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Leveraging the social neuroscience of prosocial behavior to advance our understanding of pro-environmental behavior

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Abstract

This chapter explores the intersection of social neuroscience and pro-environmental behavior to understand how prosocial neuroscientific approaches can inform and enhance climate change mitigation efforts. It emphasizes the critical role of understanding cognitive, affective, and motivational antecedents of behavior to address climate change effectively. By examining the neural underpinnings of prosocial behavior, we argue that leveraging insights from social neuroscience fosters pro-environmental decisions and actions. It discusses methodologies like functional magnetic resonance imaging and transcranial magnetic stimulation, underscoring their potential to reveal determinants of pro-environmental behavior. The text highlights the importance of empathy, social cognition, and the neural mechanisms underlying prosociality, suggesting that these can provide a foundation for investigating and encouraging pro-environmental behavior. The chapter aims to pave the way for a new subdiscipline, Environmental Social Neuroscience, focusing on the cognitive, affective, and social drivers of environmental decision-making and behavior. Integrating neuroscientific and environmental psychology approaches requires innovative research to understand and mitigate the impacts of climate change, ultimately contributing to a sustainable future.

Chapter

Man-made climate change and its mitigation are major pressing challenges for humanity. As the term man-made suggests, humans are both the source and the possible remedy for the climate changes we have been inducing over the centuries. Mitigation requires the coordination of system-level and individual-level strategies and changes in decisions and behaviors (IPCC, 2023). In order to be targeted and effective, we need to better understand the reasons that brought us into this situation and the mechanisms by which we may get out of this, or at least slow it down to a considerable extent. In this, the fields of psychological and behavioral sciences can play a major role, as one of their main foci is to advance our understanding of the drivers and obstacles of individual and collective behaviors. Within these fields, knowledge of the neural underpinnings of psychological and behavioral phenomena has become highly influential over the last decades.

Driven by the advent of modern brain imaging and brain stimulation methodologies, such as functional magnetic resonance imaging (fMRI) or transcranial magnetic stimulation (TMS), and their recent more pervasive combination with neuro-computational approaches, fields such as cognitive and affective neuroscience complement the behavioral approaches and provide key insights into the cognitive, affective and motivational antecedents of behavior both at the individual, group, and collective-societal levels. It is thus surprising that these approaches have rarely been exploited to advance our understanding of the cognitive, affective, and motivational factors that drive pro-environmental decision-making and behavior, as well as their harmful counterparts (but see Doell et al., 2023 for a recent review).

One particular subdomain where this lack of research seems a particularly missed opportunity is the domain of social neuroscience. Humans, after all, are often labeled as “social animals,” and large parts of evolution may have driven neural adaptations geared towards expanding our “social brains” and fostering ever more complex social cognition and behavior (Adolphs, 2009). Moreover, man-made climate change not only has strong social causes but has and will have increasingly stronger effects on our societies and social cohesion. Finally, fostering system- and individual-level changes geared towards more pro-environmental and sustainable behavior shares many features, on a conceptual as well as applied level, with fostering prosocial behavior.

The analogies between prosocial and pro-environmental behavior are obvious: both are behaviors that require weighing costs and benefits for the individual against costs and benefits for others, or for the (local or global) environment (here defined as the ecological aspects of the environment). Moreover, the latter will naturally include other humans, in the sense that climate

change mitigation will also benefit others, including ourselves. Costs are broadly defined, including monetary costs, and include effort or time costs – e.g. helping a colleague move house, or bringing recycling goods to the recycling containers. Also, pro-social and pro-environmental behaviors are at their core social dilemmas of a similar structure. They often create a conflict between acting to maximize the self-interests of the individual vs. foregoing some benefits or incurring costs for the self on behalf of benefitting others, or the environment, respectively.

This weighing of self-focused against other-focused ("altruistic") interests has fascinated scholars of various disciplines for centuries, with (possibly ill-posed) questions such as whether we are genuinely selfish or altruistic being heavily researched and debated up to today. It will come as no big surprise, then, that social neuroscience, since its establishment not much more than 30 years ago (e.g. Cacioppo & Berntson, 1992), has devoted considerable thought and research to prosociality as well (e.g., Lamm & Forbes, 2022 for recent review). While this has, of course, not been a magic bullet that all of sudden allowed us to answer all open questions, it has yielded conceptually and practically relevant insights into the drivers, obstacles, and moderators of prosocial cognition, emotion, motivation, and behavior. Of central importance for the present context, it has provided us with key insights into how prosociality can be investigated with methods from human neuroscience, and how their integration with cognitive and behavioral methods may yield better knowledge and insights into what makes us more or less prosocial.

The aim of this book chapter is, thus, to outline and reflect on the analogies between these approaches and the investigation of pro-environmental behaviors, with a clear focus on the former. Here, pro-environmental behaviors are defined as a class of behaviors that help to mitigate environmental issues, particularly climate change (Lange & Dewitte, 2019). Importantly, such behaviors can include the commission of acts that benefit the environment (e.g., recycling), and the omission of acts that harm the environment (e.g., opting out of driving to work). Similarly, environmentally harmful behaviours are defined as those that specifically worsen the environment, either directly (e.g., air travel), or via omission (e.g., opting not to recycle; Thøgersen, 2014).

In drawing such analogies, we will also review the empirical research that has already been performed in that respect. Considering that such research is rather scant, though, our main intention is to highlight future research avenues and to provide a possible framework, which will foster research and ultimately establish a new subdiscipline we propose to call *Environmental Social Neuroscience*.

