posterior callosal projections are necessary for an interhemispheric exchange of visual information. Interestingly, they also found that the commissurotomy patient was not capable at

correctly comparing bilaterally presented letters, but that the patients with callosal agenesis—with an intact anterior commissure—carried out the task successfully, indicating that the anterior projections are sufficient to allow for a bilateral visual matching.

To conclude, the “callosal syndrome” is mainly evident in higher order deficits occurring in the left hemispace (Zaidel, 1983). The classical view of the CC as a mere connection between the two hemispheres (Seymour et al., 1994) is now out of date, in favor of an integrative view of interhemispheric communications taking place by both white matter connections and bilateral subcortical projections. Anatomical and functional studies on the interhemispheric commissures allowed neuroscientists to define the specific functional role of each portion of the CC (Fabri et al., 2014; Gawryluk et al., 2009), and the evidence collected with patients with different degrees of callosal resection further confirmed these findings (e.g., Fabri and Polonara, 2013).

2 HUMAN FACES AS SPECIAL STIMULI

Humans are able to recognize identity, gender, age, and a number of different characteristics from the face of conspecifics, and this ability seems to be innate, being also present in newborns (e.g., Johnson et al., 1991). It has been consistently shown that face processing mainly takes place in the right hemisphere (e.g., Bruce et al., 1981; Gross et al., 1972; McCarthy et al., 1997; Prete et al., 2015e; Rizzolatti et al., 1971; Yovel, 2015), and that a right temporal region, the fusiform gyrus, is specifically devoted to facial analysis, so much so that this area has been defined “fusiform face area” (FFA; Kanwisher and Yovel, 2006; Kanwisher et al., 1997). These findings are further supported by the evidence that a unilateral right-hemispheric lesion can cause the inability to recognize faces (prosopagnosia), whereas a unilateral, left-hemispheric lesion does not alter face recognition (e.g., Barton et al., 2002), even if some evidence suggest that prosopagnosia is more severe with bilateral than unilateral lesions (Barton, 2008).

The right-hemispheric superiority in face processing has been supported by behavioral, electrophysiological, and neuroimaging studies examining healthy participants. Starting from the behavioral findings, a right-hemispheric superiority has been shown in the processing of facial stimuli by means of the divided visual field paradigm (e.g., Bourne and Hole, 2006; Verosky and Turk-Browne, 2012). For instance, in a face identity recognition task, it has been shown that when a sample and a target face were serially presented in different orientations (e.g., sample upright and target upside down) and decomposed (e.g., different portions of the images presented detached from each other), the right hemisphere is more efficient than the left hemisphere in identity recognition, with a better performance for target stimuli presented in the left than in the RVF (Prete et al., 2015e). Moreover, electroencephalographic studies corroborate this evidence, showing enhanced and faster ERP components in the right than in the left hemisphere during face perception (e.g., Prete et al., 2015a; Yovel, 2016). Also, brain stimulation techniques provide

further evidence of this asymmetry (Jonas et al., 2015; Parvizi et al., 2012; Rangarajan et al., 2014) and fMRI definitively supports the strong right-hemispheric involvement in face analysis (e.g., Dricot et al., 2008; O'Neil et al., 2014). This hemispheric asymmetry has been explained with reference to the right-hemispheric superiority for global vs local analysis of faces (Karim and Kojima, 2010), for configural vs analytic processing of faces (Chance, 2014), and for low vs high spatial frequency detection of faces (Faubert et al., 2017; Keenan et al., 1989), among others.

Despite the amount of evidence in support of the right-hemispheric superiority in face processing, interhemispheric cooperation in face analysis has been revealed in different studies. For instance, Davies-Thompson and Andrews (2012) presented a sample of 72 right-handed participants with the images of faces, bodies, inanimate objects, places, and scrambled images, during fMRI acquisition. The results suggest the involvement of a face-processing network, including FFA and occipital face area (OFA), as well as different temporal sites, inferior frontal cortex, and subcortical structures such as amygdala and superior colliculus. The authors found that facial processing increased the functional connectivity among these areas, mainly in the right hemisphere—particularly between FFA and OFA. Importantly, they also reported that the covariation in activity between corresponding areas in the two hemispheres (e.g., left and right FFA) was stronger than the intrahemispheric connectivity among different facial processing areas (e.g., right FFA and right OFA). This result supports the hypothesis that, in addition to the right-hemispheric superiority for facial stimuli, interhemispheric connections are involved in face processing. In line with this evidence, Geiger et al. (2016) found a strong interhemispheric connectivity between the left and right fusiform gyrus during memory consolidation of facial images. Finally, in a divided visual field paradigm during fMRI carried out with 20 right-handed and 20 left-handed participants, Frässle et al. (2016) found a stronger left-hemispheric FFA involvement during face processing in left handers compared to right handers, whereas no difference between the two groups was found for objects and scrambled images. The authors concluded that handedness preference affects cerebral asymmetries for faces.

To conclude, the right-hemispheric superiority in face processing is widely accepted: it has been shown by means of behavioral paradigms (Bourne and Hole, 2006; Prete et al., 2015e; Verosky and Turk-Browne, 2012), neurological patients (Barton et al., 2002), electrophysiological findings (Prete et al., 2015a; Yovel, 2016), brain stimulation methods (Jonas et al., 2015; Parvizi et al., 2012; Rangarajan et al., 2014), and neuroimaging techniques (Dricot et al., 2008; O'Neil et al., 2014). Despite this unquestioned cerebral asymmetry, the interhemispheric connections have been proven to have a crucial role in facial processing (Davies-Thompson and Andrews, 2012; Geiger et al., 2016).

2.1 HEMISPHERIC ASYMMETRY FOR FACES IN THE DISCONNECTED BRAIN

The performance of callosotomized patients could shed more light on the issue of hemispheric asymmetry for face perception and on the possible hemispheric imbalance for the different features constituting the complexity of facial stimuli.

