

The repurposed social brain

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Human social intelligence depends on a diverse array of perceptual, cognitive, and motivational capacities. Some of these capacities depend on neural systems that may have evolved through modification of ancestral systems with non-social or more limited social functions (evolutionary repurposing). Social intelligence, in turn, enables new forms of repurposing within the lifetime of an individual (cultural and instrumental repurposing), which entail innovating over and exploiting pre-existing circuitry to meet problems our brains did not evolve to solve. Considering these repurposing processes can provide insight into the computations that brain regions contribute to social information processing, generate testable predictions that usefully constrain social neuroscience theory, and reveal biologically imposed constraints on cultural inventions and our ability to respond beneficially to contemporary challenges.

Neural repurposing across and within lifetimes

Evolution uses whatever is in the room. Working as a tinkerer, it borrows and modifies pre-existing structures [1] for new uses. For instance, it is thought that feathers originally evolved for thermoregulation, were co-opted for flight, and underwent subsequent adaptations to increase their utility for flying [2]. Most complex biological structures are thought to emerge through similar cascades of re-purposing and adaptation [2,3]. Through descent with modification (see Glossary) [4], functional organization emerges as ‘a patchwork of makeshifts pieced together . . . from what was available when opportunity knocked’ [5]. Neuroscience has increasingly embraced the concept of evolutionary reuse in theories of brain function [3,6–10]. Comparatively less well developed is an understanding of how human behavior and brain organization are shaped by analogous processes that operate within the lifetime of an individual, through which pre-existing neural architecture is redeployed to process cultural inventions [11] and to flexibly manipulate other minds. We suggest here that these phenomena can also be understood as the repurposing of limited ingredients to serve novel ends, and discuss how this perspective can help inform our understanding of human sociality.

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Neural repurposing across lifetimes

Evolutionary repurposing

Human sociality is somewhat of a mystery. It is remarkable compared with many other species that have only aggressive or reproductive encounters with non-kin. From childhood we prefer collaboration to acting alone, with isolation causing negative health outcomes [12,13]. Human social networks are also vast and unusually enduring [14], built often merely on common interests with otherwise would-be strangers. What underlies the human propensity to cooperate and form lasting non-reproductive ties with non-kin?

Repurposing reward

One possible mechanism underlying human social connectedness is evolutionary repurposing involving oxytocin pathways (i.e., oxytocin, vasopressin, and their receptors [15]). The functions of vasopressin include promoting pair-bonding, territoriality, and selective aggression toward

Glossary

Cultural invention: a way of thinking or behaving that is shared by group members and transmitted across generations (e.g., literacy, arithmetic, religion, technological skills, music, art, social structures) through communication or social learning.

Cultural repurposing: the process by which cultural inventions are acquired by co-opting pre-existing sets of brain circuits (neuronal niches) [11]. The term ‘cultural repurposing’ is used here to refer to what Dehaene and Cohen have termed ‘neuronal recycling’ [11] so as to more clearly distinguish this process from other kinds of repurposing (i.e., evolutionary and instrumental repurposing) discussed in this article.

Descent with modification: Darwin’s suggestion that new morphological structures tend to be generated by borrowing and modifying pre-existing structures (i.e., through evolutionary repurposing/tinkering) [1,4].

Evolutionary repurposing: the process through which a structure with a pre-existing function is co-opted for a novel use over the course of evolution, with or without changes to its original form.

Instrumental repurposing: the creative and intentional evocation of evolved responses in novel contexts.

Neuronal niche: a set of neural circuits with sufficiently related antecedent functionality and adequate plasticity to support the acquisition of a given cultural invention [11].

Oxytocin: a mammalian neuropeptide involved in modulating social and reproductive behavior. Across mammalian species, oxytocin is involved in promoting maternal behavior (e.g., lactation, mother-infant bonding); in some mammalian species, oxytocin supports the formation and maintenance of additional kinds of selective social bonds (e.g., pair-bonds [15,16]).

Psychological distance: the extent to which an object is removed from the current, first-hand experience of the perceiver. Objects can be psychologically distant in terms of multiple dimensions (e.g., space, time, social ties, hypotheticality). Psychological distance and proximity promote attention to abstract decontextualized mental representations and to concrete situational details, respectively [26].