The chapter is structured as follows. We will start with an overview of the current methodologies available and previously used to investigate the neural bases of human prosocial behavior and we will describe their basic advantages and limitations for investigating pro-environmental decision making and behavior. This will be followed by a reflection on overall principles driving (social) decision making and their specific relevance for research on sustainable decision making and pro-environmental behavior. We will then use a selective review of the social neuroscience literature on the drivers and barriers of prosocial behavior to outline specifically how the conceptual, experimental, and methodological approaches in this domain may inform the neuroscientific investigation of pro-environmental decision-making and behavior, outlining wherever possibly already existing research, or possible concrete examples for such research.

Neuroscientific approaches for studying prosocial and pro-environmental behavior

The integration of neuroscientific insights into the study of human decision-making has gained popularity in recent years. In prosociality research, adding a neural level to the analysis has enabled inferences that help evaluate competing theories and make more accurate predictions about the proximate causes of behavior (e.g., Wyss & Knoch, 2022, for a review). However, the potential of neuroscience for shedding light on the determinants of pro-environmental behavior has remained largely untapped (Doell et al., 2023). Therefore, we elaborate on three neuroscientific approaches that have the potential to further expand our understanding of pro-environmental decision-making.

One way to investigate the processes that underlie human prosociality has been task-based brain imaging. Here, brain activity is recorded while participants are engaging in experimental tasks designed in a way that they recruit the psychological and brain processes of interest. The aim is, then, to analyze the data in a way that allows to associate the brain data to cognitive, affective, or behavioral processes relevant for the task performance. In terms of the brain imaging techniques, functional magnetic resonance imaging (fMRI) has been particularly popular. It provides images showing functional activity within or connectivity between brain regions during the execution of a task. While the use of fMRI has yielded many insights into the mechanisms underlying prosocial decision-making (e.g., Bellucci et al., 2020; Cutler & Campbell-Meiklejohn, 2019; Rhoads et al., 2021) and extended theoretical debates about the nature of cooperation (e.g., Hackel et al., 2020; Pärnamets et al., 2020), its application to understand pro-environmental behavior is still in its infancy, with a few notable exceptions (e.g., Baumgartner et al., 2023; Brevers et al., 2021; Sawe et al., 2022; Sawe & Knutson, 2015; Vezich et al., 2016). For instance, Baumgartner et al. (2023) combined fMRI with a consequential intergenerational sustainability

paradigm to assess task-dependent functional activity and connectivity. They found that decision-making was linked to activity and connectivity within and between brain areas of the mentalizing and cognitive control network, suggesting that differences in perspective-taking and self-control mechanisms may be associated with individual differences in intergenerationally sustainable behavior. This study also illustrates how novel-innovative experimental paradigms adapted for their use in fMRI scanners may advance our insights into the processes involved in sustainable decision-making (see also below).

Research not only in the area of prosociality but also in environmental sustainability has underscored the importance of internal values and contextual constraints in shaping decision-making (e.g., Berger & Wyss, 2021; Thielmann et al., 2020; Wyss et al., 2022). An alternative to task-based neuroimaging is, thus, the so-called neural trait approach which does not analyze activation during task performance but exploits brain-based measures of individual differences connected to a phenomenon of interest. Exploring sources of interindividual differences in pro-environmental motives may significantly contribute to our understanding of environmentally sustainable behavior and its determinants. The neural trait approach provides a valuable tool to explain such interindividual variation. More specifically, it seeks to explain behavioral heterogeneity with task-independent neural characteristics – so-called neural traits (Nash et al., 2015). These traits have so far been mainly identified using electroencephalography (EEG) while participants are at rest, or structural magnetic resonance imaging (sMRI), but other methods (such as magnetoencephalography or functional near infrared spectroscopy) are conceivable as well.

sMRI provides information about neuroanatomical differences in white matter (i.e., structural connections) or gray matter (i.e., cortical thickness and volume). As a pioneering example, Guizar Rosales et al. (2022) investigated trait-like neural markers (i.e., cortical thickness) of interindividual differences in intergenerational sustainability. They found that individuals displaying more sustainable behavior in an intergenerational sustainability dilemma game showed greater cortical thickness of the dorsomedial prefrontal cortex (dmPFC) and dlPFC. Supported by further mediation analyses, the authors argue that greater cortical thickness of these brain areas might help individuals to better adopt the perspective of future others and to resist the temptation of their own personal gains for the benefit of said generations.

Brain imaging techniques have certainly advanced our understanding of the processes involved in prosocial behavior and provide considerable potential to similarly do so in pro-environmental decision-making. Their nature as so-called “neural correlate” measures present a major limitation towards our aim to establish more causal-mechanistic insights, such as which brain processes

are the proximate drivers of certain behaviors. To overcome this limitation, research on prosociality has been relying on non-invasive brain stimulation methods, such as transcranial magnetic stimulation (TMS) and transcranial electrical stimulation (TES). These methods allow the safe modulation of brain activity, which is, however, limited to areas a few centimeters beneath the scalp (Brunyé, 2021; Polanía et al., 2018; but see also Luber et al., 2022). More recently, a novel approach based on functional ultrasound stimulation has also emerged, which allows for stimulation of sub-cortical areas involved in emotion processing, such as the amygdala or nucleus accumbens (Yaakub et al., 2023). In the prosocial domain, combining these methods with neuroimaging has provided key insights into the specific role(s) of certain brain areas, and their interplay (e.g., Bukowski et al., 2020; Silani, Lamm, et al., 2013; see also below). Like brain imaging methods, brain stimulation has rarely been applied in the context of environmental sustainability, with two notable exceptions. In one study, (Langenbach et al., 2022) investigated whether intergenerational mentalizing (i.e., taking the perspective of people in the future) is causally involved in sustainable behavior. They applied high-definition transcranial current stimulation (HD-tDCS) to the temporo-parietal junction (TPJ) while participants engaged in a consequential intergenerational dilemma. Excitatory HD-tDCS over the TPJ increased sustainable decision-making, suggesting that reduced engagement in mentalizing might be one of the drivers of inadequate behavioral responses to environmental issues.