For instance, patients with callosal agenesis showed no difficulties in a facial gender discrimination task, but they revealed poor performance with respect to a control group in facial emotion coding, which seems to be related to a different pattern of gaze pointing involving the lowest part of the facial stimuli rather than the eye region (Bridgman et al., 2014). The authors suggested that this peculiarity in facial scanning could be the reason why acallosal patients often show a deficit in social interactions and in particular in facial emotion detection, attributable to the reduced interhemispheric connectivity. Also in callosotomy patients the gender recognition of facial stimuli has been tested (Prete et al., 2016), but the results are controversial. In a divided visual field paradigm with a male split-brain patient (DDC), the accuracy of gender categorization resulted at chance level when stimuli were presented tachistoscopically in the RVF and thus directly projected to the left hemisphere. Nevertheless, when facial stimuli were presented in the LVF, the patient carried out the task successfully, but only when stimuli were male faces (Prete et al., 2016). Thus the study revealed a right-hemispheric lateralization of the Own-Gender Bias; the preference in recognizing persons belonging to the same gender as the observer's (e.g., Wright and Sladden, 2003). The bias, often found in favor of the right hemisphere for those stimuli having the same characteristics as the observers', has been explained by making reference to the right-hemispheric involvement in self-recognition (Keenan et al., 2005). In fact, the substrates of self-representation and self-consciousness are lateralized to the right hemisphere, mainly involving temporal and prefrontal areas (e.g., Devue and Brédart, 2011; Feinberg and Keenan, 2005; Keenan et al., 2005).

However, the same gender categorization task as the one carried out by patient DDC was also administered to a control group of healthy female and male participants did not reveal the same asymmetry as DDC (Prete et al., 2016). Healthy participants showed a right-hemispheric superiority for female face, and a left-hemispheric superiority for male face categorization, independently of the gender of participants (see also Parente and Tommasi, 2008; Prete et al., 2017b). This crossed bias in healthy participants has been attributed to an innate right-hemispheric superiority in the processing of female faces (Parente and Tommasi, 2008; Prete et al., 2017b). This asymmetry would be due to the fact that newborns are mainly cradled on the left side of the maternal body, so that the "social" right hemisphere of both newborn and mother is more directly connected, favoring an optimal social interaction between cradler and newborn. The specular left-hemispheric superiority for male faces has been attributed to a complementary cerebral specialization (the leftward cradling bias being present only in females; Todd and Banerjee, 2016). A different result was found by Luo et al. (2011) who tested a male patient with a lesion involving the splenium and the left medial occipitotemporal region. When the patient was presented with chimeric faces constituted by a female hemiface juxtaposed to a male hemiface to form one face, he reported not to see the chimeras and based his gender categorization on the left hemiface, showing a right-hemispheric superiority in this task. It has to be noted that the combination of the left-hemispheric lesion and the partial callosal resection does not allow for a clear-cut conclusion about the patient's performance in gender discrimination.

A different divided visual field paradigm was used by [Mason and Macrae \(2004\)](#) during a gender categorization task and an identity recognition task, carried out by both the male split-brain patient JW and a control group. In two different blocks, participants had to respond whether two faces presented together either in the left or in the RVF were of the same gender (gender categorization) or the same person (identity categorization). Results showed no asymmetry during the gender categorization task, neither in the patient nor in the control group, but a right-hemispheric superiority was found for identity matching. A similar right-hemispheric superiority for facial identity recognition was also described in a seminal study involving four split-brain patients described by [Levy et al. \(1972\)](#).

A possible explanation of the different results found in gender recognition paradigms could be the specific task required. On one hand, the task carried out by DDC ([Prete et al., 2016](#)), revealing the right-hemispheric lateralization for the Own-Gender Bias, was a pure categorization task (response: female/male). On the other hand, the task carried out by JW ([Mason and Macrae, 2004](#)), revealing no asymmetries, was a gender matching task in which a direct comparison between two stimuli was required (response: same/different). Moreover, JW was also tested by [Turk et al. \(2002\)](#) in a divided visual field paradigm in which morphed faces, created by mixing the photograph of the patient and that of a familiar person, were presented in one visual field at time. The authors found a right-hemispheric superiority in the recognition of familiar faces, but a left-hemispheric superiority in self-face recognition, even if both disconnected hemispheres carried out the identity task with an accuracy higher than chance (response: yes/no, for both blocks of trials in which JW was required to respond whether the stimulus was either the familiar face, or it depicted his own face). The authors attributed this left-hemispheric bias to a “self-memory system,” i.e., a distributed network responsible for the autobiographical knowledge and the idea of self ([Turk et al., 2002](#)). On the other hand, some months later the opposite pattern was described by [Keenan et al. \(2003\)](#), who presented morphed faces centrally and required the left-handed male patient ML to use the left or the right hand to respond whether the stimulus contained his own face or a familiar person’s face. They found that the patient reported seeing his own face more frequently when the left hand was used, showing a right-hemispheric superiority in self-face processing, in accordance with previous galvanic recordings described by [Preilowski \(1977\)](#). They also found a better performance in classifying familiar persons’ faces with the right hand (left hemisphere). Finally, the female patient NG was tested by [Uddin et al. \(2005\)](#) in a divided visual field paradigm in which stimuli were facial morphs, mixing the patient’s own face and an unknown face, or mixing a familiar female face and an unknown female face. Results showed that both hemispheres were capable of self-recognition, but that only the right hemisphere could also successfully recognize the familiar face. All these findings seem to suggest that individual differences, together with the specific experimental manipulations used, lead to different patterns of hemispheric asymmetries.

To summarize, it is still uncertain whether the recognition of familiar faces in general, or that of self-face in particular, is clearly lateralized to one hemisphere.

One possibility is that the left- and right-hemispheric superiorities found from time to time could be specifically attributed to the task required. In general, we can conclude that the majority of studies have revealed a superiority of the right hemisphere in the processing of faces, mainly for those faces having the same characteristics as the observer's, e.g., own-gender (Luo et al., 2011; Prete et al., 2016), own-face (Keenan et al., 2003; Preilowski, 1977), and a right-hemispheric superiority has also been consistently found for facial identity (Levy et al., 1972; Mason and Macrae, 2004) and familiarity (Turk et al., 2002; Uddin et al., 2005).

2.2 EMOTIONS AS VIEWED BY A DISCONNECTED BRAIN

A crucial piece of information conveyed by a face is the emotional state of that person. Emotional expressions are automatically detected (e.g., Stefanics et al., 2012), and this ability allows us to understand the mood of other person and to adequately respond in terms of both behavioral reactions and physiological adjustments (e.g., Jessen et al., 2016). Emotional coding has been widely studied by psychologists, neuroscientists, and clinicians, due to its central role in our daily interactions. A debated point in this frame is concerning hemispheric asymmetries for emotional processing. Two main theories are alternatively supported by research (for a meta-analysis see Fusar-Poli et al., 2009): on one hand, according to the valence hypothesis (VH), a left-hemispheric/right-hemispheric superiority exists for positive and negative valence emotions, respectively (Baijal and Srinivasan, 2011; Davidson et al., 1987); on the other hand, according to the right hemisphere hypothesis (RHH), positive and negative emotional processing both take place in the right hemisphere (Gainotti, 1972, 2012; Levy et al., 1983; Lindell, 2013).