Vasopressin: a mammalian neuropeptide similar in structure to oxytocin that modulates social behavior by binding to vasopressin 1a receptors [16]. Vasopressin promotes monogamy-related behaviors (e.g., selective mate preference, paternal care, mate guarding [15]) in pair-bonding species. Both vasopressin and oxytocin are necessary for the formation of selective social bonds in mammals [15,16].

non-mate conspecifics; oxytocin triggers maternal behavior, promotes pair-bonding, reduces vigilance for unfamiliar conspecifics in group-living primates, and promotes cooperation between unrelated humans [15–17]. Changes in oxytocin and vasopressin receptor expression patterns may have allowed these neuropeptides to support new social behaviors through interactions with existing neural circuitry. For instance, increased vasopressin receptor 1a expression in mammalian basal forebrain structures allows reward circuitry common to all mammals to be exploited for the formation of conditioned partner preferences in some species [18]. Less is known about how these neuropeptides came to support other aspects of social behavior in primates, but recent evidence suggests that oxytocin and vasopressin receptor gene variations correlate with human pair-bonding, pro-sociality, trust, and empathy [19–21]. Furthermore, exogenously administered oxytocin promotes in-group favoritism, self-sacrifice to benefit one's in-group, and out-group derogation, even when the groups reflect arbitrary, experimentally defined distinctions [22,23]. It should be noted that because oxytocin and vasopressin activate each other's receptors, it is difficult to ascertain whether the effects of exogenous administration of these neuropeptides reflect specific activation of oxytocin or vasopressin receptors [15]. Thus, further research will be necessary to elucidate the mechanisms underlying these effects. However, a growing body of literature supports the recent suggestion [6] that, through evolutionary repurposing, the functional profiles of neuropeptides (e.g., oxytocin, vasopressin) involved in regulating basic reproductive behaviors across mammalian species have been extended to include the regulation of increasingly complex patterns of social behavior among group-living primates.

Repurposing circuitry for operating on external space Psychological distance. Humans and other primates routinely form non-reproductive bonded relationships of a type that are only observed between pair-bonded mates in other taxa [24]. Human social networks are particularly vast, stable, and complexly organized [14]. Our interactions with others are shaped both by our direct social ties with others and by relationships between third parties (e.g., our trust in others is intensified if they are friends with our friends [25]). To successfully navigate our complex social world our brains must track and encode the psychological space between ourselves and others. A growing body of research suggests that representing distance from the self in social ties relies on mechanisms also involved in representing distance from the self in physical space [26,27], suggesting that phrases such as 'close friend' and 'distant relative' may be symptomatic of how the brain itself is organized (Box 1).

Throughout evolution, humans have attained the ability to represent and traverse increasingly diverse and extensive psychological distances [26]. Our mental lives consist not only of our immediate, first-hand experiences of the current environment but also of events occurring in other places, the experiences of other people, and thoughts about possible futures. In other words, we can consider information that is removed from our current experience along

Box 1. Do metaphorical mappings imply repurposing?

Several interrelated theories posit that intangible concepts (e.g., time, moral purity, psychological warmth) are often referred to in physical terms (e.g., 'the past is behind us', 'clean conscience', 'icy stare') because knowledge of the physical world scaffolds mental representations of abstract concepts (e.g., [56,75,76]). Extant behavioral, patient, and neuroimaging data on concepts of time and space are consistent with this view. Brain lesions that compromise the ability of patients to represent physical space (e.g., hemispatial neglect) produce analogous deficits in representing events on a mental timeline [77], and some brain areas appear to house shared representations of temporal and spatial distance [27] (Figure 1). Although culture and other aspects of experience influence exactly how we use space to think about time [54–56], the tendency to think about time using cognitive architecture with a precursory role in dealing with space is thought to be innate, and to be an example of evolutionary repurposing [78].

Although shared linguistic labels may sometimes reflect the recruitment of common representational resources for processing concrete (e.g., spatial distances) and abstract (e.g., temporal distances) contents [27,78], it is important to note that metaphorical mappings do not necessarily reflect neural reuse, or vice versa. For example, despite the use of shared linguistic labels to describe objects' vertical positions in space and people's positions in power hierarchies (i.e., 'high', 'low'), this information may be encoded by distinct neural mechanisms [86]. Additionally, physical pain and social rejection, which are often described using similar language (e.g., 'heartache', 'hurt feelings'), appear to involve both shared [79,87] and distinct [79] mechanisms. For example, experiencing physical pain and remembering social rejection (i.e., a past breakup) evoke dissociable representations in some brain areas (e.g., regions implicated in affective processing) and shared representations in other areas (e.g., regions implicated in endogenous regulation, memory, and motivated action [79]). Additional research is needed to delineate the shared and unique components of directly experiencing physical and social pain.

Furthermore, some associations between abstract and physical concepts may reflect associative learning. For example, through correlations in early experience (e.g., between caregiver proximity and temperature), social warmth may come to be associated with physical warmth [75,76,88]. Of course, such associations do not necessarily imply that our understanding of physical warmth provides a representational scaffolding for our understanding of friendliness, or even that understanding these concepts requires any shared mechanisms (although accumulating evidence suggests that this might be the case [75,88]).