Taken together, this brief overview of methodologies illustrates how studying human behavior using neuroscientific approaches may provide valuable insights into the determinants pro-environmental behavior. Similar to the domain of prosociality, it will be key not only to develop the technological or analytic side of the neuroscientific measurements themselves but that developments and further innovation regarding the experimental paradigms will be key as well. In fact, one reason for the scarcer use of neuroscientific methods in research on pro-environmental behavior so far may stem from a lack of suitable task paradigms. Such paradigms have been a cornerstone of prosociality research (see Van Dijk & De Dreu, 2021, for an overview), where they mirror some of the critical contingencies of real-life situations, but are more abstract and stylized and thus provide more control over key parameters. Within pro-environmental behavior research, the development of similar tasks is still in its infancy (e.g., Berger & Wyss, 2021; Lange, 2022, for a review). However, as methodologies continue to evolve and the interdisciplinary efforts intensify, the prospect of harnessing neuroscientific approaches to shed more light on the determinants of pro-environmental decision-making appears increasingly encouraging, and we hope this chapter will instill some more efforts and avenues in that direction.

Humans as (ir)rational decision-makers

Research on the mechanisms underlying human decision-making and behavior has identified several psychological barriers that may prevent sustainable behavior, thus contributing to climate change (Gifford, 2011). Rational-agent models of decision-making assume that people base their decisions on consistent preferences while aiming to maximize the utility of their actions (Becker, 1976). When determining their preferences, people are thought to have complete access to all the information that is relevant to the decision, to engage in an exhaustive analysis of the potential costs and benefits of the available outcomes as well as the probability they will occur, and to identify and choose the most favorable behavioral option (Ajzen, 1991). Preferences can be informed by diverse factors such as people's belief structures (e.g., whether they believe in man-made climate change or not; van Valkengoed et al., 2021), core values (e.g., whether they think that protecting the planet should be an important priority in one's life; Steg, 2016), or perceived social norms (e.g., whether they think that other people engage in climate action; (Constantino et al., 2022).

When it comes to the capacity to make rational, utility-maximizing decisions in the face of climate change, several complicating factors come into play. Perceiving the threat that is posed by climate change can be cognitively as well as emotionally challenging. Climate change is an abstract and complex phenomenon. It is composed of disparate and seemingly incongruous events (e.g., increased rainfall in one region and increased droughts in others), and it is often communicated using probabilities and increases in average temperature that can appear relatively minor (e.g., attempts to keep warming to 1.5°C). At the same time, climate change information and communication often appeal to affect and emotions, with climate change anxiety being one prevalent factor that leads to changes in pro-environmental beliefs and behaviors (Chapman et al., 2017). In the absence of direct personal experience with the consequences of climate change, however, it can be difficult to understand the gravity of the problem, and to infer the utility related to changing one's way of life (Markowitz & Shariff, 2012; Weber, 2006). Moreover, many competing and conflicting motivations can drive behavior in the context of climate change. Successful and impactful climate action will be costly and will require substantial shifts of consumption patterns resulting in less greenhouse gas emissions (requiring, e.g., much less flying and meat consumption; Ivanova et al., 2020). Giving up currently held comforts and securities to achieve a more livable future stands in conflict with many self-focused values and motivations (Steg, 2016).

Over the last few decades, an alternative to the rational-agent model of decision-making has gained influence, and this model is likely to be informative in the context of the thoughts outlined in the present chapter as well. This approach acknowledges that people are limited in their ability to make rational decisions. Rooted in dual-process theories of cognition and information processing (Evans, 2008), it recognizes that human behavior is usually not driven by the elaborate and rational thought processes assumed by rational-agent models. Instead, it relies on more automatic and computationally less intensive forms of decision making that allow people to navigate the countless demands of everyday life in the face of limited time, available information, and computational power (Gigerenzer & Gaissmaier, 2011). So-called "boundedly rational" decision-makers tend to construct their preference in an ad hoc fashion, based on cognitive shortcuts and biases, which makes decision outcomes highly susceptible to contextual influences (Payne et al., 1992). This explains e.g. why climate change beliefs may vary depending on the season and the occurrence of some major weather events. Moreover, decisions and display of behaviors are often based on automatic processes, reflecting an adaptation of underlying social preferences to a context where they may or may not be appropriate, and where behaviors may thus seem more or less "(ir)rational". This will be the case especially in situations or contexts where information or prior experience are scarce.

One such preference is whether humans are genuinely selfish or prosocial-altruistic. While the field of economics has pervasively argued for the former, and advocated views of a "homo oeconomicus" that maximizes self-benefit, research in behavioral economics and neuroeconomics has consistently indicated that humans can be strongly driven by prosocial motives and preferences (e.g. Fehr & Schmidt, 1999; Morishima et al., 2012). The "default" preference and thus the one selected in automatic decision-making and behavior has even suggested to act cooperatively-prosocial rather than selfishly. This has even led to the proposal that humans may rather be "intuitively prosocial" than "intuitively selfish" (e.g., Zaki & Mitchell, 2013).

