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Review Article

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Cerebral Lateralization of Pro- and Anti-Social Tendencies

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Mounting evidence suggest that the right-hemisphere (RH) has a relative advantage, over the left-hemisphere (LH), in mediating social intelligence – identifying social stimuli, understanding the intentions of other people, awareness of the dynamics in social relationships, and successful handling of social interactions. Furthermore, a review and synthesis of the literature suggest that pro-social attitudes and behaviors are associated with physiological activity in the RH, whereas unsocial and anti-social tendencies are mediated primarily by the LH. This hemispheric asymmetry is rooted in several neurobiological and functional differences between the two hemispheres. (I) Positive social interactions often require inhibiting one's immediate desires and considering the perspectives and needs of others. Given that self-control is mediated by the RH, pro-social emotions and behaviors are, therefore, inherently associated with the RH as it subserves the brain's self-restraint mechanisms. (II) The RH mediates experiences of vulnerability. It registers the relative clumsiness and motor weakness of the left limbs, and it is involved, more than the LH, in processing threats and mediating fear. Emotional states of vulnerability trigger the need for affiliation and sociality, therefore the RH has a greater role in mediating pro-social attitudes and behaviors. (III) The RH mediates a holistic mode of representing the world. Holistic perception emphasizes similarities rather than differences, takes a long-term perspective, is associated with divergent thinking and seeing other points-of-view, and it mediates a personal mode of relating to people. All these features of holistic perception facilitate a more empathetic attitude toward others and pro-social behaviors.

Key words: cerebral lateralization, hemispheric asymmetry, laterality, altruism, self-control, holistic perception, need for affiliation, need for power, pro-social, anti-social

INTRODUCTION

Psychological theories on motivation postulate that human beings have an intrinsic need for affiliation - being connected with and accepted by other people. This fundamental need motivates people to seek warm, stable and intimate interpersonal relationships, form friendships, and affiliate with specific groups (which are often based on shared ethnicity, religion, socio-economic class, intellectual interests etc.). On the other hand, humans also have an innate need to maintain their individuality and independence. This need motivates people to acquire power in order to achieve autonomy and freedom that will enable them to master and influence their environments and social relationships, instead of being influenced by them [1-9].

Ideally, these two coexisting needs - for affiliation and power - would complement and balance each other. Nevertheless, oftentimes they are in conflict and lead to opposite directions. Naturally, the need for affiliation sustains social interdependence and promotes a pro-social mindset and corresponding emotions

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and behaviors; egalitarianism, closeness between people, feelings of togetherness, cooperation and assistance. The need for power and independence, however, facilitates self-sufficiency, distance between people, competitiveness and hierarchical social relationships. It also has the potential to lead one astray toward anti-social attitudes and actions; the pursuit of power, when untempered, can turn into a desire to dominate other people, manipulation, exploitation - treating other human beings as mere instruments to be used for one's benefit - and generally to a disregard for the welfare of others.

Research suggests that these two basic motivations are lateralized in the brain. The need for affiliation is mediated primarily by neural structures within the right-hemisphere (RH), whereas the need for power is mediated mainly by the left-hemisphere (LH) [10-12]. Accordingly, pro-social tendencies, emotions and behaviors are associated primarily with physiological processes in the RH, while unsocial emotions and behaviors are linked mainly with the LH neurophysiology. This article summarizes the evidence for this lateralization of social tendencies and further discusses its neurobiological origins.

Before proceeding further on the issue of brain lateralization, a clarification is needed to avoid simplifications such as 'the RH is doing X and the LH is doing Y' etc. Almost all human experiences are mediated by neural assemblies from both the RH and the LH. Nonetheless, as previous research on cerebral lateralization has shown, the two hemispheres mediate different modes of experiencing the world and dealing with it. These two modes are qualitatively different and mutually antagonistic. Under normal circumstances we are unaware of an asymmetry between the RH and LH, since both hemispheres share information, via the corpus callosum, and the integrated and combined input results in a unified and coherent experience of ourselves and the environment. However, extreme conditions which amplify (or minify) the contribution of one hemisphere to the mental experience provide vivid manifestations of the two hemispheres' fundamental differences. For instance, in split-brain patients whose corpus callosum has been severed (to prevent dangerous epileptic seizures) the inter-hemispheric flow of information is disrupted and each hemisphere functions as an independent brain within the same person. Similarly, patients with unilateral brain lesions perceive the world primarily through the intact hemisphere; that is, the damaged hemisphere is the minor contributor, and the intact hemisphere the major contributor, to the patient's overall mental experience and impression of the world. Likewise, researchers have devised ingenious experimental paradigms that create similar conditions in the laboratory, with healthy persons with intact brains, by producing a temporary change in the activity pattern of one hemisphere, thereby creating optimal conditions for a particular hemisphere to manifest its unique processing style or superiority in executing a specific task. All these unusual conditions reveal that our ordinary conscious experience is actually a synthesis of the output of both hemispheres, while at source each hemisphere mediates a different mode of experiencing the world [13-22].

Lateralization of social tendencies

A large body of evidence indicates that the RH has a relative advantage, compared to the LH, in mediating social intelligence - the ability to perceive subtle social cues, awareness of the dynamics in social relationships, and understanding of the intentions of other people. Neuroimaging and behavioral studies show a clear RH superiority in detecting and processing stimuli with social relevance - e.g. faces, voices, gestures etc. [23-27]. Neuropsychological assessments of patients with RH lesions and abnormalities, whose mental experience is mediated primarily by the intact LH, often show significant impairments in their understanding of social concepts and interpersonal dynamics as well as difficulties in their ability to decide on the proper behavior in various social situations [28-31]. Moreover, a positive correlation was found between RH cortical atrophy and deficits in understanding social signals [32]. In addition, the RH is involved, to a greater degree than the LH, in coding and understanding the intentions behind other people's actions [33-35].

The literature further suggests that the two hemispheres are associated with processing different types of social relationships. In several experiments, using divided visual-field techniques, words and images that describe affiliation, attachments and closeness between people were recognized faster when they appeared in the left-visual-field, which is initially processed by the RH. On the contrary, descriptions of power, dominance and hierarchical relationships between people were processed faster when presented in the right-visual-field - i.e. to the LH [10, 36, 37]. These behavioral findings were corroborated by neuroimaging studies. Viewing a movie clip of an affiliation scene (e.g. nostalgic moments of romance and love) was associated with greater neural activity in RH regions, whereas watching a power scene (e.g. a conversation between a dominant mafia boss and his subordinate) has been linked with neural activity in regions within the LH [11]. In another study, participants viewed pairs of celebrity pictures and their task was to judge whether the two public figures were friends or enemies (social alliance judgments) or whose social rank is higher (social hierarchy judgments). Contrasting the brain activity patterns in the two tasks revealed that judgments of social status and hierarchies activated mainly regions within the LH,

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while judgments of social alliance between people activated also RH regions [38].

Not only impersonal judgments about social dynamics are lateralized. The need and desire for social connections as well as the pain of social rejection are mediated primarily by regions within the RH. Electroencephalography (EEG) measurements found that a low need for affiliation correlated with lower neural activity in the right prefrontal cortex [12]. Functional magnetic resonance imaging (fMRI) and near-infrared spectroscopy (NIRS) studies showed that exclusion of a player in a ball-tossing game stirred up feelings of social rejection and activated pain regions within the RH [39-42]. On the other hand, individuals with a greater left frontal activity at baseline were more resilient and less affected by social rejection [43]. Similarly, in split-brain patients, with a severed corpus callosum that prevents inter-hemispheric communication, researchers interpret the patient's left-hand responses as reflecting their RH experiences, and the right-hand responses as indicative of their LH mental state. A study where two split-brain patients were asked personal questions and their motor responses were analyzed revealed that their RH was disturbed, significantly more than their LH, by childhood memories of being bullied and loneliness [44], indicating the RH greater involvement in mediating the need for affiliation as well as the distress when this need is unsatisfied.

