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Experts in action: why we need an embodied social brain hypothesis

Louise Barrett[1], S. Peter Henzi[1] and Robert A. Barton[2]

[1]Department of Psychology, University of Lethbridge, Lethbridge, Canada
[2]Department of Anthropology, University of Durham, Durham, UK

LB, 0000-0003-1841-2997; SPH, 0000-0001-6175-1674

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Author for correspondence:
Louise Barrett
e-mail: louise.barrett@uleth.ca

The anthropoid primates are known for their intense sociality and large brain size. The idea that these might be causally related has given rise to a large body of work testing the 'social brain hypothesis'. Here, the emphasis has been placed on the political demands of social life, and the cognitive skills that would enable animals to track the machinations of other minds in metarepresentational ways. It seems to us that this position risks losing touch with the fact that brains primarily evolved to enable the control of action, which in turn leads us to downplay or neglect the importance of the physical body in a material world full of bodies and other objects. As an alternative, we offer a view of primate brain and social evolution that is grounded in the body and action, rather than minds and metarepresentation.

This article is part of the theme issue 'Systems neuroscience through the lens of evolutionary theory'.

1. A tale of two brains

Today, the social brain hypothesis (SBH) is well established as an explanation for the link between large brains and intense sociality among the anthropoid primates [1–5]. The SBH argues that the need to live in large groups selected for increased brain size and, by extension, the cognitive capacities needed to ensure that these groups remain functional and cohesive. In other words, it is an evolutionary hypothesis that explains how primates have solved the ecological problem of predation risk through the evolution of group-living, [6,7], and then solved the problem of inter-individual competition—which arises inevitably when animals are forced to live in close proximity to one another—by evolving large brains and complex cognitive capacities [1–5]. Support for this hypothesis has come from comparative studies of brain size and social life, in which Robin Dunbar and colleagues [1–5] have played a major role, as well as from studies of primate social behaviour and cognition, in both the wild and captivity [8–16]. In the case of the latter, the evidence presented is not directly tied to brains as such; rather, the objective is to establish the existence of the kinds of cognitive capacities that only a large brain can support (e.g. understanding of third-party relations [10,11], attribution of mental states to others, also known as 'theory of mind' [14] and other forms of perspective taking [9], tactical deception [15] and cooperation [8,12]).

Back in the late 1980s and early 1990s, however, another SBH was on offer [17–19]; one that was less concerned with functional explanations for why large brains have evolved in the primate order, and was instead focused on the question of whether regions of the primate brain were specialized for sensing and responding to particular kinds of bodily social stimuli—facial expression, eyes gaze, head and body orientation and biological motion [17–19]. This view of the social brain was associated mainly with the work of Lesley Brothers, along with David Perrett [17–23], where the aim was to establish what particular circuits of the primate brain were doing, and whether these were dedicated to a specific category of objects—other animate beings—as distinct from the broader category of physical objects.

Over time, this latter conception of the social brain has slipped from view in the study of primate social cognition, and Dunbar's more cognitively oriented

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version of the SBH is what most people now think of when they think of primate brain evolution. This is perhaps understandable given that, as noted above, many studies of primate cognition are aimed at establishing the existence of advanced cognitive capacities that can justify the necessity for large, expensive brains and, in many cases, to identify these as likely pre-cursors of unique human cognitive capacities, like language. To give just one illustrative example, Seyfarth & Cheney [24] have argued that the origins of spoken language can be found in the structure of baboons' social knowledge, which is construed as a language of thought. Specifically, that, '[w]hen a baboon hears vocalizations, she forms a mental representation of call meaning. The meaning of a call sequence includes the representation of an actor who performs a specific action on a recipient and causes the recipient's response. These discrete elements are combined according to the 'rules' of call delivery to create a message whose meaning is more than just the sum of the meanings of its constituent elements' [24, p. 7]. This then licenses the conclusion that '[a] baboon's assessment of call meaning thus constitutes a discrete, combinatorial, rule-governed and open-ended system of communication in which a finite number of signals can yield a nearly unlimited number of meanings' [24, p. 7], a definition that non-coincidentally maps neatly onto the definition of human language, such that 'several of the cognitive mechanisms that have long been thought to mark a clear separation between language and non-human primate communication can, in fact, be found—in admittedly simpler form—in the communication and social cognition of non-human primates.' [24, p. 7]. Thus, although sensitivity to social signals and cues obviously informs the design of these studies, and is also relied on to provide the empirical evidence, the questions of interest are not related to a sensitivity to social signals/cues *per se*. The focus, instead, is on whether the animals possess the ability to make inferences about the underlying causes that produce these cues, and then to generate further predictions about others' behaviour on the basis of such inferences. Further, no cognitive mechanisms are specifically identified in most studies. Instead, Dennett's intentional stance [25] is used to inform this methodological strategy, which requires only that animals' behaviour can predicted accurately on the grounds that they behave 'as if' they possess the capacity in question (e.g. 'listeners responded *as if* they parsed a call sequence as a dramatic narrative' [26, p. 152] and 'in their natural behaviour, therefore, non-human primates certainly act *as if* they are capable of thinking (as it were) in sentences' [26, p. 151] (emphasis added). Cognitive complexity of this order thus supports the SBH by offering evidence for the kinds of social strategizing that allows large social groups to be maintained, and for individual animals to thrive within them.