More recent research on contextual factors and moderators, however, indicates that no matter what our preferences ultimately may be, they seem much less automatic and universal than previously thought. For instance, when targeting implicit prosocial learning processes using a reinforcement learning approach, somewhat discrepant findings have been reported (Lengersdorff et al., 2020; Lockwood et al., 2016). This was also associated with a difference in neural networks involved in the learning and decision-making processes: when money was at stake, participants showed behavior more in line with selfish preferences, while prosocial

preferences prevailed when participants had to learn to avoid harm (painful shocks) being inflicted on another person. Findings such as these fit well into the overall insight that research should not focus on whether we are either genuinely selfish or altruistic, but that we should rather investigate the contextual, situational, and person-level factors that determine whether or not our preferences come more or less into play. In analogy, we should also not investigate whether humans are genuinely pro-environmental, but rather which factors influence our pro-environmental decision making and behaviors.

From prosocial to pro-environmental behavior – hindrances, obstacles, and barriers

Prosocial behavior is not an automatism, and there are many factors that can prevent or suppress its occurrence. We now turn to discuss a few of them, against the backdrop of how this may inform research on obstacles for pro-environmental and sustainable decision-making and behavior, especially in the context of climate change.

Diffusion of responsibility and social discounting

We start with the bystander effect, when the presence of others deters an individual from acting during an emergency. Research on this phenomenon was strongly influenced by the case of Kitty Genovese in 1968; she was murdered, and even though there were 38 witnesses that saw or heard the attack, not one intervened nor called the police. This tragic case spurred the creation of entire lines of research that helped identify factors such as diffusion of responsibility (i.e., when people who need to make a decision wait for someone else to act first) or pluralistic ignorance (i.e., when people mistakenly believe that everyone else holds an opinion different from their own; Latané & Darley, 1970). These factors prevent individuals from acting because they think that others are more qualified to help, or where they think that others are not helping either and that this justifies their own inaction.

While no direct neuroscientific investigation of the bystander effects exists, to our knowledge, a neuroimaging study by Cui et al. (2015) provided interesting insights into the neural networks that underpin how we perceive being responsible for another's pain, and the possible diffusion of such responsibility. When participants were solely responsible for pain being inflicted on another person, they showed more activation in pain affect sharing neural regions (including the anterior insular and mid-cingulate cortex), than when they shared the responsibility for causing the pain with another participant. This suggests that the affective response to another person's suffering,

and thus the likelihood to engage in actions that alleviate that suffering, is reduced when the supposed or actual responsibility is socially distributed.

It seems obvious, then, to use a similar design to test whether thinking of climate change as something for which we are all collectively responsible, as compared to which we all individually contribute could lead to a weakened aversive response and thus a reduced likelihood to engage in pro-environmental action. Importantly, such a study would enable insights into whether similar affective factors (as measured by activation of affect-related areas) account for diffusion of responsibility regarding pro-environmental action, or whether more cognitive-evaluative factors (such as, e.g., pluralistic ignorance) play a role instead, or whether these factors may even operate in parallel.

Diffusion of responsibility and pluralistic ignorance are cases that demonstrate a weakening of affective responses and a related reduced tendency to act. The underlying mechanism seems to be predominantly cognitive-evaluative, in the sense that attributions as to who should help (others rather than myself) reduce empathy and related prosocial motivations and behavior.

Related, but possibly more affect-driven mechanisms are social discounting and compassion collapse, to which we turn to next (Hagman et al., 2022). Social discounting describes the fact that the farther away a person is perceived to us (in terms of our social-affective closeness to them), the less we seem to care about and behave pro-socially towards them (note that this is related to, but not identical to ingroup/outgroup mechanisms, which we will discuss further below). It has been investigated in a series of studies, using a variety of methodological approaches from hormone administration to neuroimaging (e.g. Forbes et al., 2023a; Sellitto et al., 2021; Sellitto & Kalenscher, 2022). Their findings indicate that areas such as the temporo-parietal junction (TPJ) and the anterior insula, and thus what seems to be an interaction between supposedly “cognitive” and “affective” representations, underpin and shape the discounting of the needs of more distant others. More specifically, when disruptively stimulating the right TPJ using TMS, increases in the discounting of delayed and prosocial rewards were observed (Soutschek et al., 2016). Moreover, this effect was connected to decreases in perspective taking, and thus interpreted as a suppression of the ability to take a less self- centered (and thus more other-oriented) perspective. This finding and experimental logic could be easily exploited in research on pro-environmental behavior, with distance being varied either in terms of time, geographic, cultural, or other aspects that are relevant drivers of pro-environmentalism and sustainable behavior. For instance, one would predict that pro-environmental behavior would be diminished by disruptive stimulation of the right TPJ or other areas connected to perspective taking and mentalizing (Lamm et al., 2016,

for review). The research on social discounting could also be used to address questions related to inter-generational perceptions and behaviors, such as when framing decisions to be on behalf of either future generations, or of different generations currently alive.

