Morality and the Brain: The Right Hemisphere and Doing Right

Christopher M. Filley, MD,†‡ Isaiah Kletenik, MD,*§ and Patricia S. Churchland, PhD‖¶*

Abstract: Morality, the set of shared attitudes and practices that regulate individual behavior to facilitate cohesion and well-being, is a function of the brain, yet its localization is uncertain. Neuroscientific study of morality has been conducted by examining departures from moral conduct after neurologic insult and by functional neuroimaging of moral decision-making in cognitively intact individuals. These investigations have yielded conflicting results: Acquired sociopathy, a syndromic surrogate for acquired immorality, has been reported predominantly after right frontotemporal lesions, whereas functional neuroimaging during moral decision-making has demonstrated bilateral activation. Although morality is bilaterally represented, the right hemisphere is clinically more critical in light of focal lesion data suggesting that moral behavior is subserved by a network of right frontotemporal structures and their subcortical connections. Evolution may have endowed the brain with bilaterally represented but unilaterally right-dominant morality. The unilateral dominance of morality permits concentration of an essential social cognitive function to support the perceptual and executive operations of moral behavior within a single hemisphere; the bilateral representation of morality allows activation of reserve tissue in the contralateral hemisphere in the event of an acquired hemispheric injury. The observed preponderance of right hemisphere lesions in individuals with acquired immorality offers a plausible hypothesis that can be tested in clinical settings. Advances in the neuroscience of morality promise to yield potentially transformative clinical and societal benefits. A deeper understanding of morality would help clinicians address disordered conduct after acquired neurologic insults and guide society in bolstering public health efforts to prevent brain disease.

Key Words: morality, focal lesion, right hemisphere

(*Cogn Behav Neurol* 2020;33:304–307)

Received for publication July 10, 2020; accepted July 13, 2020.

From the Departments of *Neurology; †Psychiatry, Behavioral Neurology Section, University of Colorado School of Medicine, Aurora, Colorado; ‡Marcus Institute for Brain Health, Aurora, Colorado; §Department of Neurology, Division of Cognitive and Behavioral Neurology, Brigham and Women's Hospital, Harvard Medical School, Boston, Massachusetts; ‖Department of Philosophy, University of California San Diego, San Diego, California; and ¶Salk Institute, San Diego, California.

The authors declare no conflicts of interest.

Correspondence: Christopher M. Filley, MD, 12469 East 17th Place, Mail Stop F429, Aurora, Colorado 80045 (email: christopher.filley@cuanschutz.edu).

A vital question for all humans is why individuals act to help or harm others. Morality, the set of shared attitudes and practices that regulate individual behavior to facilitate cohesion and well-being (Churchland, 2019), is an essential brain capacity without which human society could not exist. As the neuroscientific examination of behavior has matured, the study of prosocial and antisocial behaviors has begun to inform long-standing considerations in philosophy in light of steadily accumulating evidence on brain–behavior relationships. Lesion analysis of individuals who display immoral behavior after brain injury (Boccia et al, 2017; Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Garrigan et al, 2016; Mendez, 2009), as well as functional neuroimaging studies of cognitively intact individuals making moral decisions (Boccia et al, 2017; Garrigan et al, 2016), have brought to light the role of specific frontotemporal structures and their subcortical connections in moral cognition and behavior. An important clinical question is whether moral behavior exhibits laterality. Here we explore the question of hemispheric lateralization of morality and examine emerging evidence that moral behavior is organized more in the right cerebral hemisphere than in other regions of the brain.

Moral behavior in humans, as well as protomoral behavior in nonhuman mammals and birds, depends on strong instincts for sociality. Humans are motivated by their social instincts to learn the norms and customs of their community, which then guide their social decision-making. The process of making social decisions is complex, not least because prosocial options may require self-sacrifice, and all animals, including highly social mammals and birds, have strong self-regarding instincts. How the brain adjudicates between competing interests such as morality and immorality is unclear, although this process has been illuminated by data on multi-alternative decision-making in nonhuman animal models (Churchland and Ditterich, 2012) and by computational theories of homeostatic control that specify the optimization of competing values (Hulme et al, 2019).

A number of functional components contribute to moral decision-making, including recognition of the emotional states of others, empathy, predictions of the consequences of possible options, integration of competing values, and cognizance of the normative values of the community (Churchland, 2019). These elements of social behavior share much in common with what has been termed *social cognition*, which is an area under intensive

study by neuroscientists. The philosophical concept of morality can likewise be considered a feature of social cognition, facilitating its examination as a manifestation of brain structure and function.