Similarly, evolutionary repurposing of cortical circuitry does not always imply that a new domain is thought of in terms of an old domain. Redeploying existing cognitive infrastructure to perform a new task does not necessarily imply the reuse of mental models [10] or even that the old and new domains will be related in conscious experience. Thus, although metaphorical mappings and neural repurposing sometimes go hand-in-hand, it is important to distinguish these phenomena, and to note that one does not necessarily imply the other.

various dimensions of psychological distance – for example in space, time, and social ties. Psychological distance along any dimension carries a common meaning with important implications for the perceiver: proximity for action, and thus how concretely or abstractly information should be construed [26]. To the extent that information is psychologically distant, abstract and decontextualized representations are more likely to be attended to rather than immediate contextual details [26]. Converging lines of evidence from social and developmental psychology, cognitive linguistics, and cognitive neuroscience have previously suggested the possibility of a common mechanism for encoding different types of egocentric psychological

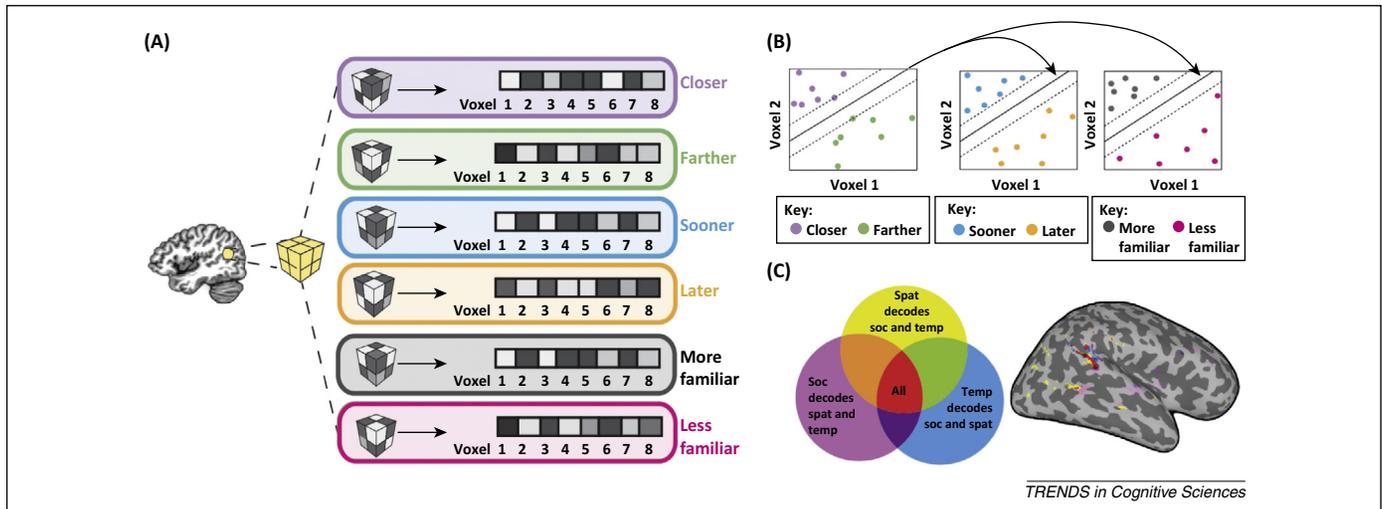


Figure 1. Shared mechanisms for encoding distance in space, time, and social ties. Multivoxel pattern analysis (MVPA) provides one way to probe the information content of particular brain regions. We recently applied MVPA to test for a common representation of spatial, temporal, and social distance from the self [27]. (A) Distributed local response patterns were extracted throughout the brain corresponding to viewing increasing and decreasing spatial, temporal, and social distances for each fMRI run for each participant (for clarity of visualization, eight- and two-voxel response patterns are depicted in (A) and (B), respectively). (B) A linear support vector machine learning algorithm was trained to distinguish trials from one domain according to direction of distance change, then tested on each of the remaining two distance domains. Dots represent two-voxel response patterns to examples of each condition for a given participant. (C) In the aRTPJ, it was possible to decode relative egocentric distance across all distance domains. Convergent results were obtained using representational similarity analysis. These results are consistent with mechanisms for computing self-relevance in terms of peripersonal space being repurposed to operate analogously on increasingly abstract contents as this region expanded over the course of human evolution [7,8]. Abbreviations: aRTPJ, anterior right temporoparietal junction; Soc, social distance; Spat, spatial distance; Temp, temporal distance. Figure adapted and reproduced from [27], with permission from the Society for Neuroscience.

distance [27]. Consistent with this possibility, we recently found that the anterior right temporoparietal junction [aRTPJ; see [28] for a recent parcellation of the temporoparietal junction (TPJ)] encodes egocentric distances in space, time, and social ties similarly (Figure 1). Social and temporal egocentric distances may have come to be encoded using mechanisms already involved in egocentric spatial distance encoding partly because the characteristics of aRTPJ connectivity and structure afford encoding information in self-centered coordinates [29], as well as switching between internally directed attention to emphasize decontextualized representations, and externally directed attention to emphasize current contextual details [27,30].