In a divided visual field task (Stone et al., 1996) each of the disconnected hemispheres of the split-brain patient JW was better than chance at matching facial expressions with emotional words. However, in accordance with the RHH, only the right hemisphere appeared to be able at matching two facial expressions, suggesting a right-hemispheric superiority for emotion processing. Nevertheless, other evidence support the validity of both the VH and the RHH (Prete et al., 2014b): it was suggested that the number of emotional stimuli which have to be processed at once could be the main variable influencing hemispheric asymmetries for emotional stimuli. In this view, when just one emotional face is presented, a right-hemispheric superiority appears (in accordance with Stone et al., 1996); when the load increases—due to the presentation of two emotional stimuli—each hemisphere shows its specialization for positive or negative emotions. Support for this speculation can be found in a task carried out by both a patient with an anterior callosal resection saving the splenium (AP) and a patient with a complete callosal resection (DDV; Prete et al., 2014b). Both patients and a control group of healthy participants were asked to rate the emotional content of chimeric faces constituted by a combinations of happy, sad, and neutral hemifaces, and auditory stimuli constituted by a syllable with happy or sad emotional valence presented in one ear and white noise simultaneously presented in the other ear. AP's responses were driven by the stimulus directly projected to the right

hemisphere during unimodal presentation (left hemiface and syllable presented in the left ear), but his performance supported the VH during audiovisual presentations (chimeric faces and dichotic stimuli presented simultaneously). However, DDV's judgments were based on the emotional expression of the right hemiface in all conditions. This pattern of results supports the need of an intact splenium in order to maintain the hemispheric imbalance for positive and negative emotions found in healthy participants.

2.3 SUBLIMINAL EMOTIONS AND THE DISCONNECTED BRAIN

Besides the evidence of hemispheric asymmetries for consciously perceived emotional stimuli, different studies also revealed a subcortical asymmetry concerning subliminal emotions: as reviewed by [Johnson \(2005\)](#), a number of neuroimaging, electrophysiological, and neuropsychological studies suggest the existence of a subcortical route specifically involved in a fast and subliminal analysis of facial features. This subcortical route primarily includes the amygdala and is responsible for emotional encoding, based on the analysis of low spatial frequencies (LSF). The output of this route would be then conveyed to cortical areas, which are mainly responsible for the processing of the high spatial frequencies (HSF); it also modulates the cortical activity in a bottom-up pathway. A dissociation in hemispheric lateralization for subliminal and supraliminal emotion processing was revealed by [Làdavas et al. \(1993\)](#), in a split-brain patient. The authors exploited a divided visual field paradigm in order to investigate the possible lateralization for emotional (disgusting and sex-related) and neutral stimuli presented below the conscious perceptual threshold (20ms) and above the conscious perception threshold (150ms). For both subliminal and supraliminal conditions the heart rate (HR) raised when emotional contents were presented, with respect to neutral stimuli. Moreover, when the stimuli were consciously perceived by the patient, both behavioral responses and HR did not differ across LVF and RVF presentations. However, when the stimuli were presented below the consciousness threshold, the HR was increased when emotional stimuli were presented in the LVF (right hemisphere) but not in the RVF (left hemisphere). The authors concluded that the right hemisphere is dominantly involved in the physiological modulation due to emotional detection, even in the absence of conscious perception of the stimulus.

The involvement of the subcortical route in LSF emotional detection has also been found in a study with emotional "hybrid faces" ([Laeng et al., 2010](#)). These stimuli are created by superimposing the photograph of an emotional face filtered at LSF to the photograph of the same person with a neutral pose filtered at HSF. Emotional hybrid faces have been then exploited in a number of paradigms involving both healthy participants and split-brain patients, in order to investigate the relationship between emotional detection, spatial frequencies, and hemispheric asymmetries. The emotional expressions mostly used have been happiness and anger, namely, those receiving the highest and lowest friendliness evaluation in the original study by [Laeng et al. \(2010\)](#), meaning that their LSF emotional content was correctly decoded

by observers. In a divided visual field paradigm, hybrid happy, hybrid angry, and neutral faces were presented to healthy participants in a divided visual field paradigm (Prete et al., 2014a). The results showed that the hidden LSF content also modulates the friendliness judgments when presented lateralized. Importantly, stimuli were evaluated as less friendly when they were presented in the LVF than in the RVF, supporting the VH (the left/right hemisphere were more prone to express positive/negative judgments, respectively). In a following study, a different divided visual field paradigm was used: pairs of hybrid or unfiltered angry, happy, and neutral faces were shown in a bilateral presentation task. Two facial stimuli were simultaneously presented, one in each visual field, and a friendliness evaluation task was carried out by healthy participants, the complete split-brain patient DDC, and AP (with the anterior callosal resection; Prete et al., 2015b). The results revealed that when stimuli were hybrid faces, the friendliness judgments were influenced more by the emotional expressions presented in the LVF, supporting a stronger involvement of the right hemisphere in the detection of all subliminal emotions (as suggested by the RHH). This pattern of results was also revealed with unfiltered stimuli both in healthy participants and in AP, whereas the evaluation by the split-brain patient DDC was mainly based on the emotional expression shown in the RVF. The interpretation was that the processing of implicit emotions, contingent upon the LSF analysis of the stimuli, does not require the integrity of callosal fibers and involves the subcortical route lateralized in the right hemisphere. In a further study the patient AP and a control group were presented with hybrid faces during a unilateral presentation paradigm at three different tachistoscopic presentation times (28, 75, 128 ms), and during a bilateral presentation paradigm obtaining by means of chimeric hybrid faces (Prete et al., 2015d). Consistent with previous results, findings showed the unilateral presentation led to a right-hemispheric superiority for all emotions (i.e., RHH), whereas the bilateral presentation revealed a right-hemispheric superiority for negative emotions and a left-hemispheric superiority for positive emotions (i.e., VH). This pattern of results can be considered as a further support for the hypothesis that hemispheric asymmetries for emotions are contingent upon the number of emotional stimuli presented at once: with just one emotional stimulus, the RHH is confirmed, when two different emotional stimuli are presented together, the results support the VH.

Finally, ERPs recorded during the central presentation of hybrid stimuli in healthy participants showed a persistent enhancement of the emotional components P1 and P2 in the right hemisphere for both positive and negative emotions (Prete et al., 2015a), a pattern further supported also by using unfiltered emotional faces (Prete et al., 2018a).