Conversely, the need for power is mediated mainly through the LH. In an experiment participants wrote an essay about a personal experience in which they felt either, having power over other individuals (high social power condition), or that someone else had power over them (low social power condition). This task evoked corresponding feelings of being socially powerful or powerless, and the EEG measurements revealed a greater activity in the left frontal cortex of the former group [45]. In contrast, the latter group demonstrated a greater tendency to bump into the right wall while walking through a narrow corridor and an inclination to bisect horizontal lines to the left of the veridical center - perceptual biases that indicate a RH dominance [46].

Accordingly, the anatomy and functioning of several regions within the RH were found to correlate positively with pro-social personality traits. Affiliativeness - the desire for closeness with other people in social and spousal relationships - was associated with a larger right anterior cingulate cortex [47-49]. Agreeableness - the tendency to be pleasing and cooperative in social situations - correlated with the gray matter volume in the right middle orbital gyrus [50] and with the right orbitofrontal cortex [51]. The tendency to trust other people - an important facilitator of positive social relationships - was found to correlate with activity in the right ventrolateral prefrontal cortex [42]. An inclination for gratitude - being appreciative and thankful of others' kindness - correlated with the volume of the right inferior temporal cortex [52]. In contrast, the volume of the left lateral orbital gyrus correlated with Machiavellianism - the tendency to manipulate other people in order to control and exploit them for one's own benefit [50].

Patients with neurodegenerative diseases often demonstrate behavioral and personality changes. Analyses of patients with damage mostly in their LH (i.e. a condition presumed to reflect RH dominance) revealed greater frequencies of interpersonal warmth, sociability and agreeableness, whereas RH-damaged patients often try to dominate and control their environment including other people [53, 54]. Other studies reported that RH lesions can lead to sexual aggression, physical assaults and acquired sociopathy [55-57]. The RH greater involvement in affiliative emotions and behaviors is reflected also in mother-baby interactions. Neuroimaging studies show associations between activity in RH regions and mothers' attachment and sensitivity to their infants [58-61].

Taken together, the aforementioned studies suggest that the human need for social connection and the desire to be accepted by others are associated with neurophysiological activity in the RH. The need to have power, on the contrary, is associated with physiological processes within the LH. This entails that the two hemispheres mediate different social attitudes; pro-social emotions and behaviors are primarily mediated by the RH, whereas unsocial and anti-social emotions and actions are mediated mainly by the LH. The following sections elaborate this hemispheric asymmetry further by demonstrating how specific social emotions, attitudes and behaviors are lateralized in the brain.

Pro-social attitudes and emotions

Moral reasoning

The RH plays an important role in our ability to tell right from wrong. In experiments where participants assessed a person's moral conduct and criminal responsibility (e.g. whether the harm caused by his/her actions was intentional or accidental etc.) these judgments were associated with enhanced metabolic activity in several regions within the RH [62-66]. These studies demonstrate the RH involvement in the promotion of pro-social behavioral norms through the juridical enforcement of moral conduct. Furthermore, a properly functioning RH is necessary for moral reasoning. Generally, actions that were intended to do harm but failed (e.g. trying to poison someone with a powder which turned out to be non-toxic) are judged harshly. People judging these acts focus on the intention (to kill) and tend to ignore the (lucky) outcome. Nevertheless, in experiments were the physiological

activity in the right temporo-parietal junction (TPJ) or right dorsolateral prefrontal cortex (DLPFC) was temporarily disrupted with transcranial magnetic stimulation (TMS), participants judged moral dilemmas in a more forgiving attitude; even attempted murders were judged as less serious when no harm was caused in the end [67, 68]. Likewise, split-brain patients tend to base their moral judgments more on the outcomes and less on the intentions. Presumably, because the LH is disconnected from the moral reasoning networks in the RH, these patients cannot make a comprehensive and integrated moral assessment [69]. Patients with RH-lesions show a similar tendency to judge moral dilemmas in a calculated fashion [70], and to ignore the agent's intentions [71]. In contrast, when participants were engaged in mental simulations of immoral acts, there was a remarkable shift in their brain activity towards the LH [72]. These studies suggest that moral and immoral thinking are associated with activity in the RH and LH, respectively.

Fairness

A pro-social attitude promotes norms of fairness and reciprocity in social interactions. In the ultimatum game, one player (the proposer) receives a sum of money and he/she makes an offer to the second player (the responder) on how to divide it between them. If the offer is accepted both players keep their parts, but if the offer is rejected, neither receives anything. Studies show that unfair proposals (such as 75:25) are usually rejected even though rejecting an offer results in no money for the responder. It seems that people prefer to give up a small gain in order to punish unfair behaviors [73]. Nevertheless, experiments have shown that a brief interruption of the physiological activity in the right frontal cortex with transcranial magnetic or direct current stimulation (TMS or tDCS) resulted in more unfair offers being accepted, while stimulation of the same region in the LH did not have any effect [74-77]. Similarly, people with a resting-state EEG indicating a greater right frontal activation are more likely to reject unfair proposals, than those with a greater activation in the LH [78]. These studies demonstrate the RH important role in mediating an egalitarian attitude - i.e. the promotion of equality and fairness in the distribution of resources.

Empathy

Several EEG studies suggest that empathy - the ability to take someone else's emotional perspective - is mediated by neural structures within the RH. Expressing empathy for someone in distress activated the right temporal region [79]. Feeling the empathy expressed by gentle and kind touching is mediated by the right primary somatosensory cortex [80]. Furthermore, a positive correlation was found between empathy scores and resting-state activity in the right frontal cortex [81]. Similarly, when professional musicians observed music played in ensemble - a condition that requires reading the performers' emotional state - the activity in their right ventral-lateral frontal gyrus correlated positively with their empathy levels [82]. Likewise, fMRI and tDCS studies show that the right TPJ plays a critical role in various aspects of social interactions, especially in the ability to take the perspective of another person [83, 84].

In an fMRI study, brain activity was recorded while participants were involved in sentencing offenders in murder cases. Two scenarios were contrasted; in one, the jurors read a text describing the desperate situation of the defendant (e.g. suffering from domestic violence, disease or poverty etc.) - a condition that was meant to elicit sympathy for the defendant - and in the other scenario, the jurors did not read this text. The results showed that individual differences in the activity of the right mid-insula correlated with the tendency to accept the mitigating circumstances. That is, the judges with the higher activity in that RH region were more compassionate and reduced the defendant's prison years more than the jurors with the lower RH activity [85]. Furthermore, during the reading of the defendant's desperate situation - a mental activity that the authors describe as "an engagement with a reasoned simulation of what the defendant was thinking when committing the crime" - a greater activity was observed in the left TPJ [85]. That is, pro- and anti-social mentalizations were lateralized; simulating the justification for the anti-social act engaged the LH, whereas the juror's pro-social and compassionate decision correlated with activity in the RH.

Comparisons between patients with RH and LH lesions showed that the former group is relatively more impaired in their ability to express empathy and compassion toward other people [86-93]. In contrast, when healthy people saw a cartoon depicting one person enjoying another person's misfortune, they quickly recognized that emotion as gloating (schadenfreude). Patients with lesions in the frontal parts of the LH, however, had difficulties in understanding the scene and the emotion expressed in it [94]. Collectively, the studies with healthy and brain damaged participants suggest that the RH is involved, to a relatively greater extent than the LH, in mediating empathy and compassion. The LH, on the contrary, is more involved in mediating anti-social emotions and mental states (e.g. gloating and justifying a crime).