Compassion collapse or compassion fade (Västfjäll et al., 2014) is another intriguing phenomenon with direct relevance for understanding pro-environmental behaviors and collective action. It describes the decrease of feelings of compassion and of prosocial acts with increasing numbers of persons in need of help. Such a decrease seems paradoxical, as from a moral-utilitarian perspective, it would be considered rational that helping proportionally increases with the number of people that need help. As discussed above, humans do not always follow rational principles, and compassion collapse may be "bounded" by perceptual and attributional factors. For instance, being able to single out individuals from a larger mass of people and attending to their concrete emotional expressions seems to be more effective in causing empathic responses, than the more abstract and necessarily mediated representations of the suffering of thousands (Kogut & Ritov, 2005; Västfjäll et al., 2014).

The theoretical insights and empirical approaches from research on compassion fade seem highly promising and relevant to inform and better understand what one could call pro-environmental or sustainable behavior loss or fade. It is indeed a well-documented finding that we tend to engage in particular circumscribed pro-environmental actions (such as e.g. recycling, switching off the lights) that may not always be the most effective ones, while at the same showing a seemingly irrational reluctance to address challenges that are much larger in scale and putative effect (such as changing our mobility and consumption behavior, or more systemic changes of the economic system; Nielsen, et al., 2021a; Nielsen, et al., 2021b). Using the theoretical framework of compassion fade and a neuroscientific approach, it would be highly interesting to investigate which neural networks and associated psychological processes may explain such phenomena, and thus which angles of interventions – i.e., cognitive, affective, or motivation – should be used to remedy them. Hypotheses to be tested could be, e.g., whether computations involved in numeracy, such as in the parietal cortex, underpin the seeming failure to respond to different levels of impact, or whether it is rather (as suggested by the literature on prosocial discounting) networks linked to affect and closeness, including insular and cingulate cortex, or to cognitive appraisal and perspective taking, such as the temporo-parietal junction and dorsomedial PFC (see, e.g., Majdandžić et al., 2012; Ugazio et al., 2021; Ye et al., 2020).

Social groups and identities

Another aspect with a major role in the social psychology and neuroscience of prosocial behavior are social identities, and ingroup vs. outgroup phenomena (see Doell, Pärnamets, et al., 2021). In brief, whether someone is perceived as being or not being part of the group I associate myself with, i.e., an in- or outgroup member, can have a major impact on empathy and prosocial behavior towards that person (see e.g., Hein et al., 2010, for neuroimaging evidence).

Notably, it has been argued that our tendency to engage in- vs. out-group categorizations is strongly biologically rooted and a highly prevalent feature that affects many aspects of social cognition and behavior. One such root may be the evolution of mammalian rearing and parental behavior, where the ingroup is one's own offspring or other genetically related individuals (Decety & Svetlova, 2012). It has thus been intensely debated how the resulting biases, stereotypes, prejudices and preferential behavior of some individuals and groups speak for a "dark side" of empathy (Bloom, 2017), in the sense that empathy *per se* is not a moral or ethical emotion, but that it needs to be combined with virtues, moral and ethical stances that counteract or even eliminate such biases (such as, e.g., that all human beings should be treated equal; see also Decety & Cowell, 2014; Lamm & Majdandžić, 2015). The research on in-/out-group biases in prosociality as well as the debate of how this may induce "dark" aspects of social cognition, emotion and behaviors is of high and direct relevance for advancing our understanding of pro-environmentalism and sustainability.

Whether we perceive ourselves as part of nature and identify nature or elements of it (such as certain habitats, or specific types of flora and fauna) as belonging to our ingroup, or instead perceive nature as something "out there" that may even need to be fought or controlled (a view held extensively for extended periods in human history, Cronon, 1996) will certainly have effects on pro-environmental concern and behavior. While this aspect, to our knowledge, has not yet been investigated explicitly, indirect insights can be gained from an fMRI study on how vegetarians, vegans, and omnivores respond to pictures of animals in negative situations (e.g., being wounded; Filippi et al., 2010). This revealed that vegans and vegetarians showed neural responses indicative of a stronger engagement of (partially distinct) affect-related (insula or amygdala), visual-perceptual, as well as prefrontal areas than omnivores. Of course, such findings may be explained by a variety of other factors, unrelated to in-/out-group mechanisms, and they also do not align fully with the modulation of responses to human in- vs. out-group members and their suffering. Moreover, we cannot know whether vegans and vegetarians already showed such different responses before becoming vegan or vegetarian, or whether they are a consequence of their dietary choices.

Future research in this domain could try to manipulate in- vs. out-group perceptions experimentally, geared towards reducing inter-group boundaries. In that respect, it is interesting to note that Baumgartner et al. (2014) show that TMS of the right TPJ reduces parochialist punishment, and this logic could be easily extended towards investigations of how this right TPJ disruption increases decisions to protect the environment. Ideally, such an approach would also include elements of social-psychological manipulations, such as framing paradigms, vignettes, or other types of interventions used in research on inter-group conflict (De Dreu et al., 2023). This should also include a focus on how anthropomorphization and humanization (e.g., Kteily et al., 2015; Majdandžić et al., 2012; Waytz et al., 2010) could be exploited to foster pro-environmental and nature-protective actions. It would, for instance, be intriguing to investigate how such interventions could influence the well-documented preferences to be concerned by the needs of other mammals, and in particular for the ones that by means of their physical appearance and visual display activate stronger feelings of care and concern (Mishra & Mehta, 2023). Ideally, such interventions would help us extend our in-group circle to animals such as insects or mollusks that often are much more relevant for biodiversity but are usually met with disgust, rejection, or just plain disinterest. Neural measures would allow us, in this case, to pinpoint whether such manipulations engage similar networks and processes as those when breaking up human-to-human boundaries, or whether human-to-animal boundaries engage distinct mechanisms (see Boch et al., 2023, for research showing distinct as well as similar brain areas involved in human-human and human-animal interaction).