We can conclude that both healthy participants' and split-brain patients' performances reveal different patterns of hemispheric asymmetries depending on the specific paradigm used. When one emotional face is presented, the superiority of the right hemisphere in emotion detection appears, supporting the RHH (Prete et al., 2014a). However, when the cognitive load becomes heavier due to the presentation of different emotional stimuli, the left and the right hemispheres appear to be

specialized in positive and negative emotion detection, respectively, supporting the VH (Prete et al., 2015d). This conclusion is true when posterior callosal connections, namely, the *splenium*, are intact and it allows for a sensory information exchange between the two hemispheres (Prete et al., 2015b).

3 CONCLUSIONS

Evidence collected with split-brain patients provide us with a better understanding of the cerebral correlates of cognitive processes. The “split-brain literature” has been a very important resource for shedding more light on hemispheric asymmetries in the most disparate domains of perception and cognition. The growing introduction of pharmacological treatments for epilepsy has resulted in a reduction in the exploitation of invasive surgical resections of the callosal projections, even if callosotomy is still performed in the most drug-resistant forms of epilepsy (Englot et al., 2017; Prete and Tommasi, 2017). The view according to which each disconnected hemisphere reflects—in an amplified fashion—the functioning of that hemisphere in the intact brain is now less supported than in the past decades (Corballis and Häberling, 2017). The overall clinical condition of split-brain patients best explains some extreme evidence of asymmetry due, for instance, to the cerebral plasticity and to the effect of patient medications (e.g., Corballis and Häberling, 2017). Evidence collected in split-brains precipitated Roger Sperry’s 1981 Nobel Prize in Physiology or Medicine for the discoveries on the functional specialization of the cerebral hemispheres and constitute a milestone for the neurosciences. With regard to facial processing, split-brain patients’ results have revealed a right-hemispheric superiority for the processing of facial features, primarily when they are shared between the observed face and the observer (e.g., own-race bias), as well as a right-hemispheric superiority in emotional detection. The scarce group of split-brain patients still available to be tested today could provide an invaluable contribution to the unresolved issues concerning facial processing and hemispheric asymmetries.

REFERENCES

- Akelaitis, A.J., 1941a. Studies on the corpus callosum: II. The higher visual functions in each homonymous field following complete section of the corpus callosum. *Arch. Neurol. Psychiatry* 45 (5), 788–796. <https://doi.org/10.1001/archneurpsyc.1941.02280170066005>.
- Akelaitis, A.J., 1941b. Studies on the corpus callosum: VIII. The effects of partial and complete section of the corpus callosum on psychopathic epileptics. *Am. J. Psychiatry* 98 (3), 409–414. <https://doi.org/10.1176/ajp.98.3.409>.
- Akelaitis, A.J., Risteen, W.A., Herren, R.Y., Van Wagenen, W.P., 1942. Studies on the corpus callosum: III. A contribution to the study of dyspraxia and apraxia following partial and complete section of the corpus callosum. *Arch. Neurol. Psychiatry* 47 (6), 971–1008. <https://doi.org/10.1001/archneurpsyc.1942.02290060109008>.

- Baijal, S., Srinivasan, N., 2011. Emotional and hemispheric asymmetries in shifts of attention: an ERP study. *Cogn. Emot.* 25, 280–294. <https://doi.org/10.1080/02699931.2010.492719>.
- Barnett, K.J., Corballis, M.C., 2005. Speeded right-to-left information transfer: the result of speeded transmission in right-hemisphere axons? *Neurosci. Lett.* 380 (1), 88–92. <https://doi.org/10.1016/j.neulet.2005.01.025>.
- Barton, J.J., 2008. Structure and function in acquired prosopagnosia: lessons from a series of 10 patients with brain damage. *J. Neuropsychol.* 2 (1), 197–225.
- Barton, J.J., Press, D.Z., Keenan, J.P., O'Connor, M., 2002. Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology* 58 (1), 71–78. <https://doi.org/10.1212/WNL.58.1.71>.
- Bayne, T., 2008. The unity of consciousness and the split-brain syndrome. *J. Philos.* 105 (6), 277–300.
- Berlucchi, G., 2012. Frontal callosal disconnection syndromes. *Cortex* 48 (1), 36–45.
- Berlucchi, G., Vallar, G., 2018. The history of the neurophysiology and neurology of the parietal lobe. *Handb. Clin. Neurol.* 151, 3–30. <https://doi.org/10.1016/B978-0-444-63622-5.00001-2>.
- Berlucchi, G., Aglioti, S., Tassinari, G., 1997. Rightward attentional bias and left hemisphere dominance in a cue-target light detection task in a callosotomy patient. *Neuropsychologia* 35 (7), 941–952.
- Bogen, J.E., 1997. Does cognition in the disconnected right hemisphere require right hemisphere possession of language? *Brain Lang.* 57 (1), 12–21.
- Bourne, V.J., 2006. The divided visual field paradigm: methodological considerations. *Laterality* 11 (4), 373–393. <https://doi.org/10.1080/13576500600633982>.
- Bourne, V.J., Hole, G.J., 2006. Lateralized repetition priming for familiar faces: evidence for asymmetric interhemispheric cooperation. *Q. J. Exp. Psychol.* 59 (6), 1117–1133. <https://doi.org/10.1080/02724980543000150>.
- Bridgman, M.W., Brown, W.S., Spezio, M.L., Leonard, M.K., Adolphs, R., Paul, L.K., 2014. Facial emotion recognition in agenesis of the corpus callosum. *J. Neurodev. Disord.* 6 (1), 32. <https://doi.org/10.1186/1866-1955-6-32>.
- Brown, W.S., Jeeves, M.A., Dietrich, R., Burnison, D.S., 1999. Bilateral field advantage and evoked potential interhemispheric transmission in commissurotomy and callosal agenesis. *Neuropsychologia* 37 (10), 1165–1180.
- Bruce, C., Desimone, R., Gross, C.G., 1981. Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J. Neurophysiol.* 46 (2), 369–384.
- Catani, M., ffytche, D.H., 2005. The rises and falls of disconnection syndromes. *Brain* 128 (10), 2224–2239. <https://doi.org/10.1093/brain/awh622>.
- Chance, S.A., 2014. The cortical microstructural basis of lateralized cognition: a review. *Front. Psychol.* 5, 820. <https://doi.org/10.3389/fpsyg.2014.00820>.
- Chen, Y.C., Spence, C., 2017. Hemispheric asymmetry: looking for a novel signature of the modulation of spatial attention in multisensory processing. *Psychon. Bull. Rev.* 24 (3), 690–707. <https://doi.org/10.3758/s13423-016-1154-y>.
- Colvin, M.M., Marinsek, N.L., Miller, M.B., Gazzaniga, M.S., 2017. Split-brain cases. In: Schneider, S., Velmans, M. (Eds.), *The Blackwell Companion to Consciousness*. Wiley Blackwell, pp. 634–647.
- Corballis, M.C., Häberling, I.S., 2017. The many sides of hemispheric asymmetry: a selective review and outlook. *J. Int. Neuropsychol. Soc.* 23 (9–10), 710–718. <https://doi.org/10.1017/S1355617717000376>.