Guilt

Violating one's own moral standards usually leads to guilt feelings. When guilt is felt in a social context it is often a motivator for pro-social activities in hope of rectifying past mistakes and

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receiving forgiveness. Studies have shown that guilt feelings are associated with RH activity and/or LH deactivation. In an fMRI study participants were engaged in re-experiencing situations from their past that were associated with strong feelings of guilt. A positive correlation was found between the levels of guilt felt and the activation of the right orbitofrontal cortex [95]. Similarly, in an experiment where participants played a game of stealing an item and then being interrogated about the theft, the guilty condition was associated with right frontal activity [96]. Furthermore, in another study participants were allowed to keep the stolen money if they could convince the interrogator about their innocence. Prior to the interrogation participants received a tDCS which either facilitated or suppressed the physiological activity in their right anterior prefrontal cortex (aPFC). The results showed that temporarily hampering activity in the right aPFC facilitated lying and reduced the levels of guilt participants had felt about their deceptive behaviors [97]. In another experiment, white university students watched series of faces of Whites, Blacks and Asians, while their brain activity was recorded with EEG. At the end of the session, the experimenter offered the students to see the pattern of their brain responses and presented them with a bogus graph showing that they responded positively to White faces and negatively to Black faces. The students' brain activity was still recorded while they watched the fake EEG data, and their verbal reports of guilt feelings were associated with decreased activity in the LH [98]. Together, these studies suggest that guilt feelings are mediated primarily by the RH.

Anti-social emotions and behaviors

Anger, hostility and aggression

EEG and NIRS studies show that anger, aggression and hostility are associated with a relatively greater activity in the frontal parts of the LH compared to the same regions in the RH [99-106]. Similarly, experiencing anger affected a subsequent dichotic listening task and resulted in a right-ear (i.e. LH) advantage, presumably as a consequence of a temporary enhancement of LH activity [107, 108]. Furthermore, the link between aggression and the LH is bi-directional; aggression increases LH activity and enhanced LH activity can intensify aggression. In two experiments the physiological activity of each hemisphere was selectively enhanced, either with tDCS or with contralateral hand clenching. Participants were then insulted and in a subsequent game they had an opportunity to retaliate with aggression. The results showed that when the LH activity was selectively enhanced (with anodal tDCS or by activating the right-hand muscles) participants expressed higher levels of anger and aggression [109, 110]. These studies demonstrate that anger and aggression are associated with physiological activity in the LH.

Not only aggression as a transient state is linked with LH activity. Aggression as a stable personality trait is also associated with a greater LH activation and/or a reduced RH activation. Comparing EEG patterns of normal people and extremely violent offenders with long-term prison sentences revealed that within the aggressive group there was an increased cortical activity in the anterior parts of the LH [111, 112]. Similarly, an fMRI study compared the brain activity of adults who experienced severe physical abuse in their childhood and went on perpetrating serious violence in their adulthood, with people who suffered severe physical abuse early in their life but refrained from violence. The results showed that the latter group had a relatively higher activity in the RH, whereas the violent anti-social group did not [113].

In the same line, neuroanatomical studies found that aggression is associated with a larger left orbitofrontal cortex [114], and a reduced right anterior cingulate cortex [115]. Clinical reports of unilateral lesion patients indicate that RH injuries, which presumably shift the inter-hemispheric balance toward LH dominance, often lead to aggressive behaviors and inappropriate social conduct [116, 117]. Likewise, a study on postpartum depressed women found that greater activity in their right amygdala was associated with less hostility toward their infants [118]. Together, these findings suggest that aggression and hostility are mediated by the LH, while the RH is involved in tempering and buffering these anti-social emotions and behaviors.

Jealousy

When a person feels that his/her connection with someone significant may be lost in favor of another person it can lead to jealousy. This emotion, when uncontrolled, can potentially facilitate anti-social behaviors. EEG studies show that jealousy is associated with an increased left frontal activation. In an experiment, participants played a computerized ball-tossing game with two other players; a same-sex player assigned by the computer and an opposite-sex player chosen by the participant. Photographs of both players were visible on the screen throughout the game to facilitate a real-life play experience. After playing several rounds, the opposite-sex player started tossing the ball only to the other player and ignored the participant. A debrief confirmed that the participants felt jealousy after being ostracized by the opposite-sex player. Analysis of the EEG signals during the exclusion phase revealed an increased activation in the frontal parts of the LH [119]. In another study, EEG was measured from 1-year-old babies when they lost their mother's attention for a doll (a social rival) or for a book (a non-social rival). A comparison of the infants' behaviors in both conditions showed that they made more efforts

to regain their mother's attention in the doll condition, compared to the book condition, indicating that in addition to the loss of the caregiver's attention there was also a particular sense of jealousy in the doll condition. The EEG pattern revealed that the babies whose LH was more active than their RH expressed significantly more jealous behaviors than the other babies [120]. These studies indicate that jealousy is mediated by the LH.

Othello syndrome is a psychiatric disorder of delusional jealousy, in which patients believe that their spouse is unfaithful, although it is clear to outside observers that there are no grounds for these allegations. The disorder is named after the Shakespearean character 'Othello' who murdered his wife while falsely believing she had been unfaithful to him. These episodes of obsessive jealousy delusions can occur after a brain injury in people who were completely normal prior to their brain damage. Several reviews of delusional jealousy cases found that most frequently the neurological damage occurred in the RH [121-124], suggesting that the jealousy was mediated primarily by the (intact) LH.

Abnormal social behaviors

As can be expected, the lateralization of pro- and un-social tendencies is demonstrated across the whole range of social behaviors and relationships from the normal to the abnormal and psychopathologies.

Williams syndrome

Williams syndrome (WS) is a rare genetic neurodevelopmental disorder with distinct facial appearance and mental retardation. A characteristic feature of individuals with WS is their outgoing personalities and over-friendliness. Children and adults with WS usually have a cheerful demeanor, they are remarkably at ease with strangers, and they seem to be highly motivated to greet and interact with other people [125-127]. WS, therefore, represents an extreme case of friendliness and desire for social interactions. Brain imaging studies of WS patients revealed several abnormalities in the anatomy and functioning of their RH. For instance, the right perisylvian and inferior temporal areas were thicker and larger in WS as compared with healthy people [128, 129]. Likewise, a better micro-structural integrity was found in the right superior longitudinal fasciculus of individuals with WS as compared with matching control participants [130]. In addition, a positive correlation was found between the volume of the right amygdala and the willingness to approach strangers. That is, the WS children with the largest amygdala in the RH were the most interested in approaching and befriending new people [131]. These studies suggest a link between the friendliness and pro-social tendencies observed in WS and their unique RH neurophysiology.

Dependent personality disorder

Dependent personality disorder (DPD) is characterized by a pervasive emotional dependence on others. Individuals with DPD typically show chronic and extreme docility, submissiveness, undue compliance with the wishes of others, difficulty in expressing disagreement with others or making even reasonable demands on them because of fear of losing their support or approval, exaggerated anxiety and fear of being abandoned by their close friend(s), as well as a limited capacity to make everyday decisions without excessive reassurance from others [132, 133]. For DPD patients, the relationship with the significant other(s) is seen as a matter of survival. Very often, due to their pathological dependence on supportive social relationships and intense need to be approved by others, these patients will avoid even the slightest expressions of anger. In addition, they tend to be admiring, loyal, affectionate and considerate towards people in their close social circle [134-136]. In a study where the performance of DPD patients and healthy controls was compared in a line bisection task, the patients deviated leftward of the veridical center significantly more than the healthy participants [137]. This perceptual bias which indicates a RH dominance, further suggests a link between an excessive need for affiliation and the RH.