Directing attention inward. Different posterior parietal cortex (PPC) regions [e.g., aRTPJ, superior parietal lobule (SPL), intraparietal sulcus (IPS)] may contribute distinctly to evolutionarily recent cognitive functions owing to differences in the affordances of their connectivity and internal structure. For instance, whereas the aRTPJ appears to serve as part of a ventral attention network that switches between internally and externally directed activities [30], depending in part on the relative self-relevance, or psychological distance, of the information at hand [27], SPL circuitry originally evolved for allocating attention within the external environment may have been repurposed over the course of evolution to perform similar operations within internal space. Consistent with this possibility, the human SPL supports flexible, top-down attentional allocation within external space and within internal representations [31–34]. Moreover, cross-domain multivariate pattern classification analyses suggest that voluntary shifts of attention in external space (e.g., when performing

saccades) and in internal representations (e.g., when performing mental arithmetic, which can be thought of as a shift of internal attention along a culturally learned number line [35]), involve shared encoding mechanisms in the SPL [36]. Similarly, when greeting an old friend, common SPL circuitry may support efforts to orient externally (e.g., to her voice in a noisy room) as well as internally (e.g., to relevant personal knowledge) to facilitate conversation [31,33,37].

Thus, areas of human PPC involved in encoding and operating on external environmental space in our distant mammalian relatives [38] may perform similar operations on internal representations, including internal representations of relatively abstract contents (e.g., social and temporal distances). Throughout primate evolution, PPC circuitry for encoding, tracking, and manipulating objects in the environment may have been repurposed to perform similar operations on objects and abstract concepts in working memory [7,8,31].

Mechanisms of evolutionary repurposing

Theories involving evolutionary repurposing are increasingly widespread in cognitive neuroscience [3,6–10]. Even so, the mechanisms underlying purported examples of neural reuse remain underspecified [9,10] and are likely heterogeneous. For instance, brain areas can take on new functions through changes in patterns of local postsynaptic receptor expression, connections with other regions, or duplication and divergence of subdivisions [10,18,39,40]. Future work should integrate our emerging understanding of the mechanisms that produce phenotypic diversity in neocortex [41,42] with theories about how evolutionarily recent aspects of human sociality relate to ancestral systems.

Neural repurposing within lifetimes

All animals are subject to evolutionary repurposing. It is, after all, the way evolution works. Repurposing within lifetimes is far rarer, relying, at least in part, on language and mentalizing. The distinctive social-cognitive capacities of humans, which appear to set us apart from our nearest primate relatives – such as our capacities for social learning, communication, and theory of mind [43] – allow us to create and transmit cultural inventions [43] and to manipulate one another's minds with considerable flexibility. We describe here two forms of repurposing that operate within the lifetime of an individual: the borrowing or modifying of pre-existing brain function to acquire cultural inventions (cultural repurposing) and to exert social influence (instrumental repurposing).

Cultural repurposing

In the same way as evolutionarily novel ways of thinking, perceiving, and behaving tend to emerge through borrowing and modifying pre-existing structures [3,9], culturally invented ways of thinking, perceiving, and behaving must also borrow and modify pre-existing structures

[11]. However, unlike evolutionary repurposing, which takes place through genetic changes over generations, cultural repurposing must occur within the lifetime of an individual through neural plasticity [11]. This reuse of brain systems already shaped by evolution substantially constrains how we process information peculiar to today's world and the associated possibility space of our cultural inventions. That is, co-opting circuitry with sufficiently related antecedent functionality and adequate plasticity to be repurposed, or neuronal niches, necessarily entails inheriting the quirks and constraints of the pre-existing circuitry [11]. Sociality contributes to both sides of this equation. First, cultural inventions often serve social purposes: language facilitates long-term reciprocal exchanges and collaborations; literacy and internet use extend identity/reputation-tracking beyond the limits of individual cognition and provide access to others' perspectives [44–48]. Second, because living in complexly bonded groups likely drove human brain evolution [24], many neuronal niches likely have pre-existing social functions. For example, reading co-opts circuitry for face and object recognition [49] (Box 2), and deducing why a computer fails to

Box 2. How learning to read affects the neural and behavioral signatures of face perception.

Literacy likely comprises the best-studied and most dramatic example of how acquiring a cultural invention can co-opt, and sometimes reshape, an invaded neuronal niche. Reading recruits a common neural substrate in the left fusiform gyrus (FG; the visual word form area—VWFA) across cultures, but emerged too recently for this regularity of functional brain organization to be attributable to natural selection [11]. Compelling recent data suggest that literacy competes with face and object processing for cortical real estate, dampening and displacing face processing in the left fusiform gyrus, and promoting right-lateralization of face processing [49,80] (Figure 1).