The current incarnation of the SBH also identifies high-level cognitive abilities (such as mentalizing and the inhibition of prepotent responses) as key to maintaining cohesive social groups, and stresses that these abilities are tied to brain areas unique to primates, specifically the so-called 'default mode network' and frontal pole (the most anterior part of the prefrontal cortex), respectively [5]. There is also a continued emphasis of the SBH on the neocortex as the comparative neuroanatomical measure that best reflects cognitive ability [4], which itself reflects the anthropocentric origins of the hypothesis [27] and the idea that the neocortex is 'the crowning achievement of evolution and the biological substrate of human mental prowess' [28, p. 274].

Here, we wish to make a case for reincorporating a more Brother's-like view into theories of primate brain evolution for three inter-related reasons: (i) recent comparative analyses have called into question the link between group size and neocortex size in the terms put forward by the SBH [29–31], as well as demonstrating the importance of non-cortical areas, particularly the cerebellum, in primate brain evolution [32,33]; (ii) there is growing recognition that brains evolved first and foremost to control bodies, such that cognition is better conceived of as a set of processes that mediate the adaptive control of bodies in dynamic, unpredictable environments—so-called '4E cognition' [34–41]—and a move away from the traditional 'disembodied' view of cognition as a purely brain-based process involving the elaboration, manipulation and transformation of mental representations of the outside world; and (iii) the concept of 'neural reuse' [42,43], which suggests that much local neural structure is evolutionarily (and developmentally) conserved, but combined and recombined in different ways across different organisms and species to serve a diverse array of purposes. These three points, therefore, suggest that, rather than looking for human-like cognitive representations in the neocortex of non-humans, a more productive research programme would attempt to understand how both human and non-human cognition emerge from the reuse of systems that have evolved for embodied sensory-motor control.

In what follows, we offer a brief review of recent work on the selection pressures shaping primate brains, consider how work on primate visual and motor systems provides an alternative view of the complexities of primate social life, and conclude with a consideration of some of the implications of non-cortical, particularly cerebellar, evolution. Our suggestion is that a focus on embodied action may open up our understanding of primate brain neurocognitive evolution in ways that recognize the somewhat messy and mosaic nature of the evolutionary process, help identify the relevant differences between apes and other primate species, and enable us to identify more accurately the unique features of hominin cognitive evolution.

2. Multiple pressures, mosaic evolution

Although the relationship between brain size and group size that supports the SBH has been described as 'remarkably robust' [4, p. 5], recent comparative analyses do not support such a conclusion. One such study, using a much larger sample of primates (more than 140 species, tripling the samples of previous analyses) and more sophisticated statistical analysis, showed that brain size, after controlling for body size and phylogeny, was best predicted by diet, with frugivores having larger brains than folivores [29]. By contrast, no measure of sociality (mating system, social system, average group size per species) could be linked to brain size. This outcome is thus more consistent with hypotheses concerning the cognitive demands imposed by extractive foraging of fruits and seeds and the complex spatio-temporal distributions of fruiting trees, than with the cognitive demand of sociality. The study concluded that it was the primary demands on foraging efficiency that then set the stage for selection on social skills [29]—a conclusion that reverses the SBH argument that animals solve their ecological problems by means of social strategies.