Psychopathy

A callous disregard for the rights of others and a propensity for predatory and violent behaviors characterize psychopathy. Without empathy, a sense of responsibility or remorse, psychopaths manipulate, lie and exploit others for their own gain, with no consideration for other people's feelings [132, 133]. Neuroanatomical and functional studies on psychopaths' brains suggest a hypofunctioning RH, and a dominant LH. Significant cortical gray-matter thinning were found in the right frontal and temporal cortices of individuals with psychopathy, compared to normal participants [138-140]. Furthermore, across both groups, there was a negative correlation between scores on the affective facets of the psychopathy check-list (PCL-R [141]) and cortical thickness in the anterior and medial temporal regions, selectively in the RH [140]. In addition, while both amygdalae volumes are reduced in psychopaths, compared to controls, there is a trend for higher reduction in the RH, and a correlation was reported between the affective and interpersonal facets of psychopathy and the amygdala reduced size [142, 143]. In the same line, fractional anisotropy analyses of the brains of psychopaths and adults with antisocial personality disorder have found abnormalities in several regions within the RH [144, 145], implying poor inter-neuron connectivity specifically in the RH.

The information flow between the two cerebral hemispheres

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can be inspected by computing the inter-hemispheric transfer time (IHTT). Poffenberger [146] reasoned that when a stimulus is presented to the same hemisphere that controls the motor response, [e.g. left-hand responses (controlled by the RH) to a stimulus presented in the left visual field (initially processed by the RH)], reaction times would be shorter than trials where information must be communicated across the hemispheres in order to initiate a motor response, [e.g. right-hand responses (controlled by the LH) to a stimulus presented in the left visual field (initially processed by the RH)], since an extra step of cross-callosal transmission is required. Indeed, cross-hemispheres trials consistently produce longer response times (ranging from 2 to 6ms) than same-hemisphere trials [147, 148]. When psychopathic and non-psychopathic criminals were compared, in a motor response task, a substantially prolonged IHTT was found among the psychopaths [149]. Remarkably, however, the increased IHTT in psychopathy, was on average larger in the right-hand, compared to the left-hand, responses, implying a relatively slower transfer of information from the RH to the LH than in the opposite route. Likewise, a physiological study on the inter-hemispheric connectivity in psychopaths found that while left-to-right signal propagation was intact, the right-to-left connectivity was abnormal [150]. This direction-specific difference in information flow across the hemispheres suggests that in psychopathy the LH is less modulated and balanced by the RH.

Similarly, in a facial affect recognition task, where responses were made either with the right or left hand, the accuracy of psychopaths was higher when they responded with the right hand [151], suggesting a LH superior functioning in psychopathy. When measuring hemispheric differences in the auditory modality with a dichotic listening paradigm, psychopathic individuals demonstrated a smaller left-ear (i.e. RH) advantage for the detection of emotion targets, compared to controls [152]. Collectively, these studies suggest that psychopathy is associated with a hypofunctioning RH and/or a hyperfunctioning LH [153].

Pedophilia

Sexual relations between adults and young children include an element of exploitation, i.e. taking advantage of a young person who lacks the basic cognitive and emotional capacities to make an informed decision on a matter with significant social consequences. Pedophilia is therefore seen by society as selfish and immoral behavior [154]. Brain imaging studies show dysfunctions and reduced metabolic activity in the right orbitofrontal and temporal regions of pedophiles [155-157]. Anatomical comparisons between the brains of individuals with pedophilia and normal participants found that various regions within the RH of pedophiles were smaller [158]. In addition, a study on the effects of hormonal therapy for pedophilia found that, before treatment, viewing pictures of young boys activated various LH regions in the pedophiles' brains. Five month into the hormonal treatment, however, these brain activations disappeared [159]. Taken together, these studies imply that pedophilic urges are mediated by the LH, and are further facilitated by an under-activated RH that fails to temper and control those unsocial behaviors.

The right and left hemispheres: mediating altruism and selfishness?

The aforementioned studies provide clear evidence for a fundamental difference in the right and left hemispheres' mediation of social interactions. The RH is involved, to a relatively greater degree than the LH, in mediating pro-social reasoning, emotions and behaviors, while the LH seems to mediate a self-centered mode - pursuing one's self-interests without having other people's interests in mind - which is reflected in the LH relatively greater involvement in unsocial (and sometimes anti-social) tendencies and behaviors (see summary in Table 1). A somewhat similar idea was proposed by James Henry. Based on several lines of evidence from neuroendocrinology and the psychology of interpersonal relationships, Henry suggested that the LH is mainly involved in self-preservation activities, while the RH mediates species-preservative behaviors, initially in the context of mother-newborn attachment and bonding, and later on in adult affiliative behaviors [160-165].

This framework that associates pro-social behaviors with the RH, and unsocial tendencies with the LH, intuitively raises the concept of altruism vs. selfishness. Indeed, an fMRI study, reported a positive correlation between activity in the right posterior superior temporal cortex (pSTC) and altruistic tendencies and behaviors [166, 167]. Activity in the same brain region (right pSTC) also correlated positively with participant's willingness to donate money to a charity [168]. Likewise, gray matter volume and activation in the right TPJ correlated positively with altruistic choices, in an experiment where participants decided how to share a sum of money [169].

Nevertheless, although it is generally true to describe the RH as a mediator of altruistic tendencies and the LH as the mediator of selfishness, it is necessary to apply caution when attributing altruistic motives to pro-social tendencies and behaviors. Altruism in its broader sense is the concern for the welfare of others. However, despite the fact that all pro-social behaviors share an element of altruism, there is still a unique meaning to the concept of altruism as acting selflessly with the intention to benefit others and without expecting any recompense.[1] Several

Table 1. The lateralization of pro- and anti-social tendencies

	Left-hemisphere	Right-hemisphere
Mediates the need for	Power	Affiliation
Primarily involved in	Unsocial and anti-social tendencies	Pro-social attitudes
Associated with	Anger, Hostility, Aggression, Jealousy, Resilience to social rejection, A sense of being socially powerful, Dominance, Control of others, Machiavellianism (manipulation and exploitation of other people), Gloating (enjoying another person's misfortune), Moral judgments based mostly on the outcome	Empathy, Agreeableness, Trust, Gratitude, Fairness, Guilt feelings, Social intelligence (Identifying social stimuli, understanding the intentions of other people, awareness of the dynamics in social relationships, and successful handling of social interactions), Pain of social rejection, Moral reasoning based on the agent's intentions, Juridical enforcement of moral conduct
Abnormal conditions	Psychopathy Pedophilia	Williams syndrome (over-friendliness) Dependent personality disorder

neurophysiological studies suggest that the RH mediates pro-social tendencies and behaviors even in the absence of altruistic drives, i.e. when the pro-sociality is driven by 'selfish' ulterior motives.

In an fMRI experiment, participants played a game where in each trial the participant received a sum of money which he could keep for himself or share it with an anonymous play partner. Two versions were tested; in one, the play partner could punish the participant and reduce/annul his earnings, and in the other, the play partner was powerless. A behavioral analysis found that participants who acted selfishly in the 'no punishment' version changed their strategy and shared a great portion of the money with their anonymous partner when punishment was possible. Their brain activity also showed an increased activation in the right DLPFC when they played more fairly [174]. This study shows a RH activation during a pro-social decision, even though it was motivated by the fear of losing previously earned gains, rather than by morality and genuine altruism.