Consistent with literacy being constrained by pre-existing circuitry for visual face and object recognition, distributions of contours across writing systems correspond closely with what this circuitry has been tuned to detect in the natural world [11,81]. More specifically, line junctions observable from most viewpoints (e.g., the points at which an animal's legs would meet its torso; the points where separate lines meet in letters such as L or T) are especially important for both object recognition and reading [82], and comprise the fundamental building

blocks of diverse writing systems [81]. In fact, the frequency distributions of particular configurations of vertices are remarkably similar across the world's writing systems, and bear a striking resemblance to the frequency distribution of particular configurations of vertices found in environmental images [81]. Thus, across cultures, writing systems appear to be constrained by the pre-existing competencies of their neuronal niche [11].

Interestingly, learning to read also changes aspects of face and object processing, breaking mirror-image generalization and decreasing holistic processing of faces and objects [83,84]. Mirror invariance, present from infancy and useful for recognizing the same faces, objects, and potential predators from different angles, is disadvantageous for differentiating letters in many alphabets (e.g., discriminating 'b' from 'd'), and is unlearned as we learn to read (Figure 1). Literates fare worse than illiterate adults at recognizing faces and objects from their mirror images [83]. Thus, intensive engagement with cultural inventions can also reshape the pre-existing functions of neuronal niches.

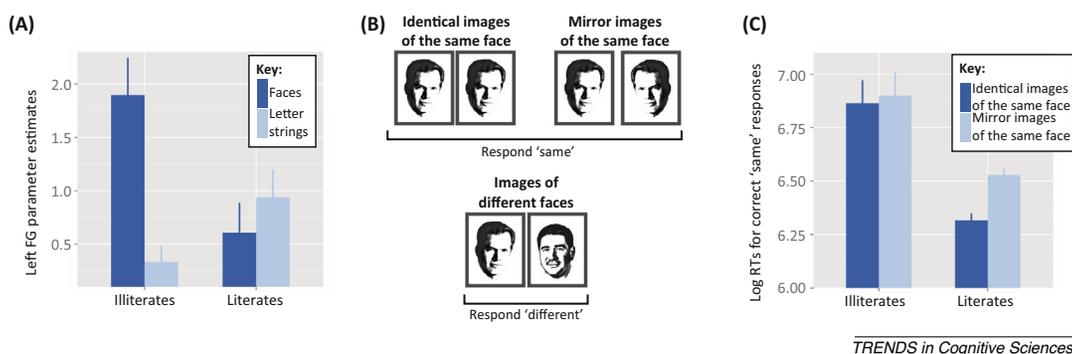


Figure 1. Learning to read impacts brain systems involved in social perception. **(A)** Learning to read increases responses to letter strings and attenuates responses to faces in the left FG (i.e., the VWFA), demonstrating that cultural inventions sometimes compete with representations corresponding to neuronal niches' pre-existing functions for cortical space [49] (in other cases, cultural inventions may more subtly extend or enhance the representational capacity of a niche [11]). **(B,C)** When instructed to judge if face image pairs depict the same individual (regardless of orientation) or two different individuals, literate adults are slower to recognize the same individual from mirror images than from identical images of his face, whereas illiterate adults are not [83]. Mirror-image generalization can be advantageous for learning and survival because it facilitates the immediate recognition of a given individual, object, or predator from different viewpoints. However, learning to read requires 'unlearning' mirror invariance. These effects are observed in individuals who learn to read as adults or as children [49,83], suggesting that even relatively modest experience with cultural inventions can influence the neural and behavioral signatures of neuronal niches [49]. Data and stimuli adapted from [49,83], with permission from the American Association for the Advancement of Science and the American Psychological Association.

understand one's intentions, or forecasting market behavior, may recruit mechanisms for social sense-making [50].

Cultural repurposing has been most extensively studied with respect to literacy (Box 2). It remains to be seen how brain systems are co-opted by other cultural inventions which can extend or dramatically transform the representational capacities of their neuronal niches [11]. Examples of subtly extending neuronal niches' pre-existing representational capacities may include the use of IPS circuitry to understand cultural hierarchies. The IPS, a brain region with a well-documented role in processing magnitude information, is also recruited when processing signals indicating relative status (e.g., words, military insignia) in cultural hierarchies [51]. Similarly, although evolutionary repurposing may have led circuitry in the SPL and in other areas of the dorsal attention network to play a general role in orienting attention internally [52], specific cultural inventions (e.g., mathematics, calendars) make use of this circuitry in culturally prescribed ways that, although somewhat variable across cultures [53–55], are also constrained by the pre-existing functions of their neuronal niche (e.g., almost all languages use spatial terms to refer to time [56]). It has also been suggested that cultural traditions that define non-kin in familial terms (e.g., fraternal orders) repurpose and reshape individuals' mental conceptions of natural relatedness [57]. Additionally, training in novel, culturally invented musical forms induces cortical plasticity in sensorimotor brain regions [58], suggesting that these regions provide a neuronal niche for music in humans. Consistent with music co-opting circuitry involved in biological motion processing, the expression of emotion in music and movement is supported by a common dynamic