Similarly, using two large comparative datasets, Powell *et al*. [30] found evidence that, while brain size was positively associated with home range size, frugivory and activity period, there was no relationship with social group size. More importantly, the authors stressed that all these results were rather unstable and sensitive to the use of different predictor datasets; an outcome they discussed in relation to data quality, intra-specific variance in group size and ecology, statistical power and, crucially, the fact that different selection pressures probably acted on different brain systems at different times. This led them to caution against drawing strong inferences from any attempt to tie brain size evolution to individual selection pressures and to any general measure of cognitive ability. In this regard, it is notable that the original brain size-group size relationship may have been largely dependent on the particular sample of species included in the smaller dataset used in these studies [30].

This sentiment has been echoed by Wartel *et al*. [31] in their analysis of the drivers of brain size, as they also found inconsistent results to be the rule rather than the exception. Given this, they concluded that there is no compelling reason to favour any the adaptive hypotheses on offer—all could either be supported or refuted depending on the datasets used, the choice of variables to include, and the particular observations used to populate those variables [31]. Although they considered relationships between sensory and motor systems and brain size likely to be robust—for example, a more motor-flexible animal will possess a more complex musculature, with more brain tissue devoted to its control (e.g. [44])—identifying the drivers of brain size and 'mental' capacities are harder to define with 'non-controversial precision' ([31], see also [45]). These findings also link to the earlier suggestion that 'cortical ballooning' (i.e. the higher ratio, or increased proportion, of neocortex to the rest of the brain) as seen in large and large-brained mammals is most parsimoniously understood as being driven by allometric scaling rules that conserve function, rather than by any special selection pressure on cognitive abilities [33]. Phylogenetically controlled analyses show a strong correlation between body size and the proportion of the brain that is neocortex—that is, large animals possess large neocortices—which seems to reflect a need for more brain space to be devoted to making cortical connections. Larger cortices are made up of more white matter than grey matter, and this white matter consists of fibres making long-range connections that require greater axon diameter and more myelination in order to preserve processing speeds over longer conduction distances [33]. Ratios between brain structure volumes are confounded by such allometric relationships, and contrary to the underlying assumption of their use, they do not correlate with relative computational capacity as measured by numbers of neurons [33].

What all these analyses show, then, is that far from neocortex size being 'a robust predictor of both social group size and many other aspects of social behaviour' [46, p. 2], the relationship flickers in and out of view, depending on sample size and composition, measures used and choice of predictor variables. This being so, we need to move away from large-scale comparative analyses aimed at identifying a single key driver of overall brain size across the primates, recognize the mosaic nature of primate brain evolution and look instead to the clade-specific ways in which brain size reflects variation in specific neural systems [32,45,47].

This is where ideas relating to neural reuse become immediately relevant. If we look at cortico-cerebellar networks, for example, we see reciprocal loops that have a remarkably similar anatomical architecture across multiple systems, and which appear to have evolved by duplicating circuits and retaining a powerful, general functional organization. In particular, these cortico-cerebellar loops mediate forward models, whereby the system makes predictions about the consequences of actions and continuously adaptively adjusts behaviour in real time [48]. Originally developed within the framework of control theory and applied to understanding sensory-motor control, it is now understood that forward models present a solution to the problem of behavioural control more generally. The precise function of a cortico-cerebellar loop thus depends on its specific connections (e.g. with motor versus pre-frontal cortex). Hence, the cerebellum is now known to be involved in a wide range of functions, including motor control, perception, language, working memory, cognitive control and social cognition [49]. This dissolves the arbitrary distinction between cortex as the 'thinking' part of the brain and the cerebellum as engaged only in sensorimotor control, and allows us to consider the range of tasks in which the cerebellum is involved, rather than worrying about whether or not the cerebellum is 'cognitive' in the manner of the neocortex [32,33].

In terms of primate brain evolution, the coordinated functioning of neocortex and cerebellum is reflected in a strong pattern of correlated evolution between them, independent of change in other regions [33]. Although it is often said that an expanded neocortex is what marks humans out evolutionarily, comparative analysis reveals more rapid cerebellar relative to neocortical expansion in human and great ape lineages than in other primates [32,33]. Cerebellar expansion in apes is reflected in their slow maturation, and cerebellar and neocortical size display distinct life-history correlates congruent with their developmental schedules [50]. In particular, cerebellum shows relatively substantial post-natal growth, particularly during the juvenile period, and its evolutionary expansion in apes corresponds to significantly slower post-natal development [50]. This suggests that environmental input is crucial for cerebellar function, pointing to the importance of well-coordinated action in the world as a key feature of primate social life, and a probable selection pressure on brain evolution. We return to the topic of the cerebellum below in our consideration of human uniqueness.