In another study, participants played a game where one player had the role of an 'investor' and another player acted as a 'banker'. Both players were anonymous to each other; they communicated via computers located in different rooms. In each round, the investor received some money which he could save or invest with the banker. Investments yielded a fixed profit of 200%, however, this earning formula was known only to the banker who had a choice, in each round, to return to the investor either 50%, 25% or none of the profits. Two versions were played; in one, the investor was informed after every 3 rounds about the average distribution of the profits - a condition that motivated the banker to build a good reputation, by returning a greater share of the profits, in order to attract investments in the future rounds. In the other version, the investor was not informed at all. TMS was applied to the bankers' left or right DLPFC in order to temporarily disrupt the activity of that region and shift the inter-hemispheric balance into a dominance of the contralateral uninterrupted hemisphere. The results showed that when the investor was unaware of the profit distributions the TMS did not affect the bankers' decisions. However, when they were motivated to build a good reputation, disruption of the left DLPFC (i.e. RH dominance) resulted in the bankers keeping for themselves only 52% of the earnings, while the same TMS applied to their right DLPFC (i.e. LH dominance) resulted in the bankers keeping more than 70% of the profits [175]. In this study the RH moderating influence came into effect only when the banker's reputation was on the line and mainly for self-serving purposes - increasing long-term gains - rather than moral considerations of fairness.

In addition, pro-social behaviors sometimes originate simply from conformity to social norms. In a study, participants judged the attractiveness of a series of faces and after each rating they were informed how a group of 200 students from the same university rated that face. There was a general tendency, in the second round, to adjust the ratings in line with the group's opinions. Remarkably, participants whose right posterior medial frontal cortex was temporarily attenuated with TMS were less affected by the group's rating [176]. This study shows that with a fully functioning RH one is sensitive to the opinions of others and adjusts to the social

[1]Whether pure altruism is possible, or that even unreciprocated acts of giving are motivated, at least partly, by the emotional gratification it generates, is an age old philosophical debate [e.g. 170–173] that is beyond the scope of this article. Nonetheless, social behaviors can be viewed as a continuum that ranges all the way from pure selfishness on one side to pure altruism on the other end, with many mixed-motives behaviors between these poles, rather than a rigid dichotomy of altruism or selfishness. With this perspective, some pro-social acts would definitely be positioned closer to the altruism pole (e.g. donating one's spare kidney to save a stranger [170]) as they primarily involve a genuine desire to enhance another person's welfare, while other pro-social acts are closer to the selfish side (e.g. sponsoring a social event when the primary motive is a cost-efficient advertisement and business promotion).

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norms. Interrupting the RH activity enables the expression of one's true opinion, likes and dislikes, with less surrender to social pressure. Therefore, the RH involvement in affiliative behaviors may not always coincide with altruistic motives, a genuine gregarious drive or an authentic joy of friendship; rather, it may reflect the RH greater sensitivity to social norms and its mediation of conformity.

Furthermore, even the RH involvement in empathy is not by itself evidence that humans have an innate neural system designed for altruistic sentiments, since empathy can be restricted to people from one's own ethnic or social group. EEG recordings showed a RH frontal activation when participants felt sadness and similar activation when they observed in-group members feeling sad. The RH activation, however, was significantly lower for scenes of out-group members in distress [177]. Similarly, people punish out-group members for selfish and unfair behaviors more severely than they punish in-group members for the same behaviors. An fMRI study showed that the harsher punishments of the out-group members were associated with an increased activity and stronger connectivity in several RH regions, compared to the lighter punishments of in-group members [178]. In addition, a TMS that transiently disrupted the neural activity in the right, but not left, TPJ reduced this in-group favoritism [179]. Therefore, the RH involvement in empathy and in the enforcement of moral codes is not necessarily indicative of empathy for humankind - an all-embracing humanism and egalitarianism with a sense of universal brotherhood. Rather, it may be parochial and limited to one's group (tribe, religion, nation etc.) at the expense of outsiders, and therefore it is ultimately based on self-centeredness, where the person's group is perceived as an extension of oneself (i.e. 'we' vs. 'them').

Thus, conceptualizing the left and right hemispheres involvement in opposite social attitudes in terms of neural systems that promote selfishness vs. altruism, respectively, would be inaccurate. The pro-social behaviors, which the RH mediates, are not always driven by an altruistic motive; sometimes they are motivated by fear (of punishment, or social rejection etc.), conformity to socially accepted conventions, self-centered ethnocentrism, or even profit-making - giving as a strategy for enhancing one's reputation and long-term profits. If pro-social activities are mediated by the RH regardless of their underlying motivations (altruism or self-interests), how can we then view the cerebral lateralization of social tendencies? What are the underlying biological mechanisms that can explain the RH disposition to mediate pro-social emotions and behaviors? More specifically, is there something in the RH and LH neurophysiology and functions that make them more suitable to mediate pro-social and unsocial attitudes, respectively?

Self-control is the foundation of a pro-social mindset

A theoretical framework that can explain the hemispheric asymmetry in social tendencies is the behavioral activation and inhibition systems that were proposed by Jeffrey Gray. Based on observations from animal studies and the principles of behavioral learning theories, Gray [180] suggested that we have two neural systems for responding to the environment; the behavioral activation system (BAS) and the behavioral inhibition system (BIS). The BAS regulates appetitive, positive-incentive motivation, and is manifested in approach behaviors toward potentially rewarding stimuli. The BIS, on the other hand, is sensitive to aversive cues, and regulates avoidance/withdrawal behaviors from potentially harmful/pain-inducing stimuli.

Correlations between participants' BAS/BIS measurements and their EEG patterns revealed that the BAS and BIS are hemispherically lateralized in the brain; the LH is generally associated with motivating one to act and approach positive/appealing stimuli, while the RH is mostly involved in inhibiting actions that may lead to unpleasant results [181-184]. Furthermore, behavioral and neurophysiological evidence link the RH with self-control and inhibition, not only in motor behavior, but across various mental functions such as speech, cognitive processes as well as emotional experiences [e.g. 185-189]. Accordingly, when the balance between these two systems (BAS/LH and BIS/RH) is altered and one system becomes more dominant it is manifested correspondingly in overactivation or overinhibition; a hyperfunctioning LH is associated with impulsiveness - a tendency to act without much forethought - in motor response selection in go/no-go tasks [190], as well as in economic decisions in time-discounting tasks [191]. In contrast, a hyperfunctioning RH is associated with more cautious, inhibited and withdrawal behaviors as can be seen in infants playing [e.g. 192-194], as well as in adults' decision making [183, 195].

Social interactions between humans are governed by a wide range of values, rules, customs and rituals that form the basis of every culture. Individuals internalize these social conventions through the process of socialization, thereby acquiring the skills and habits necessary for participating as members in their societies. As social interactions are inherently full of potential conflicts between an individual's and other people's interests, the essence and main theme of the entire socialization process is training the individual to restrain and control his/her immediate instincts, delay gratification, and think, feel and behave in a manner that considers also other people's needs and wishes. Pro-social behaviors are therefore grounded in the brain's inhibitory mechanisms.

Studies have shown that individuals with higher levels of patience

and self-control were more likely to be cooperative and help others [196, 197], to donate to charity [198], to forgive a partner's misbehavior [199], and less likely to over-exploit public resources [197]. Furthermore, the relationship between self-control and positive social interactions is bi-directional. For instance, high self-control correlated positively with one's perceived sense of belonging and acceptance by family and friends [200]. The other side of the coin - increased sense of acceptance - can bolster a person's ability to exert self-control and delay gratification [200]. Similarly, people attribute greater trustworthiness to those who are perceived as better able to control themselves [201], thereby facilitating their positive social interactions. On the other hand, poor ability to regulate one's instincts and desires is associated with a higher likelihood of engagement in a range of anti-social and aggressive behaviors [e.g. 202, 203].