- Corballis, M.C., Corballis, P.M., Fabri, M., Paggi, A., Manzoni, T., 2005. Now you see it, now you don't: variable hemineglect in a commissurotomy man. *Cogn. Brain Res.* 25 (2), 521–530. <https://doi.org/10.1016/j.cogbrainres.2005.08.002>.
- Corballis, M.C., Birse, K., Paggi, A., Manzoni, T., Pierpaoli, C., Fabri, M., 2010. Mirror-image discrimination and reversal in the disconnected hemispheres. *Neuropsychologia* 48 (6), 1664–1669. <https://doi.org/10.1016/j.neuropsychologia.2010.02.011>.
- Corbetta, M., Shulman, G.L., 2011. Spatial neglect and attention networks. *Annu. Rev. Neurosci.* 34, 569. <https://doi.org/10.1146/annurev-neuro-061010-113731>.
- D'Antonio, F., Pagani, G., Familiari, A., Khalil, A., Sagies, T.L., Malinger, G., et al., 2016. Outcomes associated with isolated agenesis of the corpus callosum: a meta-analysis. *Pediatrics*, 138 (3), pii: e20160445. <https://doi.org/10.1542/peds.2016-0445>.
- Davidson, R.J., Mednick, D., Moss, E., Saron, C., Schaffer, C.E., 1987. Ratings of emotion in faces are influenced by the visual field to which stimuli are presented. *Brain Cogn.* 6, 403–411. [https://doi.org/10.1016/0278-2626\(87\)90136-9](https://doi.org/10.1016/0278-2626(87)90136-9).
- Davies-Thompson, J., Andrews, T.J., 2012. Intra- and interhemispheric connectivity between face-selective regions in the human brain. *J. Neurophysiol.* 108 (11), 3087–3095. <https://doi.org/10.1152/jn.01171.2011>.
- De Schotten, M.T., Urbanski, M., Duffau, H., Volle, E., Lévy, R., Dubois, B., Bartolomeo, P., 2005. Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. *Science* 309 (5744), 2226–2228. <https://doi.org/10.1126/science.1116251>.
- Devue, C., Brédart, S., 2011. The neural correlates of visual self-recognition. *Conscious. Cogn.* 20 (1), 40–51. <https://doi.org/10.1016/j.concog.2010.09.007>.
- Dimond, S., 1978. Depletion of awareness and double-simultaneous stimulation in split-brain man. *Cortex* 14 (4), 604–607.
- Doty, R.W., 1989. Schizophrenia: a disease of interhemispheric processes at forebrain and brainstem levels? *Behav. Brain Res.* 34, 1–33.
- Dricot, L., Sorger, B., Schiltz, C., Goebel, R., Rossion, B., 2008. The roles of “face” and “non-face” areas during individual face perception: evidence by fMRI adaptation in a brain-damaged prosopagnosic patient. *Neuroimage* 40 (1), 318–332. <https://doi.org/10.1016/j.neuroimage.2007>.
- Englot, D.J., Birk, H., Chang, E.F., 2017. Seizure outcomes in nonresective epilepsy surgery: an update. *Neurosurg. Rev.* 40 (2), 181–194. <https://doi.org/10.1007/s10143-016-0725-8>.
- Fabri, M., Polonara, G., 2013. Functional topography of human corpus callosum: an fMRI mapping study. *Neural Plast.* 2013, 251308. <https://doi.org/10.1155/2013/251308>.
- Fabri, M., Pierpaoli, C., Barbaresi, P., Polonara, G., 2014. Functional topography of the corpus callosum investigated by DTI and fMRI. *World J. Radiol.* 6 (12), 895. <https://doi.org/10.4329/wjr.v6.i12.895>.
- Faubert, J., Vasques, R., Cravo, A., Fukusima, S.S., 2017. Task and exposure time modulate laterality of spatial frequency for faces. *Psychol. Neurosci.* 10 (2), 154. <https://doi.org/10.1037/pne0000090>.
- Feinberg, T.E., Keenan, J.P., 2005. Where in the brain is the self? *Conscious. Cogn.* 14 (4), 661–678. <https://doi.org/10.1016/j.concog.2005.01.002>.
- Frässle, S., Krach, S., Paulus, F.M., Jansen, A., 2016. Handedness is related to neural mechanisms underlying hemispheric lateralization of face processing. *Sci. Rep.* 6, 27153. <https://doi.org/10.1038/srep27153>.
- Funnell, M.G., Corballis, P.M., Gazzaniga, M.S., 1999. A deficit in perceptual matching in the left hemisphere of a callosotomy patient. *Neuropsychologia* 37 (10), 1143–1154.