3. Social coordination in physical space

Although the general relationship between neocortex size and group size has not withstood more extensive and rigorous analyses, the relationships detected between brain size, frugivory and activity period are in line with earlier work suggesting that visual specialization has been one of the important drivers of primate brain size. For example, independent correlations between relative neocortex size, activity period (diurnal versus nocturnal), degree of frugivory and group size [51] have been shown to reflect the relative expansion of the geniculo-cortical visual system and enhancements of fine-grained binocular vision [52,53].

These analyses found that both V1 and non-V1 cortex were positively correlated with encephalization [54], but only in association with the parvocellular layers of the lateral geniculate nucleus (LGN), which is the pathway mediating vision for fine detail and colour, not the magnocellular layers involved in movement detection. The relative number of neurons in the parvocellular layers of the LGN was also found to correlate with social group size, as well as with diurnality and degree of frugivory, whereas the magnocellular layers did not. Thus, there is evidence for increasing visual specialization that was linked to both social and ecological selection pressures. This accords with the proposal that visual processing of complex and rapid social interactions, and the monitoring of visual signals (most prominently facial expression and eye-gaze) were the skills linked to social group size maintenance [33]—a suggestion in line with earlier, more detailed work on specific regions of the brain [17–23]—while at the same time underpinning the fine visual discrimination and coordination needed for manipulating small fruits and seeds. That is, certain aspects of primate brain size evolution can be tied to the socioecological demands of the perceptual domain quite directly, rather than being a response to a pressing need for more 'abstract' sociocognitive skills: a 'visual brain hypothesis', if you will. It should also be noted that as variation in neocortex size is also strongly related to the evolution of the cerebellum as well as visual structures, it is perhaps more accurate to describe this as a visuo-motor brain hypothesis [33].

With respect to a reconceptualization of the SBH along more embodied lines, we suggest that the findings above steer us toward a 'second person participatory' perspective on social interaction [54–56], i.e. one that concerns itself with how animals interact with other physically, rather than with the generation of inferences about the inferences they might generate about each other. Here, cognition is construed as flexible action *in* the world, not as internal propositions directed *at* the world. Consequently, neurophysiological and behavioural work on motor coordination, and in particular, peripersonal space (PPS) [57–59] also offers a promising avenue of exploration with respect to understanding the demands of social coordination in the physical environment. This is work that can be married to the evidence on visual specialization that emphasizes the importance of monitoring facial expression, eye-gaze and other social signals.

The term 'peripersonal space' (or 'near space') was first used to describe the area within an arm's reach of the body. In this original conception, PPS designated the range within which physical objects could be grasped and manipulated [60]. As work has continued, however, this notion of PPS has been expanded and refined, as we describe below. To characterize PPS more precisely in neurobiological terms, studies on monkeys have identified neuronal populations in parietal cortex, including the ventral intraparietal area (VIP) and area 7b, areas of frontal cortex, including ventral premotor cortex (vPMC) and areas 6 and F4, as well as subcortical areas, like putamen [58]. These are areas that respond not only to tactile (somatosensory) stimuli, but also to visual or auditory stimuli presented in close proximity to the somatosensory receptive field (it is worth noting here that the bimodal nature of these neuronal responses undermines the notion that perception and action can be seen as separable processes). These receptive fields are 'anchored' to a specific body part (e.g. the face, the hand, the arm), forming a body-part-centred 'mapping' of space around the body (see [58,59] for review). The responses of these multi-sensory neurons, and the notion of PPS, was thus argued to be crucial for guiding effector-specific movements in relation to nearby objects [59–63]. Further work, however, found evidence for a defensive function of PPS—where, for example, sudden puffs of air presented near the face of macaques produced distinctive startle responses that could also be produced by stimulation of the neurons in the VIP, and the polysensory zone [64,65]. Thus, in addition to guiding action with respect to non-threatening objects, PPS is argued to provide a 'margin of safety' that allows animals to avoid threatening objects (including conspecifics) as well as collisions with physical hazards [66].