structure (Figure 2) that is strikingly consistent across far-off cultures [59]. The human capacities for cultural invention and transmission have allowed us to produce a huge variety of music and dance traditions, the breadth of which is unmatched by otherwise analogous displays in other species (e.g., [89]). Such examples may become increasingly readily observed as technology accelerates the pace at which we adopt new ways to convey information and interact. It has been suggested that as artificial agents (e.g., robots) become more prevalent, human perceptual systems may become retuned to treat them as social partners [60]. This possibility, as well as further outstanding questions for future research, are discussed in Box 3.

Additional research will be necessary to clarify how the construction, processing, and interpretation of cultural inventions are constrained by the neuronal niches they co-opt. For example, it appears that highly familiar, multipart visual objects of expertise that co-opt fusiform face-area circuitry become characterized by behavioral hallmarks of face processing (e.g., holistic processing [61]). In addition, human reasoning may sometimes be limited by applying faculties evolved for social cognition in non-social contexts [62]. Using brain systems that evolved for predicting the behavior of other people to make sense of our physical environment may shape how many cultural belief systems explain, and often anthropomorphize, natural forces [63–65]. Similarly, mechanisms involved in mentalizing may be co-opted to deal with large-scale, anonymous social structures (e.g., financial markets), with sometimes advantageous and sometimes deleterious consequences [66,67]. Investigating how neuronal niches shape, and are reshaped by, sociocultural