Stress and pro-sociality

Closing up our selective review, we turn to the role of stress as an example of how challenging aversive situations may influence prosociality as well as pro-environmental behavior. Despite a clearly bad reputation in terms of its folk psychological understanding, stress is scientifically understood as an adaptive response of the organism, triggered by challenging situations that require the mobilization of extra efforts and energy to cope with them. The literature on how stress influences social cognition and prosocial behavior is surprisingly scarce, and controversial. A recent meta-analysis (Nitschke et al., 2022; see also Faber & Häusser, 2022; von Dawans et al., 2021) found no consistent differences between stressed and control groups in their prosocial behaviors. Stress, depending on the context or individual factors, may thus have beneficial and adverse effects alike on prosocial behavior. In a series of neuroimaging and psychoendocrinological studies, we have extensively investigated how stress influences empathy and prosocial behavior (Forbes et al., 2023b; Tomova et al., 2017, 2019, 2020). This, again, has

painted a mixed picture. While one fMRI study showed that stress increases prosocial behavior (Tomova et al., 2017; see also Tomova et al., 2020), another fMRI study showed that stress made us more self-focused (Forbes et al., 2023b). The studies differed in the way in which prosocial behavior was induced and measured. While in one case, a dictator game and thus the effortless sharing of money from a windfall was used, the other study required participants to make decisions as to whether they wanted to invest physical effort to help another person. Aversive experiences such as stress can thus have a decisive impact on behaviors that are costly and effortful, such as taking more sustainable means of transportation, or buying and procuring the more expensive organic produce.

Antecedents and ways to foster pro-social and pro-environmental behavior

Depending on the scientific discipline, different aspects of the antecedents of prosocial behavior will be highlighted. Our review is guided by social psychological approaches. We start by discussing antecedents that pertain to social cognition, i.e., empathy, (empathic) concern, and perspective taking, then review research on more behavioral-motivational factors such as prosocial preferences, and then focus on antecedents that connect behaviors to social norms and morality.

Social-cognitive aspects: empathy

Emotions play a strong role in driving human behavior, and prosocial and pro-environmental behaviors are no exception. As the origin of the term “emotion” (from the Latin “e-movere”) indicates, emotions’ primary function is to set things in motion. In the case of prosocial behavior, empathy, which according to one definition is the ability to share and understand the affective state of others (e.g., Lamm et al., 2019, for review), may act as a strong driver to motivate prosocial behavior. For instance, sharing the affective concomitants of another person’s pain may move and motivate us - in the very sense of the “e-movere” - to help that person by reducing their pain (e.g., Crockett et al., 2014; Hartmann et al., 2022).

The neural networks that have been associated with empathy are closely connected to affect and emotion processing, as well as the awareness of the affective states by means of interoceptive processes. They include, foremost and in particular when negative emotions are shared, the anterior insular cortex and the mid-cingulate cortex (Lamm et al., 2019, for review; Lamm et al., 2011; Schurz et al., 2021, for meta-analyses), while the sharing of positive affect and emotions has been connected to areas of the reward system and hedonic experiences (Lamm et al., 2015;

Morelli et al., 2015). This pattern of findings is highly relevant in the present context as it suggests that vicarious affective processes similar to first-hand affect play a key role in empathizing with others. This is how it may set helping behavior “in motion”.

The affective underpinnings of empathy also bring into play another important aspect, which is that empathy *sensu* affect sharing is not the same as sympathy, compassion, or concern (Singer & Lamm, 2009 for review). The latter are related, yet distinct terms and phenomena, although their occurrence may be driven by affect sharing; however, all three have to be distinguished from a decisive additional element, which is that they care a component of care or concern for the other person. As such, they have much better leverage to instigate prosocial behaviors, as care and concern are even more direct drivers of behavior than empathy *sensu* affect sharing. This, at first, may be counterintuitive, as the everyday usage of the term empathy usually implicitly suggests to carry a care and concern element.

From a scientific viewpoint, however, we need to distinguish the “feeling as” (i.e., affect felt as the affect of the other) from the “feeling for” (i.e., feelings of care and concern for the other) component – with the latter being more instrumental for prosocial behavior (Batson, 2009 for review). Finally, in this context, we also need to delineate affect sharing and concern from feelings of personal distress, which is the experience of negative affect that may occur in response to the plight of others. This distinction is particularly important when it comes to understanding pro-environmental behavior, as personal distress may result in self-centered rather than prosocial responses. More specifically, it entails a strong focus on re-establishing a neutral or positive affective state for oneself, and thus may detract from an other-oriented focus and attempts to help them overcome their plight (Decety & Lamm, 2011). Personal distress often leads to disengagement from an upsetting situation, such as when switching off the overwhelming bad news or when quickly passing and expressly ignoring a person in clear need of help. Interestingly, these related yet distinct experiences in response to the suffering of others are associated with different neural networks. While personal distress and negative affect sharing has predominantly been connected to the insular and cingulate cortex, care and concern are associated with the meso-cortico-limbic motivational and reward system as well as areas that underpin “warm and tender” compassion-related feelings (Ashar et al., 2017; Klimecki et al., 2013; Singer & Klimecki, 2014, for review).