Much of the early work on PPS depicted it as a series of clearly demarcated 'bubbles' extending from particular areas of the body—something suggested to be a legacy of the very earliest work on 'flight zones' in animals [67] and work on proxemics and the notion of 'personal space' in humans [68]. However, more recent work has shown that most multi-sensory neurons show a graded, continuous response with respect to distance from the body, rather than a simple stepwise 'in-or-out' response [57], while some cells in the vPMC have receptive fields that extend further than reaching distance (sometimes even to the end of the testing room) [57]. PPS does not seem to be confined to the narrow zone within arm's reach of the body (which was an artefact of design of the earliest studies), but shows a certain degree of flexibility, where PPS-related neurons not only respond to stimuli with graded (or even reversed) relationships to distance, but are also influenced by factors such as the motion of body parts, and the trajectory and valence of the stimulus [57]. As such, PPS is better conceived as a 'set of continuous relevance-estimation fields', or zones in space that reflect the behavioural relevance of actions aimed at either making contact or avoiding contact between objects (including conspecifics and other animals) and the body [57], and where the size and extent of such fields is adjusted continuously in relation to ongoing activity. Classic work on macaques, for example, showed that, following training with a rake-like tool that allowed them to retrieve distant food, the receptive fields of the visual neurons associated with the somatosensory receptive field of the hand were extended to include the length of the tool [69,70].

Work on PPS in general, and the field-theory of PPS in particular [57], offers us the kind of embodied view mentioned above in §1. More specifically, it pushes us away from the standard view of behaviour as a stepwise process that proceeds linearly from sensory input to motor output, and towards the kind of embodied, interactive approach described by affordance competition theory [71]. Here, the neural architecture that mediates behaviour is best characterized as a set of competing sensorimotor loops, with multiple simultaneous competing actions constantly being prepared, and selection among them occurring in response to the possibilities for action (affordances) in the environment, and how available affordances shift as part of the ongoing flow of activity [71]. Bufacchi & Iannetti [57] use a human example to illustrate this, in which they consider how the PPS field derived from reaction times to a tactile stimulus on the hand (i.e. pressing a button as soon as the stimulus is felt) varies as an auditory stimulus approaches, with reaction times being faster when the sound is closer. As they note, it is not immediately obvious why pressing a button should have anything to do with creating or avoiding contact between the hand and the sound source. However, if multiple simultaneous competing actions are being prepared at all times then, as sounds move closer to the hand, actions related to making or avoiding contact become increasingly relevant. Given that similar actions will share similar neural network activity, then any actions produced by tactile stimulation (here, a button press) should share its network with actions that create or avoid contact with the sound source. As a result, as the sound approaches, any hand-related actions should be more readily enacted, giving rise to shorter reaction times. Their argument, then, is that most PPS fields will result from the summation of the relevance of a whole set of possible actions, rather than being linked to a single specific action.

Hunley & Lourenco [59] similarly consider PPS to be a body-centred network responsible for the coordination of actions that both enables interactions with, and avoidance of, objects and other living entities. In their view, this network is described by distinct defensive and non-defensive pathways that, although dissociable, nevertheless display evidence of shared organization, and can be viewed as part of a single integrated system. In this regard, they can be considered as somewhat akin to dorsal and ventral pathways in the visual system [72,73]. Evidence from monkeys indicates that non-defensive behaviours are associated with a pathway that includes the anterior parietal area (AIP), area 7b, and premotor area F5, while defensive behaviours are associated with a pathway involving VIP and F4 [74]. There is also evidence that these pathways may correspond to different body parts, with AIP, 7b and F5 largely tied to activity related to the hand and arm, while VIP and F4 are linked to the head and face: activities that involve interactions towards and with objects and others, and those that involve protecting vulnerable areas of the body, respectively [74]. The defensive and non-defensive pathways can be conceptualized similarly to a dimensional view of neophilia and neophobia: although these are often seen as the extreme ends of a single continuum, they are better viewed as two separate dimensions, because animals require some combination of both traits to function effectively [75]. Just as an animal may need to be neophilic enough to exploit novel situations but also be sufficiently neophobic to do so in ways that protect them from danger, so PPS represents two dimensions that allow animals both to navigate the world safely, while simultaneously providing the capacity to effectively manipulate and exploit physical and social resources in adaptive and functional ways.

In our view, then, work on PPS provides a neurobiologically grounded solution to the problem of coordination through physical and social space that, in current conceptions of the SBH, relies on executive processes like inhibition and inferential reasoning. It should be readily apparent that a flexible sensitivity to the area of space around the body, and the selection of relevant actions, is crucial to the various demands of primate social life in the round: the selection and processing of particular foods, movement in and through the trees, and the ongoing back and forth of social interactions, whether this be monitoring and withdrawing from threatening encounters or coordinating affiliative behaviours like grooming, mating and infant care. One can readily see how visual specializations linked to detecting gaze direction and facial expression would form part of a coordinated sensorimotor system that allows animals to regulate their behaviour with respect to the approach and avoidance of their conspecifics. Shifts in the extent of both defensive and non-defensive PPS would thus enable the specification and selection of appropriate actions as the animal moves through space.