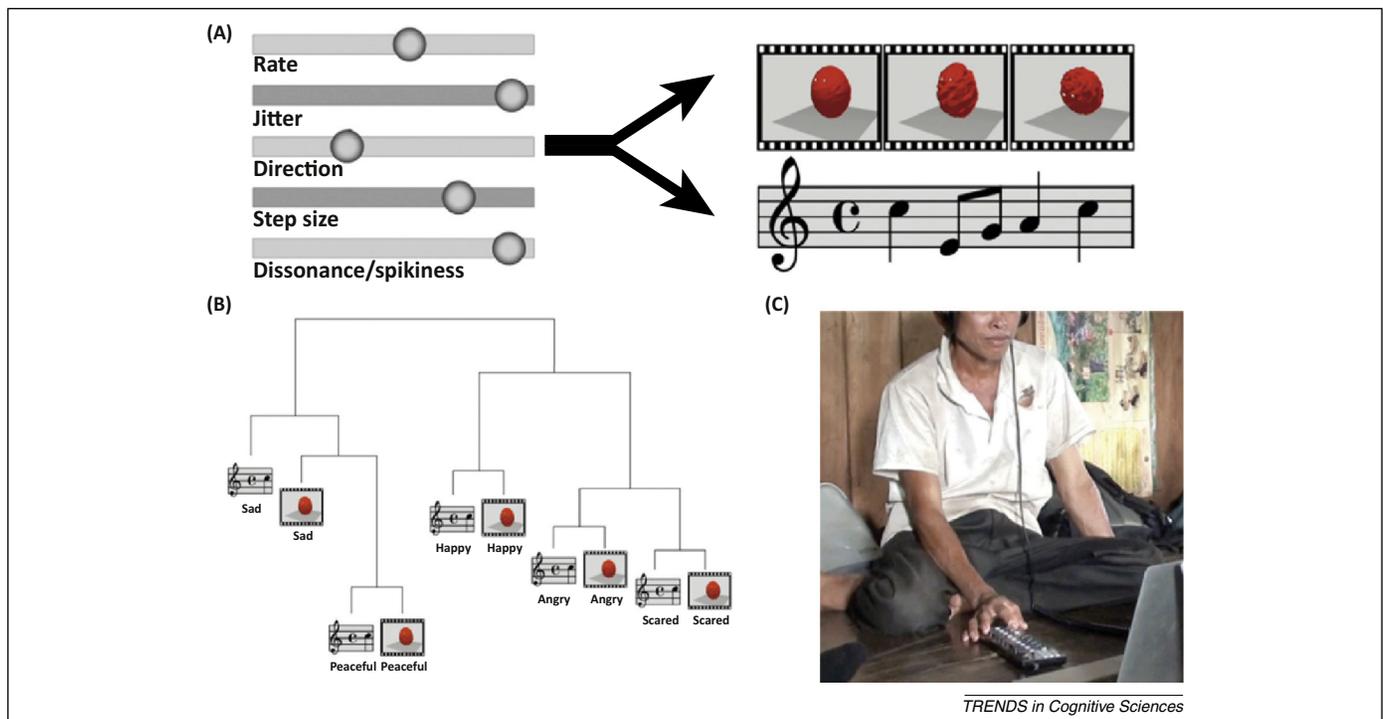


Figure 2. Cultural repurposing of biological motion processing to create music. (A) Participants manipulated five slider bars corresponding to five dynamic features to create either animations (bouncing ball) or musical clips (piano melodies) that expressed different emotions. (B) A clustering analysis of slider bar configurations revealed a cross-modal, emotion-based structure such that analogous parameters were used nearly equivalently to express emotion in music and movement. (C) These results were replicated in a remote tribal village in Cambodia. Together, these results suggest that the expression of music involves co-opting circuitry for processing biological motion, and that the musical forms that cultures use to convey emotional meaning are constrained by the neuronal niche that music co-opts. Figures adapted from [59].

inventions comprises an intriguing future direction for social neuroscience.

The same constraints that restrict the development and interpretation of cultural inventions also limit our ability to appreciate and effectively respond to modern-day challenges (e.g., climate change, awareness of far-off others' suffering). Nonetheless, humans can strategically and flexibly evoke evolved responses in novel contexts to effectively meet such challenges (i.e., instrumental repurposing).

Instrumental repurposing

Many of the threats and sources of suffering that face humanity today are very different from those that drove the evolution of human social cognition. Thus, our social cognitive information processing systems are often poorly matched to the challenges that characterize our modern world [68], such as the long-term adverse consequences of global warming or the suffering of large groups of people within our own societies and abroad, making the consequences of these phenomena difficult for us to appreciate fully or respond to rationally.

Fortunately, we are equipped with the capacity to reflect upon and understand our own psychology, as well as a remarkable ability to flexibly manipulate our own and others' behavior in response to novel challenges. Thus, we can flexibly push each other's buttons to evoke particular behavioral responses. Importantly, this flexibility is not without constraint: the buttons available for us to push are restricted to those afforded by our evolutionary heritage and cultural context. Therefore, like evolutionary innovations and cultural inventions, effective strategies for influencing each other's behavior are not free to vary boundlessly, but instead are limited by pre-existing neural architecture. By imitating the types of problems that our brains evolved to solve we can instrumentally evoke evolved responses to address the problems that characterize today's world – a redeployment process we term instrumental repurposing.

For example, the most effective manner of eliciting concern and help for problems that afflict many, such as poverty, hunger, and disease, is not a reasoned presentation of facts, but rather, a depiction of a single, vividly identified victim [66]. This may be in part because victims elicit more intense affective reactions when presented individually rather than as part of a group [69], and in part because our pro-social behavioral tendencies evolved to promote cohesion within small hunter-gatherer bands that lived together in close proximity rather than in a huge, anonymous, globally interconnected society [69]. Perhaps it should not be surprising, therefore, that we are well-equipped to respond helpfully to the single child who falls down a well but not to the plight of many anonymous children suffering in a far-off continent, or to the challenges that future generations will face because of climate change [68–70].

Recent research suggests that our proclivity to respond with concern and helping behavior to a vividly identified individual, and with indifference and inaction to anonymous victims of misfortune (i.e., the identifiable victim effect [69]), is caused by the reward that we experience when helping an individual, rather than the vicarious pain induced by confronting his or her suffering (Figure 3)

[71]. The large body of research on this topic has usefully informed charitable donation campaigns and suggestions for addressing widespread indifference about global warming that involve telescoping inward the psychological distance between those who will suffer as a result of climate change and ourselves (e.g., by focusing on the consequences for identifiable, socially proximal victims, such as one's own children [70]).

Although we may not be naturally equipped to appreciate or respond appropriately to problems that our distant ancestors did not face, we can motivate appropriate reactions by framing contemporary problems in terms of situations to which our brains did evolve to respond (e.g., the suffering of a proximal other) through the instrumental repurposing of evolved responses. However, this repurposing need not be benevolent. For example, as the philosopher Martha Nussbaum has noted:

Throughout history, certain disgust properties – sliminess, bad smell, stickiness, decay, foulness – have repeatedly and monotonously been associated with, indeed projected onto, groups by reference to whom privileged groups seek to define their superior human status. Jews, women, homosexuals, untouchables, lower-class people – all of these are imagined as tainted by the dirt of the body ([72], p. 347).