Moral reasoning, empathy for someone in distress, fair behavior, guilt feelings for an inadequate treatment of another person, and all other pro-social tendencies require one to inhibit his own desires and interest, for a while, and adopt the perspective of another person by considering his needs and wishes. Therefore, pro-social behaviors and tendencies are naturally associated with the RH neurophysiology since they involve a substantial component of inhibition - exercising self-control and restraint - a function that is mediated by the RH. This explains why the RH mediates also pro-social behaviors that are not altruistically motivated, since they comprise an element of self-restraint. That is, the two hemispheres subserve different systems (the BAS and the BIS) which are both needed for survival and proper functioning in any environment. The LH/BAS promotes the pursuit of hedonic desires. The RH/BIS, balances and moderates this drive by taking into account also other people's interests, which may not correspond with one's own wishes, and therefore may potentially have a negative effect on one's long-term wellbeing. Consequently, morals, etiquettes and pro-social behaviors are learned mainly through the inhibition system, thereby being assimilated primarily into the neural structures and networks of the RH.

The need for affiliation is rooted in a sense of vulnerability

Another plausible explanation for the RH association with pro-social attitudes, emotions and behaviors is the RH relatively greater involvement in mediating experiences of vulnerability - an emotional state that triggers the need for affiliation and sociability. There are two biological asymmetries between the right and left hemispheres that lead to the RH association with experiences of vulnerability. (a) Approximately 90% of the population is less dexterous in the left-hand, i.e. they perform motor actions better with their right-hand than with their left-hand. Anatomically, the right-hand is controlled by the LH, and the left-hand is controlled by the RH. Thus, the LH receives, through the right-limbs dexterous and fluent motor actions, a positive feedback of having power and ability to deal with environmental challenges, whereas the left-limbs relative clumsiness generate a sense of incompetence, weakness and vulnerability that is registered in the RH [189]. (b) Several lines of evidence suggest that the RH has a leading role in processing threats. For instance, frightening stimuli are better detected and trigger a greater physiological response when they are presented in the left visual-field (initially processed by the RH), compared to identical stimuli presented in the right visual-field [204-207]. In addition, higher levels of the stress hormone cortisol correlate with a greater RH activation [208-212]. Panic disorders, phobias, and the detection of fear in others are all associated with a RH physiological activity [213-220]. These studies show that the RH, more than the LH, mediates experiences of fear, stress and anxiety which engender a sense of vulnerability [189].

Vulnerability is often a motivator for pro-social behaviors. Studies have demonstrated that subtle reminders of one's mortality increased positive attitudes towards charities and the amount of given donations [221]. Awareness of one's mortality also reduced racial prejudice and increased helping behaviors [222]. Exposure to traumas or natural disasters has been shown to increase engagement in pro-social activities [223-225]. Even a laboratory manipulation that elevated participants' stress resulted in more pro-social behaviors. In an experiment, participants were randomly assigned to a group that was exposed to a stressful situation (a public-speaking task) or to a control group without stress, and their behaviors during subsequent games were analyzed. The results showed that the individuals who were exposed to stress trusted their play-partners and shared their earnings with them more often than the control group [226]. These findings are even more remarkable, given that all play-partners remained anonymous throughout the play session and the entire interaction between the players was carried out via computers that were located in separate cubicles, i.e. vulnerability can facilitate pro-social behaviors even toward anonymous strangers.

The biological mechanism behind this phenomenon - that vulnerability leads to pro-social behaviors - seems to be the fact that positive social interactions are fundamental means for dealing with fears and alleviating distress [227, 228]. Plenty of evidence show that whilst loneliness and social isolation are associated with greater stress [229, 230], positive and supportive social relationships serve as buffers against the detrimental impacts of stress in humans [e.g. 231-233] as well as in social animals [234, 235]. Studies have shown that in stressful situations even the mere presence of other people can alleviate the distress. In

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a classic experiment, participants were (deceptively) told that they were going to receive electric shocks. One group was shown the electrical apparatus and was told that the shocks would be extremely painful (high anxiety group); the other group did not see the apparatus and was told that the electric stimulation would feel like tickles and would not hurt (low anxiety group). Individuals from both groups were offered to wait, while the experimenter was finishing the last preparations, either in a waiting room by themselves or in another waiting room with other people who were also participating in the experiment. The results showed clearly that the individuals who were randomly assigned to the high anxiety condition chose to wait with other people, significantly more often than the low anxiety group [236].

Further investigations of this phenomenon in hospitals with women waiting to give birth or patients awaiting a major surgery etc. found that they preferred to wait during their stressful period with other patients, rather than alone, only when the others were perceived as capable of providing a beneficial stress-relief, but not otherwise [237-243]. This confirms the notion that the stress-induced preference for being in physical proximity to other people is linked to its utility function - the perceived benefit (i.e. stress relief) that can be achieved by being with a specific person/group in a given situation.

This association between affiliation and stress relief is rooted in our biological development. Systematic observations of infants from various cultures revealed that when an infant is exposed to an unfamiliar environment or to a stranger, situations which naturally evoke anxiety and stress, the infant maintains eye contact and physical proximity to its caregiver which the baby sees as a 'secure base' [244-247]. These studies have led John Bowlby and Mary Ainsworth to postulate that the infant's natural attachment behaviors are expressions of an innate emotional homeostasis mechanism for stress-regulation. While exploring the new environment, the infant maintains eye contact and close proximity to its caregiver because of the stress-relief that the presence of the caregiver provides, i.e. the confidence that if the need arises the 'secure base' is easily accessible. When it grows, the child seeks the love of its parents because it engenders feelings of safety and protection that reduce fear and distress [244-253].

Studies on adult social relationships revealed similar dynamics; a major driving force behind the formation and maintenance of all social relationships is the emotional support and relief from stress that positive social relationships can offer in times of need. Thus, from a neurobiological perspective, engagements in social relationships and pro-social activities are essentially adaptive behaviors, evolutionarily designed to support emotion regulation - i.e. friends and a significant other provide a 'secure base' for retreating when the need arises - thereby facilitating optimal health and well-being that enable the ultimate biological goals of survival and reproduction [245, 249, 254-258].

Taking the lead in mediating experiences of weakness and vulnerability, the RH is essentially mediating a mental condition that increases the need for affiliation and social connectedness. Consequently, a pro-social mindset and corresponding behaviors are primarily associated with the RH. The LH, in contrast, with its motor dexterity that generates a feedback of strength and ability to deal with challenges, is more involved in mediating experiences of power and a perception of high self-efficacy [10-12, 45, 189, 259], a mental state that tends to reduce the need for social relationships. Studies comparing participants with high and low sense of power found that feeling powerful was associated with an increased perception of social distance between oneself and other people [260, 261], less compassion to the suffering of others [262], greater moral hypocrisy - imposing strict moral standards on others while allowing much leniency in one's own practices [263], a tendency to maximize one's profits while ignoring other people's interest [264], treatment of other people not as valuable human beings but according to their usefulness for one's goals [265, 266], as well as a propensity to undermine the positive intentions behind other people's generous acts [267]. Accordingly, unsocial and anti-social attitudes and behaviors are primarily associated with the LH which mediates experiences of power.[2]

Holistic perception enables an empathic and pro-social attitude

Another conceivable source of the hemispheric asymmetry

[2]This view of affiliation and sociality as an innate psychobiological mechanism for coping with stress and achieving homeostasis can explain a fundamental aspect of psychopathy. The core emotional deficit of psychopaths is their shallow affect, callousness and unemotional mental state [141, 268]. In addition, the most robust neurophysiological finding about psychopaths is their low startle response to fearful and threatening stimuli [e.g. 269–272], as well as their deficits in recognizing fearful facial expressions [e.g. 273, 274], as compared to normal individuals. This archetypal feature of psychopaths – their relative lack of apprehension, fearlessness and a general immunity to psychological distress – is central and crucial to understand the biological mechanisms associated with the psychopath's anti-social tendencies and behaviors. A relative resistance to stress and anxiety entails a low need/motivation to form meaningful friendships and warm social relationships as means for emotion regulation. That is, although a low need for social affiliation per se is not a bad trait, it seems that in psychopaths this combination is the soil and substrate on which anti-social tendencies and behaviors breed and grow. When a relative immunity to stress, fearlessness and therefore a low need for warm and supportive social relations are combined with a constellation of other adverse bio-psycho-social factors, it can lead one to the extreme selfishness and anti-social behaviors manifested in psychopathy.