- Funnell, M.G., Corballis, P.M., Gazzaniga, M.S., 2000. Cortical and subcortical interhemispheric interactions following partial and complete callosotomy. *Arch. Neurol.* 57 (2), 185–189.
- Fusar-Poli, P., Placentino, A., Carletti, F., Allen, P., Landi, P., Abbamonte, M., et al., 2009. Laterality effect on emotional faces processing: ALE meta-analysis of evidence. *Neurosci. Lett.* 452 (3), 262–267. <https://doi.org/10.1016/j.neulet.2009.01.065>.
- Gaffan, D., Hornak, J., 1997. Visual neglect in the monkey. Representation and disconnection. *Brain* 120 (9), 1647–1657.
- Gainotti, G., 1972. Emotional behavior and hemispheric side of the lesion. *Cortex* 8 (1), 41–55. [https://doi.org/10.1016/S0010-9452\(72\)80026-1](https://doi.org/10.1016/S0010-9452(72)80026-1).
- Gainotti, G., 2012. Unconscious processing of emotions and the right hemisphere. *Neuropsychologia* 50 (2), 205–218. <https://doi.org/10.1016/j.neuropsychologia.2011.12.005>.
- Gawryluk, J.R., Brewer, K.D., Beyea, S.D., D'Arcy, R.C., 2009. Optimizing the detection of white matter fMRI using asymmetric spin echo spiral. *Neuroimage* 45 (1), 83–88. <https://doi.org/10.1016/j.neuroimage.2008.11.005>.
- Gazzaniga, M.S., 1967. The split brain in man. *Sci. Am.* 27, 24–29.
- Gazzaniga, M.S., Bogen, J.E., Sperry, R.W., 1962. Some functional effects of sectioning the cerebral commissures in man. *Proc. Natl. Acad. Sci. U.S.A.* 48 (10), 1765–1769.
- Geiger, M.J., O'Gorman Tuura, R., Klaver, P., 2016. Inter-hemispheric connectivity in the fusiform gyrus supports memory consolidation for faces. *Eur. J. Neurosci.* 43 (9), 1137–1145. <https://doi.org/10.1111/ejn.13197>.
- Geschwind, N., 1965a. Disconnexion syndromes in animals and man I. *Brain* 88, 237–294.
- Geschwind, N., 1965b. Disconnexion syndromes in animals and man II. *Brain* 88, 585–644.
- Geschwind, N., Kaplan, E., 1962. A human cerebral disconnection syndrome. *Neurology* 12 (10), 675–685. <https://doi.org/10.1212/WNL.12.10.675>.
- Gross, C.G., Rocha-Miranda, C.E., Bender, D.B., 1972. Visual properties of neurons in inferotemporal cortex of the Macaque. *J. Neurophysiol.* 35 (1), 96–111.
- Hausmann, M., Corballis, M.C., Fabri, M., 2003. Line bisection in the split brain. *Neuropsychology* 17 (4), 602–609. <https://doi.org/10.1037/0894-4105.17.4.602>.
- He, B.J., Snyder, A.Z., Vincent, J.L., Epstein, A., Shulman, G.L., Corbetta, M., 2007. Breakdown of functional connectivity in frontoparietal networks underlies behavioral deficits in spatial neglect. *Neuron* 53 (6), 905–918. <https://doi.org/10.1016/j.neuron.2007.02.013>.
- Heilman, K.M., Bowers, D., Valenstein, E., Watson, R.T., 1987. Hemispace and hemispatial neglect. In: Jeannerod, M. (Ed.), *Neurophysiological and Neuropsychological Aspects of Spatial Neglect*. Elsevier, Amsterdam, pp. 115–150.
- Jessen, S., Altvater-Mackensen, N., Grossmann, T., 2016. Pupillary responses reveal infants' discrimination of facial emotions independent of conscious perception. *Cognition* 150, 163–169. <https://doi.org/10.1016/j.cognition.2016.02.010>.
- Johnson, M.H., 2005. Subcortical face processing. *Nat. Rev. Neurosci.* 6 (10), 766–774. <https://doi.org/10.1038/nrn1766>.
- Johnson, M.H., Dziurawiec, S., Ellis, H., Morton, J., 1991. Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 40 (1), 1–19. [https://doi.org/10.1016/0010-0277\(91\)90045-6](https://doi.org/10.1016/0010-0277(91)90045-6).
- Jonas, J., Rossion, B., Brissart, H., Frismand, S., Jacques, C., Hossu, G., et al., 2015. Beyond the core face-processing network: intracerebral stimulation of a face-selective area in the right anterior fusiform gyrus elicits transient prosopagnosia. *Cortex* 72, 140–155. <https://doi.org/10.1016/j.cortex.2015.05.026>.

- Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. *Philos. Trans. R. Soc. Lond. B* 361 (1476), 2109–2128. <https://doi.org/10.1098/rstb.2006.1934>.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17 (11), 4302–4311.
- Karim, A.R., Kojima, H., 2010. The what and why of perceptual asymmetries in the visual domain. *Adv. Cogn. Psychol.* 6, 103. <https://doi.org/10.2478/v10053-008-0080-6>.
- Keenan, P.A., Whitman, R.D., Pepe, J., 1989. Hemispheric asymmetry in the processing of high and low spatial frequencies: a facial recognition task. *Brain Cogn.* 11 (2), 229–237.
- Keenan, J.P., Wheeler, M., Platek, S.M., Lardi, G., Lassonde, M., 2003. Self-face processing in a callosotomy patient. *Eur. J. Neurosci.* 18 (8), 2391–2395. <https://doi.org/10.1046/j.1460-9568.2003.02958.x>.
- Keenan, J.P., Rubio, J., Racioppi, C., Johnson, A., Barnacz, A., 2005. The right hemisphere and the dark side of consciousness. *Cortex* 41 (5), 695–704.
- Kinsbourne, M., 2003. The corpus callosum equilibrates the cerebral hemispheres. In: Zaidel, E., Iacoboni, M. (Eds.), *The Parallel Brain: The Cognitive Neuroscience of the Corpus Callosum*. MIT Press, Cambridge, MA, pp. 271–281.
- Làdavas, E., Cimatti, D., Pesce, M.D., Tuozzi, G., 1993. Emotional evaluation with and without conscious stimulus identification: evidence from a split-brain patient. *Cogn. Emot.* 7 (1), 95–114. <https://doi.org/10.1080/02699939308409179>.
- Laeng, B., Profeti, I., Sæther, L., Adolfsdottir, S., Lundervold, A.J., Vangberg, T., et al., 2010. Invisible expressions evoke core impressions. *Emotion* 10 (4), 573. <https://doi.org/10.1037/a0018689>.
- Lassonde, M., Sauerwein, H.C., Lepore, F., 1995. Extent and limits of callosal plasticity: presence of disconnection symptoms in callosal agenesis. *Neuropsychologia* 33 (8), 989–1007.
- Lausberg, H., Göttert, R., Müniinger, U., Boegner, F., Marx, P., 1999. Callosal disconnection syndrome in a left-handed patient due to infarction of the total length of the corpus callosum. *Neuropsychologia* 37 (3), 253–265.
- LeDoux, J.E., Wilson, D.H., Gazzaniga, M.S., 1977. A divided mind: observations on the conscious properties of the separated hemispheres. *Ann. Neurol.* 2 (5), 417–421. <https://doi.org/10.1002/ana.410020513>.
- Levy, J., 1983. Language, cognition, and the right hemisphere: a response to Gazzaniga. *Am. Psychol.* 38, 538–541.
- Levy, J., Trevarthen, C., Sperry, R.W., 1972. Perception of bilateral chimeric figures following hemispheric deconnexion. *Brain* 95 (1), 61.
- Levy, J., Heller, W., Banich, M.T., Burton, L.A., 1983. A symmetry of perception in free viewing of chimeric faces. *Brain Cogn.* 2, 404–419. [https://doi.org/10.1016/0278-2626\(83\)90021-0](https://doi.org/10.1016/0278-2626(83)90021-0).
- Lindell, A.K., 2013. Continuities in emotion lateralization in human and non-human primates. *Front. Hum. Neurosci.* 7, 464. <https://doi.org/10.3389/fnhum.2013.00464>.
- Luck, S.J., Hillyard, S.A., Mangun, G.R., Gazzaniga, M.S., 1994. Independent attentional scanning in the separated hemispheres of split-brain patients. *J. Cogn. Neurosci.* 6 (1), 84–91.
- Luo, B., Shan, C., Zhu, R., Weng, X., He, S., 2011. Functional foveal splitting: evidence from neuropsychological and multimodal MRI investigations in a Chinese patient with a splenium lesion. *PLoS One* 6 (8), e23997. <https://doi.org/10.1371/journal.pone.0023997>.
- Marzi, C.A., Bisiacchi, P., Nicoletti, R., 1991. Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia* 29, 1163–1167.