Our argument here thus resembles Cisek & Pastor-Bernier's [76] critique of neuroeconomics. The latter is a field where a great deal of energy is spent debating whether modern human decision-making is 'economically rational' and determining the kinds of deliberative cognitive mechanisms that would be required to calculate values and commit to rational action. Much of this work is focused on executive functions considered to take place in the frontal lobes and separate from sensorimotor control; reasoning that is not unlike that used in the SBH, which as we have noted, places a similar emphasis on high-level executive processes. Such a stance seemingly makes the implicit assumption that brain evolution is a process by which a 'mammalian' cerebral cortex has been draped over a more primitive 'reptilian' brain, even though this view has long since been debunked [77]. Evolution does not proceed by bolting new structures onto those already existing, but by the elaboration and specialization of ancestral neurological circuits, in ways that preserve the system's overall integrity [76]. The theory of neural reuse can also be folded into this, again offering an alternative neurobiological picture compared to the SBH. A true evolutionary perspective, then, pushes us to build theories that are addressed to the kinds of 'embodied decisions', captured by the examples described above: decisions that occur during ongoing activity, and which are mediated by sensorimotor processes that enable close coordination with the environment.

Consider a group of baboons at the beginning of the day: some remain on the sleeping cliffs grooming, others are already foraging on the grassy plain below, a few are beginning to drift off on the day's journey. Now, consider a baboon that encounters this social scene: there are decisions to make concerning hand and foot placement as she descends from the cliff while, at the same time, there are decisions about which animals she can safely approach along the route, and those to whom she should give a wide berth. Once on the ground, there are decisions to make about where to forage—which means whether and where to dig for corms—and this means monitoring who else is around, and where, and what they are doing and with whom. All this might mean having to decide where to move as others approach or move further away, and all the while she is controlling and coordinating her hand movements, as she digs and plucks corms from the ground, dusts them off on her arm, peels away tough outer layers with fingers and teeth. This baboon is constantly in action and in the moment, responding in real time to a perpetual flow of socio-environmental stimuli.

These kinds of embodied decisions are different from those considered in the highly cognitive, anthropocentric view of neuroeconomics [76] and, we would argue, the SBH. The options available to the baboon are potential action possibilities—affordances—not abstract 'values'. Options of this nature are strongly influenced by biomechanical constraints and environmental layouts, and so cannot be considered as clean-cut abstractions occurring in some independent cognitive or mental realm. In addition, decision-making under such conditions is simultaneous: our baboon may encounter a series of objects and social others, but there are always several action possibilities available for selection at any given point. Thus, embodied decisions are always highly dynamic: 'as an animal moves through its world, available actions are constantly changing, some are vanishing while others appear, and also the relevant variables (outcome values, success probability, action cost) are always in flux…each embodied decision is a single-trial situation with unique settings.' [76, p. 3]. Our baboon continuously picks up sensory information about relevant affordances as part of her ongoing activity, with no temporal distinction between choice and implementation—in many ways, the choice *is* the implementation. In other words, decisions need not be determined by a central executive of any kind, but depend instead on which of the reciprocally connected sensorimotor networks are the first to 'commit' to a given action strongly enough to pull the rest of the network into a 'distributed consensus' [76]. The notion of specialized but flexible PPS fields can be folded easily into this process of embodied decision-making: sensitivity to the proximity of threatening and non-threatening objects and others is key to action specification and selection [58]. In terms of primate brain evolution, then, our proposition is that, as with the analyses of visual specialization [51–53], there is much merit to be had in analyses that investigate the size and structure of parietal regions associated with PPS in relation to the size and structure of social groups (e.g. in relation to strength of dominance hierarchies, uni-male versus multi-male, multi-female structures, single-level versus multi-level societies), as well as the demands of the foraging environment, and the degree of terrestriality. We also need to investigate and understand potential links between the visual brain and PPS-related regions of the brain.