The neuroscientific study of morality has been conducted by parallel investigations examining (a) departures from morality after neurologic insult and (b) the process of moral decision-making in cognitively intact individuals. Disrupted morality in clinical populations has been investigated in terms of the concept of *acquired sociopathy* (Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019), a term that is based on the psychiatric diagnosis of antisocial personality disorder but that refers to individuals who develop antisocial behavior after sustaining a brain lesion (Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Mendez, 2009).

Moral decision-making in cognitively intact individuals has been investigated using functional neuroimaging (Boccia et al, 2017; Garrigan et al, 2016). Despite emerging consensus on the identification of specific brain regions subserving morality, the laterality of morality remains unresolved, as the neurologic lesion literature often discloses right hemisphere localization (Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Mendez, 2009), whereas the neuroimaging data typically disclose bilateral representation (Boccia et al, 2017; Garrigan et al, 2016). Resolution of this discrepancy can be informed by a review of reported cases of immorality that have been acquired after onset of a brain lesion.

FOCAL NEUROLOGIC DISORDERS AND MORAL BEHAVIOR

As clinicians know well from interactions with difficult patients in whom a range of diagnoses may be present, a wide variety of neurologic disorders can be associated with immorality. Among the many disorders that impact the brain to enhance the likelihood of immoral behavior, a large proportion feature diffusely distributed neuropathology (ie, Alzheimer disease) or arise from an uncertain localization (ie, delirium), precluding the precise identification of the regions involved. The study of focal brain lesions, however, permits more specific localization of the origins of morality by identifying damaged areas that can be presumed to have facilitated the emergence of immoral acts.

The major disorders relevant to acquired immoral behavior are stroke, penetrating traumatic brain injury, neoplasia, and neurodegenerative disease, most importantly behavioral variant frontotemporal dementia (de Oliveira-Souza and Moll, 2019; Mendez, 2009; Roberts et al, 2019). The most notable case setting the stage for this work was that of Phineas Gage, whose penetrating bifrontal injury in 1848 produced a dramatic personality change. The advent of structural neuroimaging in recent decades has enabled much more precision in the location of lesions than techniques that were available in the past (Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Mendez, 2009). A well-known modern example is the case of EVR in 1985, in whom a marked personality alteration with immoral conduct occurred after surgery for an orbitofrontal meningioma (de Oliveira-Souza and Moll, 2019). Nevertheless, acquired immorality is likely underreported because departures from moral conduct are common in clinical practice and hence may not be regarded as sufficiently novel to warrant reporting.

TOWARD A LOCALIZATION OF MORALITY

The localization of morality presents a daunting challenge involving discussion of many cortical and subcortical structures, and a thorough account of available information is beyond the scope of this article. However, the weight of evidence from lesion and neuroimaging studies indicates that frontotemporal regions are most crucial for the representation of moral conduct (Boccia et al, 2017; Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Garrigan et al, 2016; Mendez, 2009). A recent and very thorough review concluded that virtually all cases of acquired compromise of moral conduct followed an injury to frontotemporal structures and their subcortical connections (de Oliveira-Souza and Moll, 2019). Key gray matter regions include the medial orbitofrontal cortex, medial prefrontal cortex, anterior cingulate cortex, insula, amygdala, temporoparietal junction, and ventral striatum (Figure 1) (Boccia et al, 2017; Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Garrigan et al, 2016; Mendez, 2009; Roberts et al, 2019). Among several relevant white matter tracts, the most prominent is the uncinate fasciculus (de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Filley, 2020; Highley et al, 2002; Mendez, 2009; Oishi et al, 2015; Van Horn et al, 2012). Moral behavior appears to arise from the activity of frontotemporal networks that are organized to recognize others' emotional states, engage empathy, select from possible options, and guide conduct that is intended to achieve an outcome in accordance with community values.

With respect to lateralization, several reviews of altered moral conduct have specifically identified a preponderance of right hemisphere lesions (Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Mendez, 2009), although bilateral and unilateral left hemisphere injury may also be associated with immorality. The right medial orbitofrontal and medial prefrontal cortices stand out as critical gray matter structures (Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Mendez, 2009), and the right uncinate fasciculus is most noteworthy as a major frontotemporal connection (Van Horn et al, 2012) that is not only larger than its left counterpart in most individuals (Highley et al, 2002) but is also associated with a loss of empathy in individuals with stroke (Oishi et al, 2015). These observations are particularly intriguing given that in humans, and in phylogenetically older primates and other