- Marzi, C.A., Fanini, A., Girelli, M., Ipata, A.E., Miniussi, C., Smania, N., Prior, M., 1997. Is extinction following parietal damage an interhemispheric disconnection phenomenon? In: Their, P., Karnath, H.O. (Eds.), *Parietal Lobe Contribution to Orientation in 3D Space*. Heidelberg, Springer-Verlag, pp. 431–445.
- Mason, M.F., Macrae, C.N., 2004. Categorizing and individuating others: the neural substrates of person perception. *J. Cogn. Neurosci.* 16 (10), 1785–1795.
- Mathews, M.S., Linskey, M.E., Binder, D.K., 2008. William P. van Wagenen and the first corpus callosotomies for epilepsy. *J. Neurosurg.* 108, 608–613. <https://doi.org/10.3171/JNS/2008/108/3/0608>.
- McCarthy, G., Puce, A., Gore, J.C., Allison, T., 1997. Face-specific processing in the human fusiform gyrus. *J. Cogn. Neurosci.* 9, 605–610. <https://doi.org/10.1162/jocn.1997.9.5.605>.
- Miller, M.B., Sinnott-Armstrong, W., Young, L., King, D., Paggi, A., Fabri, M., Polonara, G., Gazzaniga, M.S., 2010. Abnormal moral reasoning in complete and partial callosotomy patients. *Neuropsychologia* 48 (7), 2215–2220. <https://doi.org/10.1016/j.neuropsychologia.2010.02.021>.
- O’Neil, E.B., Hutchison, R.M., McLean, D.A., Köhler, S., 2014. Resting-state fMRI reveals functional connectivity between face-selective perirhinal cortex and the fusiform face area related to face inversion. *Neuroimage* 92, 349–355. <https://doi.org/10.1016/j.neuroimage.2014.02.005>.
- Parente, R., Tommasi, L., 2008. A bias for the female face in the right hemisphere. *Laterality* 13 (4), 374–386. <https://doi.org/10.1080/13576500802103495>.
- Parvizi, J., Jacques, C., Foster, B.L., Withoft, N., Rangarajan, V., Weiner, K.S., Grill-Spector, K., 2012. Electrical stimulation of human fusiform face-selective regions distorts face perception. *J. Neurosci.* 32 (43), 14915–14920. <https://doi.org/10.1523/JNEUROSCI.2609-12.2012>.
- Preilowski, B., 1977. Self-recognition as a test of consciousness in left and right hemisphere of “split-brain” patients. *Act. Nerv. Super. (Praha)* 19 (2), 343–344.
- Prete, G., Tommasi, L., 2017. Split-brain patients. In: Shackelford, T.K., Weekes-Shackelford, V.A. (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer International Publishing AG, Cham (ZG), Switzerland, pp. 1–5. <https://doi.org/10.1007/978-3-319-16999-6-2764-1>.
- Prete, G., Laeng, B., Tommasi, L., 2014a. Lateralized hybrid faces: evidence of a valence-specific bias in the processing of implicit emotions. *Laterality* 19 (4), 439–454. <https://doi.org/10.1080/1357650X.2013.862255>.
- Prete, G., Marzoli, D., Brancucci, A., Fabri, M., Foschi, N., Tommasi, L., 2014b. The processing of chimeric and dichotic emotional stimuli by connected and disconnected cerebral hemispheres. *Behav. Brain Res.* 271, 354–364. <https://doi.org/10.1016/j.bbr.2014.06.034>.
- Prete, G., Capotosto, P., Zappasodi, F., Laeng, B., Tommasi, L., 2015a. The cerebral correlates of subliminal emotions: an electroencephalographic study with emotional hybrid faces. *Eur. J. Neurosci.* 42 (11), 2952–2962. <https://doi.org/10.1111/ejn.13078>.
- Prete, G., D’ascenzo, S., Laeng, B., Fabri, M., Foschi, N., Tommasi, L., 2015b. Conscious and unconscious processing of facial expressions: evidence from two split-brain patients. *J. Neuropsychol.* 9 (1), 45–63. <https://doi.org/10.1111/jnp.12034>.
- Prete, G., Fabri, M., Foschi, N., Brancucci, A., Tommasi, L., 2015c. The “consonance effect” and the hemispheres: a study on a split-brain patient. *Laterality* 20 (3), 257–269. <https://doi.org/10.1080/1357650X.2014.959525>.