4. Emergent systems of human social cognition

In addition to offering new avenues of exploration with respect to primate brain evolution, thinking of the social brain as an integrated system of sensorimotor coordination can offer new insights into the evolution of our own cognition. Graziano [61], for example, emphasizes the importance of PPS and physical coordination as the basic grounding for more sophisticated forms of human social cognition: 'personal space plays its most profound human role in the social domain. That invisible bubble of protected space, the space in which you do not want other people, creates the scaffold for all other social interactions. It places us in a great social honeycomb of decorous relationships' [61, p. 147]. Experimental data on humans tends to support Graziano's argument. A study using a cross-modal visual–tactile task to determine the bounds of PPS found that PPS expanded following an interaction with another person, but only if the action was cooperative—in other words, low-level sensorimotor processing modulated processes of high-level social cognition [78]. As a non-threatening interaction, one might imagine that cooperation would shrink PPS fields around the body, not extend them. However, we need to consider defensive and non-defensive pathways as connected but distinct [59]. While cooperative interactions should indeed involve a reduction in defensive PPS, non-defensive PPS should expand to better facilitate social coordination in the context of cooperation. Thus, the other person plays a functional role within PPS, in much the same way that monkey PPS was shown to extend to include raking tools. There is also evidence that PPS can vary in relation to particular psychological traits: expansion of PPS following tool use was affected by expressed levels of claustrophobic fear, with participants that scored high on this trait experiencing less expansion [79].

De Jaegher [80] offers similar arguments in her enactive account of autism, which posits that sensory and motor difficulties are basic to autism, rather than seeing them as separate from deficits in so-called 'higher cognitive functions', such as theory of mind. Specifically, she suggests that 'sensorimotor interactional coordination ability' lies at the base of our ability to engage in 'participatory sense-making', defined as the way that neurotypical people make sense of the world by moving around in it and with it. How, in other words, we coordinate our movements with others when interacting, such that we generate and transform meaning together. Differences in how one perceives and moves through the world may, therefore, lead to difficulties in coordinating social interactions, and hence to failures in the participatory sense-making needed to understand ourselves and others. Among other things, De Jaegher [80] discusses how, in comparison to typically developing children and those with Aspergers, autistic children display lower levels of visuopostural attunement to the environment [81,82]. Other researchers have also suggested that motor problems are basic to autism: children with autism experience difficulties with 'reach-to-grasp' movements, showing both poorer planning and execution [83]. These kinds of visuo-motor deficits are suggested to be related to anomalies in magnocellular pathways, visuo-cerebellar circuits, as well as in cerebellar–premotor cortex loops [83].

More recent work has specifically considered PPS in the context of autism. For example, using an audio-tactile integration task to assess PPS, adults with autism spectrum disorders (ASDs) were found to have smaller PPS than non-ASD adults, and one with a sharper boundary [84]. This was also associated with a lower susceptibility to the full body illusion [84]. In a comparison of autism and schizophrenia as disorders of the self, and how this might relate to PPS, it was argued that these conditions might sit at either end of a continuum, with autism reflecting a steep self-other gradient, with little variation, while schizophrenia reflects a shallow self-other gradient, associated with heightened variability in PPS [85] (schizophrenic individuals, for example, are more susceptible to the rubber hand illusion [86,87]). Such work, therefore, supports the argument that human cognitive capacities emerge from the elaboration and specialization of ancestral neurobiological circuits that enable the control of bodily actions in the environment. The deficits seen in autism and schizophrenia point to fundamental issues in coordinating physical and social space, which in turn are tied to issues relating to the nature of the self, and the recognition and maintenance of self-other boundaries [85,88]. In such a view, these conditions are not wholly psychological in nature, as this is usually understood, i.e. distinct from physical problems in the body. Rather they demonstrate how particular psychological conditions cannot be separated from how people monitor and move physically in space.

5. Cerebellar expansion, neural reuse and human uniqueness

In conclusion, we return to the role of the cerebellum in neurocognitive evolution and outline the implications for understanding what appear to be specialized human capacities. Given the rapid cerebellar expansion during ape evolution, the role of the cerebellum in organizing and comprehending action sequences [89] and apes' marked facility for sequence organization in below-branch brachiating locomotion, tool use and extractive foraging [89], it seems reasonable to propose that there has been selection for greater temporal organization, comprehension and learning of behavioural sequences in these taxa. This suggests that, in addition to placing greater emphasis on sensorimotor coordination in studies of primate brain evolution in general, we also need to give more serious consideration to ideas relating to 'technical intelligence' when considering ape and human brain evolution in particular. This includes the idea that the syntactical features of language may have been built from pre-existing sensorimotor specializations common to all apes [90], where both social and technical skills are important, and no doubt interact with each other in mutually reinforcing ways [33]. The neural reuse perspective can easily accommodate such a scenario: cortico-cerebellar loops involved in organizing coherent sequences of movements to produce tools could be repurposed to organize coherent sequences of social actions to produce social outcomes, or coherent sequences of words to produce sentences