in mediating social tendencies is the two hemispheres' different modes of information processing. The world can be perceived from different hierarchical levels. Looking at a forest, one can view it holistically in its global meaning (a forest), or focus on specific trees and attend to their local features. Many studies with healthy and brain-damaged patients have demonstrated that these two complementing modes of perception are lateralized in the brain; the RH mediates the grasp of the overall picture, while the LH is associated with attention to the details [275-285]. For instance, patients with a unilateral brain damage were shown a series of stimuli (letters or geometrical shapes) consisting of elements which had different meanings than the global feature (see example in Fig. 1), and subsequently their memory for what they saw was tested. Those with a lesion in their RH, whose mental experience is presumably dominated by the undamaged LH, recalled the smaller, local features better than the large, global ones, while the opposite occurred in people with a lesion in the LH [286, 287].

This hemispheric asymmetry in perceiving the world (holistic/global vs. analytic/local) permeates the entire mental realm. Chess and Go are board-games that emphasize different playing strategies. In Go, all stones are identical and the key factor for winning is a clever positioning of the stones on the board. In chess, however, the pieces have different ranks and functions, thus success depends on moving a proper piece to an appropriate position in a given situation. An fMRI study comparing the brain activity while participants analyzed scenarios in these two games revealed that during chess which employs a 'local battle' strategy there was a higher activity in the LH. In contrast, Go which requires a 'global strategy' was associated with a greater activity in the RH [288, 289]. Similarly, when listening to music the RH is generally attuned to the whole melody while the LH has an advantage in analyzing the subcomponents [290, 291]. Likewise, a study found that people with a right-ear preference (i.e. LH advantage) are better at tasks that exert local focused attention, whereas those with a left-ear preference (i.e. biased toward the RH) are better at tasks that require a more global view [292].

Fig. 1. The RH sees an E and a triangle, while the LH attends to the Xs and circles.

Animal behavior studies have documented this cerebral lateralization - the RH perception of the gestalt and the LH focus on the separate components - also in pigeons [293, 294], chickens [295, 296], gerbils [297], dolphins [298], baboons [299, 300], and chimpanzees [301], suggesting that the hemispheres' different (and complementing) perceptual modes is not a uniquely human phenomenon; it is shared by other species and is probably rooted in biological and evolutionary processes [302-304].

Four aspects of holistic perception seem to contribute to the hemispheric asymmetry in social tendencies. (A) Holistic (global) perception is inclusive in nature; it highlights the similarities and connections between the various elements in the scene. In contrast, analytic (local) perspective is narrow, with an emphasis on differences that exclude an item from a general category. In a study, participants were presented with a series of large letters constructed from different smaller letters (see example in Figure 1). One group of participants were required to name the big letters (global priming condition) while another group had to name the small letters (local priming condition). Then, they were introduced to pictures of various flower bunches and their task was to identify similarities and differences between the pictures. Analysis of their responses revealed that the former group, that was primed to see the global meaning, found more similarities than differences, whereas the opposite occurred with the latter group [305-307]. Likewise, when participants could choose between a small and a large set of choices, global priming led to a preference of smaller choice-sets. Presumably, a global viewpoint emphasized the similarities between the options, making many of them redundant, thereby decreasing the appeal of having more choices [308].

Applying these principles to social relationships, it is conceivable that the global/holistic perspective that the RH mediates is inherently biased to highlight the commonly shared traits between people and to overlook their differences. This mental position of seeing commonalities rather than divisions fosters a more humanistic and egalitarian perspective that facilitates pro-social attitudes and behaviors. Conversely, the local/analytic perspective, mediated by the LH, concentrates on the variation and differences between people - a viewpoint that promotes a mindset of inequality and hierarchies in social relations. This notion is supported by several experiments showing that representing events and objects on a global and broader level (rather than a narrow, concrete and detail-focused level) is associated with a tendency to see greater similarity between one and diverse others [309], and with greater tolerance toward non-normative social groups [310], suggesting that holistic perspective is associated with blurred social distinctions and a more inclusive social attitude.

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Furthermore, induction of a global, rather than a local, perspective increased liking for atypical objects [311]. That is, a holistic mindset seems to underscore the similarities even in atypical objects thereby enhancing their likeability.[3]

(B) In addition, a gestalt/holistic cognitive mode affects both space and time perception; i.e. seeing the forest vs. focusing on the trees, as well as thinking long-term vs. short-term. Studies show that individuals who adopt a global mindset tend to have longer time horizons as reflected by a lower present-bias in time-discounting choices [314], and greater self-control in the presence of temptations [315, 316]. That is, a global/abstract perspective seems to expand one's temporal horizons and bring to mind the consequences of one's current decisions and actions in the long run. These studies corroborate neurophysiological evidence linking the LH (local mode, short-term thinking) with impulsive behaviors [190, 191] and the RH (global mode, long-term thinking) with self-restraint [185, 195].

A selfish and unsocial attitude reflects a short-term perspective that focuses on immediate rewards. Conversely, a pro-social mindset often entails forbearing present inconveniences in hope of future beneficial results. Thus, the LH mediation of a relatively narrow cognitive mode that focuses on immediate pleasures and gains breeds a perspective that favors unsocial (or even anti-social) behaviors. The RH, on the other hand, with its mediation of holistic perception enables a broader perspective that takes into account the effects of one's behaviors in the long run, a viewpoint that fosters a pro-social attitude and corresponding behaviors.

(C) Another feature of the RH holistic mode of thinking is its ability to handle multiple options, representations and meanings simultaneously. Linguistic studies that compared how people resolve lexical ambiguity presented in their right or left visual field, suggest that when faced with a word or concept that has several meanings, the RH activates a broader semantic network that holds the multiple alternative meanings, while the LH is involved in selecting the single most appropriate meaning in a given scenario [317-319]. Similarly, whereas healthy people understand the sarcasm when a boss tells a lazy employee 'don't work too hard!', RH-damaged patients could not grasp the irony in that scenario as they focused on the literal meaning [320]. Presumably, their RH deficits prevent them from seeing other meanings. In studies of deductive reasoning, participants judged the logical validity of certain inferences based on given premises. LH-damaged patients (i.e. RH dominance) were more accurate when the information given was fluid and uncertain, so that several options were possible, whereas RH-damaged patients excelled in instances with a single conclusion [321, 322]. Likewise, when students were presented with the Rorschach inkblots (a set of random unstructured visual stimuli intended to elicit personal subjective associations) either in their right or left visual-field, they reported more associations when the inkblots were presented in the left visual-field (i.e. to the RH) than in the opposite hemispace [323], reflecting the RH mediation of broader horizons that enable multiple associations and possibilities. In the same line, stimulation of the RH either with tDCS or by left-hand muscle clenching, intended to temporarily shift inter-hemispheric balance toward the RH, resulted in participants finding more solutions to the puzzles and cognitive problems they had to solve [324-326]. Again, these studies reflect the RH superiority in divergent thinking and seeing things from different and unusual angles.