- Prete, G., Laeng, B., Fabri, M., Foschi, N., Tommasi, L., 2015d. Right hemisphere or valence hypothesis, or both? The processing of hybrid faces in the intact and callosotomized brain. *Neuropsychologia* 68, 94–106. <https://doi.org/10.1016/j.neuropsychologia.2015.01.002>.
- Prete, G., Marzoli, D., Tommasi, L., 2015e. Upright or inverted, entire or exploded: right-hemispheric superiority in face recognition withstands multiple spatial manipulations. *PeerJ* 3, e1456. <https://doi.org/10.7717/peerj.1456>.
- Prete, G., Fabri, M., Foschi, N., Tommasi, L., 2016. Face gender categorization and hemispheric asymmetries: contrasting evidence from connected and disconnected brains. *Neuroscience* 339, 210–218. <https://doi.org/10.1016/j.neuroscience.2016.10.021>.
- Prete, G., Fabri, M., Foschi, N., Tommasi, L., 2017a. Asymmetry for symmetry: right-hemispheric superiority in bi-dimensional symmetry perception. *Symmetry* 9 (5), 76. <https://doi.org/10.3390/sym9050076>.
- Prete, G., Malatesta, G., Tommasi, L., 2017b. Facial gender and hemispheric asymmetries: a hf-tRNS study. *Brain Stimul.* 10 (6), 1145–1147. <https://doi.org/10.1016/j.brs.2017.08.002>.
- Prete, G., Capotosto, P., Zappasodi, F., Tommasi, L., 2018a. Contrasting hemispheric asymmetries for emotional processing from event-related potentials and behavioural responses. *Neuropsychology* 32 (3), 317–328. <https://doi.org/10.1037/neu0000443>.
- Prete, G., Fabri, M., Foschi, N., Tommasi, L., 2018b. Geometry, landmarks and the cerebral hemispheres: 2D spatial reorientation in split-brain patients. *J. Neuropsychol.* 12 (2), 248–270. <https://doi.org/10.1111/jnp.12115>.
- Ptito, A., Brisson, B., Dell'Acqua, R., Lassonde, M., Jolicoeur, P., 2009. The attentional blink within and across the hemispheres: evidence from a patient with a complete section of the corpus callosum. *Biol. Psychol.* 82 (1), 64–69. <https://doi.org/10.1016/j.biopsycho.2009.06.001>.
- Rangarajan, V., Hermes, D., Foster, B.L., Weiner, K.S., Jacques, C., Grill-Spector, K., Parvizi, J., 2014. Electrical stimulation of the left and right human fusiform gyrus causes different effects in conscious face perception. *J. Neurosci.* 34 (38), 12828–12836. <https://doi.org/10.1523/JNEUROSCI.0527-14.2014>.
- Rizzolatti, G., Umiltà, C., Berlucchi, G., 1971. Opposite superiorities of the right and left cerebral hemispheres in discriminative reaction time to physiognomical and alphabetical material. *Brain* 94 (3), 431–442. <https://doi.org/10.1093/brain/94.3.431>.
- Seymour, S.E., Reuter-Lorenz, P.A., Gazzaniga, M.S., 1994. The disconnection syndrome: basic findings reaffirmed. *Brain* 117 (1), 105–115.
- Sperry, R.W., 1961. Cerebral organization and behavior. *Science* 133 (3466), 1749–1757. <https://doi.org/10.1126/science.133.3466.1749>.
- Stefanics, G., Csukly, G., Komlósi, S., Czobor, P., Czigler, I., 2012. Processing of unattended facial emotions: a visual mismatch negativity study. *Neuroimage* 59 (3), 3042–3049. <https://doi.org/10.1016/j.neuroimage.2011.10.041>.
- Stone, V.E., Nisenson, L., Eliassen, J.C., Gazzaniga, M.S., 1996. Left hemisphere representations of emotional facial expressions. *Neuropsychologia* 34 (1), 23–29.
- Todd, B.K., Banerjee, R., 2016. Lateralization of infant holding by mothers: a longitudinal evaluation of variations over the first 12 weeks. *Laterality* 21 (1), 12–33. <https://doi.org/10.1080/1357650X.2015.1059434>.
- Turk, D.J., Heatherton, T.F., Kelley, W.M., Funnell, M.G., Gazzaniga, M.S., Macrae, C.N., 2002. Mike or me? Self-recognition in a split-brain patient. *Nat. Neurosci.* 5 (9), 841–842. <https://doi.org/10.1038/nn907>.
- Uddin, L.Q., 2011. Brain connectivity and the self: the case of cerebral disconnection. *Conscious. Cogn.* 20 (1), 94–98. <https://doi.org/10.1016/j.concog.2010.09.009>.

- Uddin, L.Q., Rayman, J., Zaidel, E., 2005. Split-brain reveals separate but equal self-recognition in the two cerebral hemispheres. *Conscious. Cogn.* 14 (3), 633–640. <https://doi.org/10.1016/j.concog.2005.01.008>.
- Unterberger, I., Bauer, R., Walser, G., Bauer, G., 2016. Corpus callosum and epilepsies. *Seizure* 37, 55–60. <https://doi.org/10.1016/j.seizure.2016.02.012>.
- Verosky, S.C., Turk-Browne, N.B., 2012. Representations of facial identity in the left hemisphere require right hemisphere processing. *J. Cogn. Neurosci.* 24 (4), 1006–1017. https://doi.org/10.1162/jocn_a_00196.
- Volz, L.J., Gazzaniga, M.S., 2017. Interaction in isolation: 50 years of insights from split-brain research. *Brain* 140 (7), 2051–2060. <https://doi.org/10.1093/brain/awx139>.
- Wernicke, K., 1874. The aphasia symptom-complex. Breslau, Cohn and Weigert. Translated in: Eling P., Ed. *Reader in the History of Aphasia*. vol. 4. 1994. Amsterdam: John Benjamins; 69–89.
- Wright, D.B., Sladden, B., 2003. An own gender bias and the importance of hair in face recognition. *Acta Psychol. (Amst.)* 114 (1), 101–114. [https://doi.org/10.1016/S0001-6918\(03\)00052-0](https://doi.org/10.1016/S0001-6918(03)00052-0).
- Yovel, G., 2015. An integrative review of neural and cognitive face-selective measures. *Neuropsychologia* 83, 5–13. <https://doi.org/10.1016/j.neuropsychologia.2015.09.026>.
- Yovel, G., 2016. Neural and cognitive face-selective markers: an integrative review. *Neuropsychologia* 83, 5–13. <https://doi.org/10.1016/j.neuropsychologia.2015.09.026>.
- Zaidel, E., 1983. Disconnection syndrome as a model for laterality effects in the normal brain. In: Hellige, J. (Ed.), *Cerebral Hemisphere Asymmetry*. Praeger Publishers, New York, pp. 95–151.
- Zaidel, E., 1995. Interhemispheric transfer in the split brain: long-term status following complete cerebral commissurotomy. In: Davidson, R.J., Hugdahl, K. (Eds.), *Brain Asymmetry*. MIT Press, Cambridge, MA, pp. 491–532.
- Zaidel, E., Iacoboni, M., 2003. *The Parallel Brain: The Cognitive Neuroscience of the Corpus Callosum*. MIT Press, Cambridge, MA.

FURTHER READING

- Malpass, R.S., Kravitz, J., 1969. Recognition for faces of own and other “race” *J. Pers. Soc. Psychol.* 13, 330–335.