How may these findings inform our quest for understanding the antecedents of pro-environmental behavior? We argue they highlight that when exposing research participants to the “plight” of the natural-ecological environment (the eco- and biosphere), as induced by climate change or other ways of environmental pollution or destruction, we need to consider that this may result in different

and nuanced responses, differentially activate the associated neural networks, and in this way also influence pro-environmental (and environmentally harmful) decisions and behaviors in varying ways. For instance, portrayals of environmental destruction or “doom and gloom” styled negative emotion communications may overwhelm and personally distress people, ultimately leading to disengagement and inaction (Chapman et al., 2017).

Meanwhile, care- and concern-based portrayals may lead to a focus on support and action towards protecting the environment. However, interindividual differences in specific traits also need to be considered. For example, in participants with low levels of environmentally relevant trait affect (i.e., one’s predisposition to experience positive emotions in an environmental context), positive emotional communications resulted in the commission of fewer pro-environmental messages throughout the day (compared to neutral and even negative environmental messages; Doell et al., 2021). Thus, while concern-based or emotionally positive communication strategies may result in the commission of more pro-environmental behaviors in some, these same interventions may backfire in others.

Regardless, consistent empirical and meta-analytic evidence has shown that emotions about climate change are some of the strongest predictors of climate change related decisions and behaviors (e.g., van der Linden, 2015; Xie et al., 2019). Generally, it will be important to leverage emotional responses and not just fact- or knowledge-based responses, if the aim is to motivate changes in pro-environmental and sustainable behaviors (for a review, see (Brosch, 2021). Here, neuroscientific methodologies can help to better understand and characterize these often-conflicting results, and may even contribute to the development of better targeted interventions.

In fact, one of the few studies in environmental social neuroscience looked at neural responses to the harm of people, animals, and nature (Mathur et al., 2016). More specifically, the authors exposed participants in the fMRI scanner to images of humans, non-human animals, and nature (mostly scenes of landscapes or patches of land) in situations that could be perceived as harmful, threatening or damaging, or in neutral control conditions. The findings revealed largely overlapping networks for the three categories, including the anterior insular and the mid-cingulate cortex. This suggests that harm to nature or non-human animals may recruit similar networks as harm being inflicted in humans, a finding that may not only be exploited to foster pro-environmental action, but also confirms the conceptual analogies between pro-social and pro-environmental responses the present paper focuses on. However, further research is definitely needed. Neuroimaging studies should try to pinpoint how distinct aspects such as personal distress, “shared” affective responses, and feelings of concern may rely on representations that

are similar for humans and the environment, and whether they may predict individual differences in pro-environmental behaviors.

Social-cognitive aspects: perspective taking

Perspective taking, i.e., the capacity to view (physical or mental) situations from different stances, is a key skill for social cognition and behavior in general, but it also plays a special role in the context of empathy and prosociality. It enables us to overcome egocentric tendencies, and to gain access to inner states of others that otherwise may not be accessible. Perspective taking can be more or less implicit or explicit ("automatic" vs. "deliberate"), and it often needs to be accompanied by another process that is referred to as self-other distinction, which avoids the confusion between one's own views and inner states (thoughts, feelings, motives) from those of the other person.

Self-other distinction is of particular importance when taking the perspective of others, where it prevents that we mistakenly not just "step into someone else's shoes", but that we falsely start assuming those shoes are actually our own. In the context of prosociality and helping others, it should inform a helper whether another person is really in need of help, or whether we mis-evaluate their needs due to an egocentric stance. Adequate self-other distinction also helps to avoid becoming overwhelmed by confusing the aversive feelings of the other with one's own affective state, which is why it plays a particular role in psychotherapeutic interactions (Silani et al., 2013 for review).

Perspective taking has been shown to act as a key driver and a moderator of empathy and empathic concern. While earlier accounts had conceptualized empathy as an automatic and mainly bottom-up driven phenomenon, later findings and approaches indicated that empathy is by no means automatic, but rather malleable by variety of factors. One prevalent aspect is the stance from which stimuli about others' pain or suffering are perceived. In a study by Lamm et al., 2007, participants were instructed to adopt a more involved vs. a more detached perspective, and this recruited different areas involved in personal distress, affect sharing, or self-other distinction, suggestive of an inverted U-shape between affective engagement and empathy as well as concern. In other words, engaging in a perspective that led to overwhelmingly strong emotional responses driven by personal distress, and not or very little engagement with the plight of the other person leading to a lack of emotional involvement, led to lowest empathy and concern. What seems optimal then is a level of involvement that is neither too intense nor too detached. This logic could also be used for understanding better which areas and processes drive pro-

environmental behavior, and where the peak of the inverted U is situated so that behavior can be optimally fostered.

For instance, researchers have recently started to investigate the relationships between climate anxiety and climate action, speculating that too much anxiety might lead to “eco-paralysis” (Clayton, 2020). However, this has not yet been fully supported in the literature. Indeed, multiple studies have found a positive relationship between climate anxiety and climate action (Hogg et al., 2021; Whitmarsh et al., 2022; Wullenkord et al., 2021). It should be noted that the operationalization of how climate anxiety is measured and whether it differs from worry has been unclear and often intertwined. In contrast, one study using more stringent definition of climate anxiety (using a scale inspired by the clinical domain) found no relationship between climate anxiety and behavior, potentially reflecting a state of tension between motivating and paralyzing effects (Clayton & Karazsia, 2020). Thus, it is not entirely clear when anxiety fosters climate action and whether too much anxiety might be detrimental and overwhelming (thus leading to either a freezing or a withdrawal behavioral response).