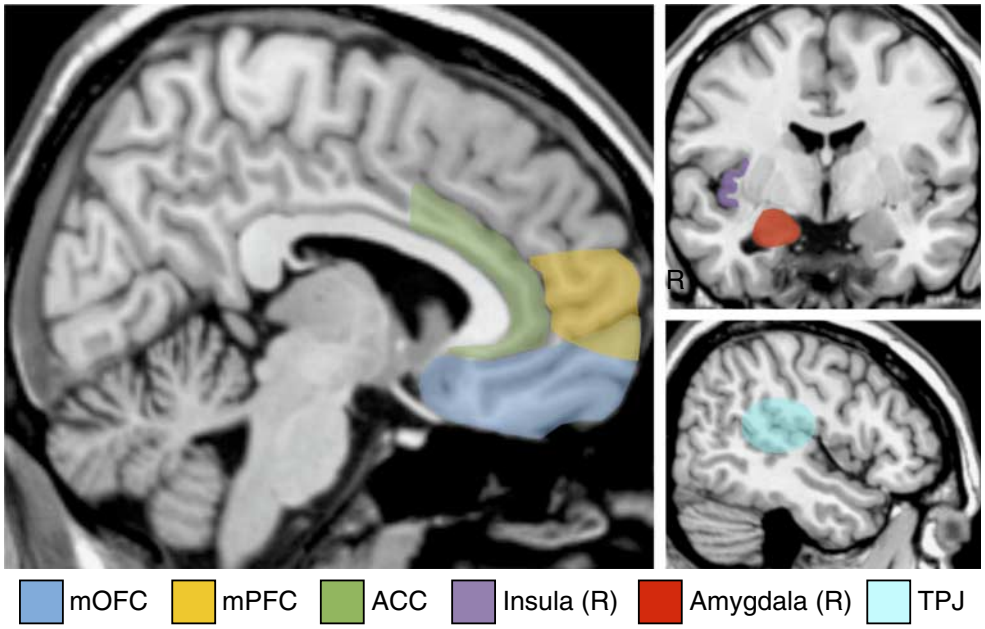

FIGURE 1. Brain regions most commonly reported in cases of lesional acquired immoral behavior (Mendez, 2009; Roberts et al, 2019). These areas likely operate as functional elements of a morality network. The structures include the medial orbitofrontal cortex, anterior cingulate cortex, and temporoparietal junction (implicated in theory of mind); the medial prefrontal cortex (involved in emotion regulation and behavioral inhibition); and limbic structures including the amygdala and insula (involved in emotional responsiveness to suffering). The uncinate fasciculus, which connects the frontal lobe with the anterior temporal lobe, and the ventral striatum at the base of the forebrain, are not shown. Acquired immoral behavior is reported at a higher rate when lesions in these areas occur in the right hemisphere (de Oliveira-Souza et al, 2019). (Regions were traced by the authors on the MRIcron CH2 template [http://www.bic.mni.mcgill.ca/ServicesAtlases/Colin27].) **ACC** = anterior cingulate cortex. **mOFC** = medial orbitofrontal cortex. **mPFC** = medial prefrontal cortex. **R** = right. **TPJ** = temporoparietal junction.

species, the right frontal lobe is typically wider, protrudes more anteriorly, and occupies more volume than the left (Toga and Thompson, 2003), raising the possibility that morality may have ancient evolutionary origins implicating the right hemisphere.

IS THE RIGHT HEMISPHERE SPECIALIZED FOR MORALITY?

The aforementioned lesion data lead to the preliminary impression that the right hemisphere plays a more influential role in moral conduct than the left. Functional neuroimaging studies of cognitively intact individuals making morally demanding decisions, however, have reported activity in both hemispheres (Boccia et al, 2017; Garrigan et al, 2016). The dilemma between right versus bilateral representation of morality remains to be resolved, and interindividual variability is probable. In some individuals, for example, morality is likely to be substantially represented on the left, similar to the right lateralization of language in other individuals. A special role of the right hemisphere in morality, however, is neurobiologically plausible in view of the propensity of social cognition in general to be more represented in this hemisphere (Darby et al, 2018; de Oliveira-Souza and Moll, 2019; de Oliveira-Souza et al, 2019; Filley, 2020; Mendez, 2009).

Evolution may have endowed the brain with bilaterally represented but unilaterally right-dominant morality for at least two reasons. First, unilateral localization permits the concentration of an essential social cognitive function so that the efficiency of information processing and transfer are optimized (Filley, 2020; Toga and Thompson, 2003; Van Horn et al, 2012) to support the perceptual and executive operations of moral behavior within a single hemisphere. Second, bilateral representation allows the activation of reserve tissue in the contralateral hemisphere in the event of an acquired hemispheric injury (Demonet et al, 2005).