The common denominator of these phenomena is that the two hemispheres subserve different (and complementary) cognitive modes of representing one's environment. The LH mediates a single, narrow, precise and determinate way of perceiving and understanding one's environment, whereas the RH mediates a wider perspective that includes multiple possibilities of representing the world [21, 22, 319, 327, 328]. In the context of social relationships, this hemispheric difference translates into a LH mediation of a narrow perspective - one's own point-of-view, here and now - whereas the RH broader scope, that enables various ways of representing the world, is more receptive to the alternatives, i.e. to other people's opinions and their unique ways of seeing things. This enhanced attunement to other viewpoints seems to contribute to the RH mediation of empathy and a pro-social attitude.

(D) Human faces are the primary social stimuli. When we look at a face, two parallel processes occur simultaneously; we see a person, an individual, and at the same time we categorize him/her by gender, ethnicity, age etc. (e.g. a young Russian woman). Studies on

[3]In the remote association test (RAT), a person is presented with three words and asked to find a fourth word that links all three. For instance, for the word triad 'cottage/swiss/cake' the word 'cheese' is the correct answer as it is related to all three words. This test measures a person's ability to see relationships, connections and a semantic overlap between words/concepts that are only remotely associated. Studies have found that priming participants with the need for affiliation enhanced their subsequent performance in the RAT [10, 312]. Similarly, people who scored higher on the need for affiliation performed better on the RAT [313]. Perhaps, the linkage between these two ostensibly unrelated mental processes (the affiliation motive and performance on the RAT) is that both processes are mediated by the same neural system – the RH. Therefore, activation of the affiliation motive stimulates a holistic/intuitive mode of thinking that sees similarities and relationships, thereby facilitating performance on the RAT tasks which specifically require this mode of thinking.

face perception suggest that the two hemispheres are differentially involved in these processes. The RH with its holistic mode is more efficient at seeing the gestalt, the complete configuration of the face as an indivisible whole, leading to the perception of the individual, whereas the LH with its analytic mode is relatively more involved in deconstructing the facial features in order to categorize the person by gender, race, age etc. [329-334]. This hemispheric specialization in face perception entails that, in social interactions, the RH mediates a more personal mode that sees the unique individual, a perspective that facilitate the ability to empathize with him/her. The LH, in contrast, mediates an impersonal mode that stereotypes the person into categories and labels. It is conceivable that this fundamental hemispheric asymmetry in the way we perceive other people - seeing a unique person vs. stereotyping him/her - contributes to the right and left hemispheres mediation of pro-social and unsocial tendencies.

Collectively, these features of holistic perception - a focus on similarities rather than differences, a long-term perspective, divergent thinking that enables seeing other points-of-view and a personal mode of relating to people - promote the RH mediation of a more open-minded and empathetic attitude toward others and facilitate the RH greater engagement in pro-social behaviors, as compared to the LH.

SUMMARY

As biological creatures that depend on their environment and its resources for survival and well-being, the human existential condition is such that a person needs power and autonomy that will enable carrying one's (own) weight, i.e. meeting one's individual needs sufficiently and independently. In addition, human beings have an innate psychobiological need for affiliation and social connection, which is necessary for both emotion-regulation and personal growth. Part of the human challenge is to achieve equilibrium between opposite and conflicting needs and desires; the need to be part of a social group and the need for independence, the longing for intimacy and closeness with significant others and the desire for some privacy and occasional solitude. Thus, whilst taking care of one's own needs, it is necessary to cultivate a pro-social mindset and corresponding actions, in order to reap the benefits that positive and supportive social relationships can offer. This includes tempering and moderating one's behavior so that other people's needs and interests are not hurt, as well as helping others to meet their needs and achieve happiness.

A review and synthesis of the literature suggests that these two (seemingly opposite, but actually complementing) biological needs are lateralized in the brain; the LH has a relatively greater role in mediating the need for power, whereas the RH is more involved in mediating the need for affiliation. The RH superiority in perceiving social cues, interpreting the intentions of other people and understanding social dynamics effectively renders the RH as the brain center of social information processing, thereby subserving and facilitating affiliative tendencies. Accordingly, pro-social attitudes, emotions and behaviors are associated mainly with physiological processes in the RH, while the LH has a leading role in mediating unsocial and anti-social mindsets and actions[4].

The biological origins of this hemispheric asymmetry in social

[4]Social behavior is a complex phenomenon that can be influenced by multiple factors. Thus, in certain situations the overt behavior may be incongruent with the inner motivation and therefore it may seem to contradict with the notion that the RH mediates pro-social tendencies. For instance, social anxiety is associated with a RH hyperfunctioning and/or a LH hypofunctioning [214, 215, 218, 335]. Similarly, shyness is associated with a higher activity in the frontal parts of the RH as compared with the homotopic LH regions [336–339], and with a larger right anterior cingulate cortex [340]. Nevertheless, the propensity of socially anxious and shy individuals to avoid social contacts should not be taken to imply disinterest in friendships or a low need for affiliation. On the contrary, shy children and adults have a strong yearning for positive social interactions; they desire to be accepted by other people and experience close and warm relationships, and yet they are still inhibited, feeling discomfort in the presence of others, thinking that they cannot handle social interactions adequately, and fearing that they will be embarrassed, rejected or otherwise socially excluded [341, 342]. Research indicates that social withdrawal, shyness and reserved emotionality arise from fear and anxiety [343], low self-esteem [344], poor parenting style and insecure attachment [345, 346], or previous negative social experiences of rejection and bullying [347]. Some individuals are oversensitive in their social interactions due to an unfortunate combination of adverse bio-psycho-social factors and past negative social experiences which intensify their fears of embarrassment, humiliation and social rejection [e.g. 348, 349]. This hypersensitivity creates an ambivalent emotional situation where the basic human need for comforting, non-judgmental, embracing and friendly social relationships propel one toward social interactions, while concurrently the deep fears of being scrutinized and judged by other people, misinterpreted and rejected, or that one's interest in social relationships might not be reciprocated, paralyze and disable the shy person from being proactive and taking the initiative in forming and maintaining social interactions. That is, in the case of shyness, the fears override the need for affiliation, thereby dictating an inhibited behavior that occurs despite the person's deep need for social connection. This behavioral inhibition serves as a protection mechanism from (real or imagined) social rejection and the pain it generates. This conflict between a deep, unfulfilled need for affiliation and a much stronger fear of rejection creates the cognitive dissonance, emotional tension and physiological arousal (the general feelings of stress, anxiety and unease) that shy and socially anxious people feel at social interactions. Very often this inner-conflict is resolved by an inhibited/withdrawal behavior – an unconstructive solution that exacerbates and perpetuates the social anxiety. Accordingly, the RH activation associated with shyness and social anxiety reflects the fear, stress, behavioral inhibition and the high need for affiliation (despite the person's inability to demonstrate proactive social behaviors).

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tendencies are severalfold. (1) Positive social interactions require a great deal of self-control - inhibition of one's immediate instincts and desires - and consideration for the perspective of others. Given that self-control is mediated by the RH, pro-social emotions and behaviors are, therefore, inherently associated with physiological processes of the RH, because it subserves the brain's inhibition system that restrains inappropriate behaviors and mental activities. (2) The RH mediates experiences of vulnerability. It registers the relative clumsiness and motor weakness of the left limbs, and it is involved, to a greater degree than the LH, in mediating fear, anxiety and stress. Emotional states of vulnerability are major triggers of the need for affiliation and sociality, and therefore the RH has a greater role in mediating pro-social attitudes and behaviors. (3) The RH mediates a holistic mode of perceiving and understanding the world whereas the LH mediates a more focused analytic perspective. Holistic perception emphasizes similarities rather than differences, takes a long-term perspective, is associated with divergent thinking and seeing other points-of-view, and it mediates a personal mode of relating to people. All these features of holistic perception facilitate the RH mediation of a more empathetic attitude and pro-social behaviors.

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