Political and moral intolerance, from religious persecution to bans against same-sex marriage, have been fueled by the language and imagery of disgust, thereby evoking

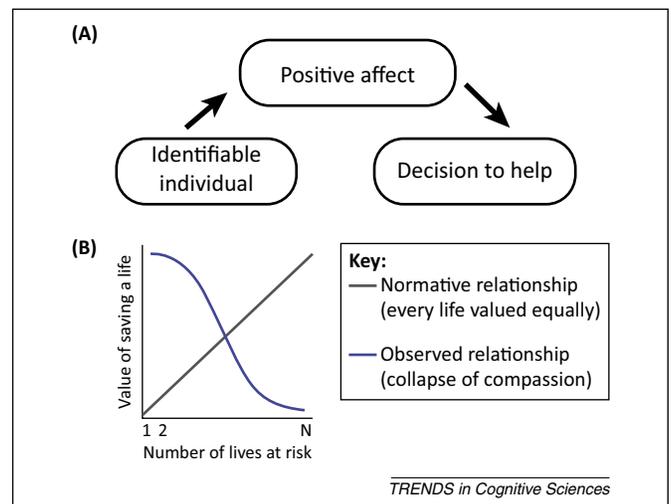


Figure 3. An example of instrumental repurposing: using emotional responses to identifiable victims to elicit helping behavior. Somewhat paradoxically, people help most when the life or wellbeing of a single individual is in question [69], especially when that individual is presented in a vivid manner. (A) Recent evidence suggests that the identifiable victim effect is mediated by stronger positive affect (as suggested by both self-report and nucleus accumbens activity) elicited when anticipating helping another person [71]. (B) Idealized curve of the value associate with saving a life, where every human life is assigned the same value [69]. (Blue) A curve suggested by Slovic [69] to approximate the observed collapse of compassion for larger numbers of victims. A single individual elicits maximally vivid and concrete mental processing, and maximally intense affective reactions [69]. Attention and emotional reactions, as well as helping behavior, decrease when multiple victims are presented, until victims are processed merely as statistics [69]. This research suggests that charitable campaigns emphasizing a single, vividly identified individual, and the benefit she or he will incur from a donor's help, are likely to be particularly successful in eliciting contributions. Curves in (B) adapted from [69], with permission from the author.

Box 3. Outstanding questions

- How are sociocultural inventions (e.g., stratified hierarchies in social organizations, musical forms) constrained by the neuronal niches that they co-opt?
- Which mechanisms for generating phenotypic diversity of neocortex (e.g., addition of new subdivisions to cortical areas, changes in connections between cortical areas, changes in size of cortical areas [42]) gave rise to various recently developed social cognitive capacities?
- In what cases does functional overlap indicated by univariate fMRI contrasts or lesion studies result from the recruitment of a common mechanism, and in what cases does such overlap result from the recruitment of overlapping but distinct mechanisms?
- Repurposing neural circuitry does not necessarily imply 'grounded cognition', or vice versa [10]. However, in some cases neural reuse appears to lead to metaphorical mappings [7,10,27]. In what cases are linguistic metaphors symptomatic of shared processing mechanisms, rather than mere linguistic flourish?
- Patients with hemispatial neglect have recently been shown to possess strikingly analogous deficits in spatial and temporal representations [77]. Do focal brain lesions causing deficits in spatial representations produce deficits in reasoning about social relationships?
- Increasingly, people rely on computers for what has been historically provided by face-to-face interaction (e.g., communicating, learning information). To what extent are we creating technology in our image? Does widespread adoption and effectiveness depend on how well technologies repurpose existing neuronal niches (e.g., giving self-driving cars human-like features increases our trust and comfort in such vehicles [85])? Conversely, how do the ways in which technology-mediated interactions differ from face-to-face interactions alter those neuronal niches and, in turn, human sociality?

evolved responses towards toxicity and disease [72–74]. Whether for helpful, harmful, or neutral ends, instrumental repurposing describes the process by which novel problems are addressed by the top-down engagement of older systems. By rapidly and flexibly framing novel problems in ways that evoke pre-existing systems, language and imagery facilitate repurposing at a timescale that evolution cannot match.

Concluding remarks

Evolutionary, cultural, and instrumental repurposing occur at vastly different timescales through distinct mechanisms: evolutionary repurposing arises from genetic reshuffling and natural selection pressures, cultural repurposing relies on brain plasticity [11] and sophisticated social-cognitive capacities [43], and instrumental repurposing is facilitated by the ability to understand and flexibly manipulate one's own and others' minds. However, all involve invoking ancestral neural mechanisms in new ways to meet novel challenges. Considering neural repurposing within and across lifetimes can shed light on how new functions are constrained by characteristics inherited from old functions. Like evolutionary innovations and cultural inventions, the tools with which we can address newly emerging societal challenges are constrained by our biological endowment. By achieving a more thorough understanding of human social cognition we can begin to more effectively shape our own and other's behavior in response to the myriad modern problems that our brains did not evolve to solve.

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