Of interest with respect to these points is that language, which is another product of evolution, also shows bilateral representation on functional neuroimaging but unilateral dominance (on the left) in lesion studies (Demonet et al, 2005). Each hemisphere may in fact "fine tune" its opposite such that right-sided moral conduct is enhanced by the social cognitive function of language (Filley, 2020), and left-sided language is enhanced by affective prosody (Demonet et al, 2005). Given that protomoral behavior has been observed in many nonhuman species (Churchland, 2019; de Oliveira-Souza and Moll, 2019; Filley, 2020), right hemisphere specialization for morality may have appeared in evolution even before the arrival of language in the left hemisphere. Thus, evolution may have optimized capacities that are important for human adaptation by the strategic lateralization of critical

hemispheric functions. The notion that morality may be right lateralized can be examined prospectively with detailed clinical assessment and advanced neuroimaging.

CONCLUSION

Morality merits attention as a brain function as surely as more established domains such as memory and language. The study of focal lesions suggests the tentative statement that moral behavior is subserved by a right-predominant network of frontotemporal structures and their subcortical connections. This hemispheric specialization is clearly provisional; immoral acts may never be committed by individuals with right hemisphere damage and are common in the absence of any demonstrable lesion. The observed preponderance of right hemisphere lesions in acquired immorality is noteworthy, however, and offers a plausible hypothesis about the localization of morality that can be tested in clinical settings.

Further advances in the neuroscience of morality promise to yield potentially transformative clinical and societal benefits. A better understanding of the neural origin of morality would not only help clinicians address disordered conduct after acquired neurologic insults but also guide society in considering that moral deficits may result from dysfunctional brains, which could in turn bolster societal efforts to foster brain health and prevent brain disease.

REFERENCES

Boccia M, Dacquino C, Piccardi L, et al. 2017. Neural foundation of human moral reasoning: an ALE meta-analysis about the role of personal perspective. *Brain Imaging Behav*. 11:278–292. doi:10.1007/s11682-016-9505-x

Churchland AK, Ditterich J. 2012. New advances in understanding decisions among multiple alternatives. *Curr Opin Neurobiol*. 22:920–926. doi:10.1016/j.conb.2012.04.009

Churchland PS. 2019. *Conscience: The Origins of Moral Intuition*. New York, New York: W.W. Norton.

Darby RR, Horn A, Cushman F, et al. 2018. Lesion network localization of criminal behavior. *Proc Natl Acad Sci U S A*. 115:601–606. doi:10.1073/pnas.1706587115

de Oliveira-Souza R, Moll J. 2019. Moral conduct and social behavior. *Handb Clin Neurol*. 163:295–315. doi:10.1016/B978-0-12-804281-6.00016-1

de Oliveira-Souza R, Paranhos T, Moll J, et al. 2019. Gender and hemispheric asymmetries in acquired sociopathy [published online March 19]. *Front Psychol*. 10:346. doi:10.3389/fpsyg.2019.00346

Demonet J-F, Thierry G, Cardebat D. 2005. Renewal of the neurophysiology of language: functional neuroimaging. *Physiol Rev*. 85:49–95. doi:10.1152/physrev.00049.2003

Filley CM. 2020. Social cognition and white matter: connectivity and cooperation. *Cogn Behav Neurol*. 33:67–75. doi:10.1097/WNN.0000000000000223

Garrigan B, Adlam AL, Langdon PE. 2016. The neural correlates of moral decision-making: a systematic review and meta-analysis of moral evaluations and response decision judgements. *Brain Cogn*. 108:88–97. doi:10.1016/j.bandc.2016.07.007

Highley JR, Walker MA, Esiri MM, et al. 2002. Asymmetry of the uncinate fasciculus: a post-mortem study of normal subjects and patients with schizophrenia. *Cereb Cortex*. 12:1218–1224. doi:10.1093/cercor/12.11.1218

Hulme OJ, Morville T, Gutkin BS. 2019. Neurocomputational theories of homeostatic control. *Phys Life Rev*. 31:214–232. doi:10.1016/j.plrev.2019.07.005

Mendez MF. 2009. The neurobiology of moral behavior: review and neuropsychiatric implications. *CNS Spectr*. 14:608–620. doi:10.1017/s1092852900023853

Oishi K, Faria AV, Hsu J, et al. 2015. Critical role of the right uncinate fasciculus in emotional empathy. *Ann Neurol*. 77:68–74. doi:10.1002/ana.24300

Roberts S, Henry JD, Molenberghs P. 2019. Immoral behaviour following brain damage: a review. *J Neuropsychol*. 13:564–588. doi:10.1111/jnp.12155

Toga AW, Thompson PM. 2003. Mapping brain asymmetry. *Nat Rev Neurosci*. 4:37–48. doi:10.1038/nrn1009

Van Horn JD, Irimia A, Torgerson CM, et al. 2012. Mapping connectivity damage in the case of Phineas Gage [published online May 16]. *PLoS One*. 7:e37454. doi:10.1371/journal.pone.0037454