Here, a neuroscientific approach may complement studies using self-reports of anxiety and be gauged to predict pro-environmental behaviors based on the engagement of distinct networks related to threat and threat coping. It would be particularly interesting to exploit recent approaches investigating the role and mechanisms of social support, which may have buffering effects on stress and anxiety (e.g., Goldstein et al., 2018; Shamay-Tsoory & Levy-Gigi, 2021), but also of stress and anxiety contagion, which may have detrimental effects (e.g., Nitschke & Bartz, 2023).

Interestingly, and somewhat surprisingly, a recent behavioral (online) study was not able to reveal an effect of perspective taking for others on climate change mitigation measures, such as donations, signing a petition, or approving of mitigation policies (Koessler et al., 2023). A neuroscientific approach could be particularly helpful to pinpoint the cognitive, affective, motivational and other potentially relevant processes that may have been involved in participants when engaging in perspective taking, and to use that information to finetune either the perspective taking instructions or to connect them better to the investigated mitigation measures. Another worthwhile research avenue would be to exploit the phenomenon that perspective taking cannot only be applied to better understand other human beings or view things from their perspective, but to pretty much any real or even hypothetical entities. One could, for instance, ask participants to adopt the perspective of “mother nature”, or of parts of the ecosystem for which humans are usually less prone to show empathic or concern responses. This could provide key insights for how to fight the global decline in biodiversity, which would require much more protection of

animals and ecosystems to which we naturally feel less connected to (such as insects, or swamps). In this respect, a neuroscientific approach may inform us whether perspective taking for such animals would increase empathy and concern-related responses in similar neural networks as those engaged in response to animals we usually feel closer to, or whether it engages distinct networks and affective response. Depending on the findings, one may then decide on optimal intervention strategies, such as whether they should involve some elements of anthropomorphisation (i.e. conveying the animals or plants as having similar attributes as humans, which, however, may come at its own risk, Williams et al., 2020), or whether other types of affect-inducing strategies (such as focusing on the benefits of the distant animals' for biodiversity) may be more effective.

Perspective taking for future selves

Perspective taking may also be exploited to better understand one's future selves, or the future selves of generations after us that will be most affected by climate change. Indeed, using brain stimulation methodology, Soutschek et al. (2016) could show that the right temporo-parietal junction (rTPJ) plays a key role in discounting future rewards for an imagined future self, but also for imagined future individuals. Moreover, these effects on discounting were linked to deficits in perspective-taking. When combining brain stimulation with neuroimaging, they moreover could pinpoint the orientation towards future rewards (and selves, as well as others) as a mechanism that enables the delay of gratification (Soutschek et al., 2020). This is an exciting finding, as it suggests that similar mechanisms could be leveraged to foster future-orientation, an important element of sustainable choices and behavior, and thus buffer the negative effects of temporal discounting (see above).

One example where related research has been performed in the domain of sustainability research comes from (Brosch et al., 2018), who exposed participants to different consequences of climate change while undergoing functional MRI. The authors manipulated the timescale from which these consequences would be experienced, such that they were either within the participants' lifetime, or several decades later (and thus presumably felt most by future generations). Participants experienced increased activation in a region involved in the encoding of the personal significance of future events (i.e., a specific portion of the vmPFC), when envisioning far future events. Importantly, the degree of activation in this region was highest for participants with high levels of self-transcendent values (i.e., high levels of benevolence and care for the welfare of others). The highly self-transcendent participants also reported higher subjective feelings of concern about the future events. Thus, this work outlines the neural substrates by which people

with differing value structures feel concern for the plight of future generations, and highlights the utility of combining neuroimaging approaches with more traditional environmental psychology approaches.

Another study where prospective thinking has been investigated is the fMRI study by Brevers and colleagues (2021). These authors could demonstrate that asking participants to engage in prospective thinking about sustainable or unsustainable behaviors activated areas involved in valuation and memory, such as the ventro-medial prefrontal cortex and hippocampus. Interestingly, areas of the social brain, such as the rTPJ, did not show up in their study. This suggests that this area may play a role only when using as framing of the future sustainable behavior as a prosocial or other-oriented act.

Conclusions and outlook

Man-made climate change poses a major threat to humanity. It not only affects the geo- and biosphere of our planet, but will globally disrupt societies and the socio-economic conditions under which we lived so far. While there is wide consensus by now that we can only tackle this challenge together and across national, political, and economic boundaries, how this joint effort should be organized and implemented is a matter of intense debate. Science and academia not only have the knowledge and tools, but also the obligation to contribute to this discourse. While the natural and life sciences have been central in documenting and understanding the causes and effects, we need concerted efforts by the social sciences to better understand mitigation of as well as adaptation to climate change and its downstream effects.

Besides behavioral science-based research approaches documenting and explaining meso- and macro-level cognition and behavior, we need to tap the potential of micro-level investigations and the insights they provide in the putative mechanisms driving individual-level processes, decision-making, and behaviors. Social neuroscience as a discipline that has emerged at the intersection of social psychology and behavioral sciences with neuroscience seems optimally positioned to lead on such efforts. In the present chapter, we have thus attempted to outline some analogies between the research on prosocial and pro-environmental behavior that we may want to exploit. We hope this will motivate research efforts that bridge across and integrate all relevant levels of observation, from molecules to collective behaviors, just as social neuroscience has attempted to for several decades now. Importantly, these efforts should not only aim at basic research on the drivers and obstacles of pro-environmental behavior, but rather be geared towards understanding

of how these insights may be used to ensure a sustainable future for us all and the generations after us on our planet.

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