Indeed, Ellis [91] offers precisely this argument, proposing an evolutionary scenario that links our remarkable manual dexterity and unparalleled ability to manipulate objects within our PPS (which he refers to as 'toolspace') to the construction and use of tools and other artefacts of various kinds. Specifically, physically coordinated, joint activity on objects is argued to have given rise to forms of social communication that eventually became symbolic language. Consequently, in a reversal of the standard view, language and other complex cognitive skills do not form the underpinnings of our sophisticated material cultures but are, instead, considered to be their manufactured products [91]. Human cognition is, therefore, 'in large part a cultural artefact invented by successive generations of especially dextrous primates' [91, p. 1]. As with our argument above, the emphasis here is on sensorimotor coordination as the foundation of, and scaffold for, our characteristically human cognitive skills. More broadly, this theory again resonates with ideas of neural reuse, where neural adaptations build upon one another and specific adaptations have multiple effects on behaviours traditionally considered to represent different 'domains'. That is, it seems possible to build on, or extend from, Ellis' theory [91], and investigate more closely how cortico-cerebellar networks potentially may support similar types of processes in different contexts, such as sequencing and prediction in brachiation, tool making and language.

Indeed, complex sequence organization and learning has long been proposed as a key aspect of human cognition that underlies tool use, language, music and other distinctive human capabilities [92]. More recently, Ghirlanda *et al.* [93] found evidence that the ability to learn arbitrary stimulus sequences distinguishes humans from non-human species. Unlike humans, where the correct representation and processing of sequential information is crucial to all kinds of everyday tasks, and also to some of our more rarefied skills, such as the creation of music and mathematics, non-human animals do not seem to be able to learn and make use of arbitrarily sequential information. For example, in studies comparing humans and macaques on the same task, humans took 30 trials per presented sequence to achieve 90% correct responses, whereas macaques required on the order of 400 trials per sequence to achieve 70% correct. Notably, however, there are no studies, to date, investigating these abilities in non-human apes. If the findings on cortico-cerebellar evolution are pointing us in the right direction, however, we might predict that apes will show improved skills in this domain.

In addition, although their survey of empirical findings, combined with a model of non-human sequence discrimination, provided good evidence to indicate that humans show a greatly improved memory for sequence formation, Ghirlanda *et al.* [93] did not show how humans have overcome the limitations of non-human memory. One suggestion that they offer is that language provides the kind of explicit verbal scaffolding needed to deal with arbitrary sequences (e.g. 'respond when you see blue first, and then yellow, but not if this comes before red'). However, as they also point out, this puts the cart before the horse, as language itself is dependent on sequence formation, and such verbal strategies could not work without understanding of concepts such as 'first' and 'before'. What they do not consider, however, are the kinds of 'external' strategies suggested by Ellis, in which the processing and making of material artefacts, and the capacity for joint action, might have scaffolded these skills, not least by generating forms of material culture that physically embody such sequences, and thereby provide a form of external memory (see [94] for an explanation of just such a process in the invention of number concepts). It may be that we are only capable of particular kinds of representational thinking (e.g. thinking in terms of the intersection in a Venn diagram) because we first generated such things in physical form, and were then able to internalize them (whatever 'internalize' might mean). One sees something similar in the counting practices shown by children who learn arithmetic using an abacus, and can then perform remarkable feats of 'mental arithmetic' without the abacus present, including complex multiplication and long-division. What is most notable here, perhaps, is how the children continue to perform the characteristic hand movements corresponding to moving beads along the bars of the physical abacus as they engage in these 'mental' calculations [95,96].

In summary, our argument, then, is that characteristic and complex forms of human cognition may ultimately depend on basic processes of physical coordination in relation to objects and social others. Investigations of primate brain evolution will, therefore, benefit from focusing more closely on how the brain has become specialized for socially and physically oriented forms of sensorimotor coordination, and how these may have scaffolded and set the stage for the evolution of unique human cognitive capacities.

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