The PROUST hypothesis: The embodiment of olfactory cognition

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30 **Abstract**

32   The extension of cognition beyond the brain to the body and beyond the body to the environment is an area of debate in philosophy and the cognitive sciences. Yet these debates

34 largely overlook olfaction, a sensory modality used by most animals. Here, I use the philosopher's framework to explore the implications of embodiment for olfactory cognition. The

36 philosopher's 4E framework comprises *embodied* cognition, emerging from a nervous system characterized by its interactions with its body. The necessity of action for perception adds

38 *enacted* cognition. Cognition is further *embedded* in the sensory inputs of the individual and is *extended* beyond the individual to information stored in its physical and social environments.

40 Further, embodiment must fulfill the criterion of mutual manipulability, where an agent's cognitive state is involved in continual, reciprocal influences with its environment. Cognition

42 cannot be understood divorced from evolutionary history, however, and I propose adding *evolved,* as a fifth term to the 4E framework. We must therefore begin at the beginning, with

44 chemosensation, a sensory modality that underlies purposive behavior, from bacteria to humans. The PROUST hypothesis (*perceiving and reconstructing odor utility in space and time)*

46 describers how olfaction, this ancient scaffold and common denominator of animal cognition, fulfills the criteria of embodied cognition. Olfactory cognition, with its near universal taxonomic

48 distribution as well as the near absence of conscious representation in humans, may offer us the best sensorimotor system for the study of embodiment.
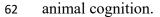
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Introduction

52   A critical question for the field of animal cognition is that of boundaries: what exactly is

cognition and who has it? Studies of minimal cognition, e.g., cognition in plants, bacteria and

54   other species lacking nervous systems, are already challenging the field (Duijn, 2006). In

philosophy and cognitive science, the definition of cognition is challenged even further by the

56   concept of the embodied and extended mind (Clark & Chalmers, 1998; Keijzer, 2017; Varela et

al., 1991). Here, a brain is only one part of a mind, which can exist embodied, embedded and

58   extended, in its environment (Carter et al., 2018). Philosophers define embodied cognition as

follows: "The properties of an organism's body limit or constrain the concepts an organism can

60   acquire." (Shapiro & Spaulding, 2021). Thus, at the very heart of embodied cognition is the

concept that different bodies will necessarily shape different minds, a fundamental tenet of

62   animal cognition.

The study of embodied cognition entertains a diversity of interpretations, each with a range

64   of propositions from the modest to the radical. One such framework is "4E cognition". Here

embodiment is parcellated into four levels of analysis: cognition of the body (*embodied*

66   cognition), cognition as related to the sensory inputs and physical affordances of the individual's

environment (*embedded* cognition), how an individual's action creates its perceptions and

68   concepts (*enacted* cognition) and finally, the information that an individual accesses that is

stored in physical and social environments externally to its brain and body (*extended* cognition)

70   (Shapiro & Spaulding, 2021).

But animal cognition could add a fifth E, *evolved.* Excellent reviews have addressed the

72   question of comparative embodied cognition, in cephalopods, domestic dogs and spiders (Cheng,

2018; Japyassú & Laland, 2017). But in the discussion of embodied cognition in both philosophy

74   and comparative cognition, there is a notable omission: olfactory cognition.

This oversight is serious; indeed one could argue that it endangers the enterprise.

76   Chemosensory perception and action is the common denominator of animal species, both aquatic

and terrestrial, from single- to multicellular species (Ache & Young, 2005; Bargmann, 2006;

78   Eisthen, 1997; Papini, 2010). It is also a primary sensory modality in minimally cognitive

species, such as bacteria and plants. In prokaryotes, it is the most important sensory modality

80   recruited for spatial orientation (Gelperin, 2014; Parsek & Greenberg, 2005). Spatial orientation

to odors may arguably have been the class of associative learning that was the impetus for the

82 radiation of animal phyla in the Cambrian (Ginsburg & Jablonka, 2010; Jacobs, 2012). It is even possible that selection for olfactory navigation in the genus *Homo* may have led to the evolution

84 of the nasal pyramid, and hence shaped the evolution of our own species (Jacobs, 2019).

For these reasons, any discussion of embodied cognition, even in humans, cannot neglect

86 chemosensation. But understanding embodiment is also critical for animal cognition. Understanding mechanisms of cognition and behavior demands an understanding of evolution

88 and adaptation (Cisek & Hayden, 2022; Krakauer et al., 2017). The surest path to this goal is through structured comparisons of convergent and divergent adaptations across taxa (Arnold &

90 Nunn, 2010; Barton et al., 1995; MacLean et al., 2012). If the question we are trying to answer is the embodiment of cognition, the logical course of action is to build structured comparisons

92 among diverse species. Ideally, such species would differ along specific parameters in embodiment (i.e., morphology), enactment (i.e., sensorimotor competency), embeddedness (i.e.,

94 sensory ecology) and extension (i.e., the structure of their cognitive niche). To do this effectively would require the widest possible sweep of taxonomic breadth. This, of course, could best be

96 accomplished by studying convergence and divergence in chemosensory cognition, building upon already impressive work in comparative and behavioral neuroscience (Ache & Young,

98 2005; Baker et al., 2018; Corey & Ache, 2016; Eisthen, 2002; Laurent, 2002).

Finally, not only is olfaction central to embodied cognition, but it is possible that the whole

100 enterprise will fail without it. This is because olfaction offers direct evidence for the radical claim of embodied cognition that the very concept of representation is misleading. Discussions

102 almost exclusively centered on visual cognition (Carter et al., 2018) overlook decades of work in olfactory cognition that questions whether an odor is represented consciously at all (Herz &

104 Engen, 1996; Zucco, 2012).

Olfaction and representation

106 The neuroanatomy of the main olfactory system (hereafter olfactory system) may explain the unique attributes of olfactory cognition. The olfactory system, a primary component of the

108 vertebrate brain Bauplan, is the only sensory system to bypass the thalamus, the relay station of the diencephalon (Striedter, 2005). The thalamus mediates conscious attention in humans and is

110 activated when the stimuli are visual or auditory stimuli, but not with olfactory stimuli (White, 2012). For this reason, Kay and Sherman proposed that the main olfactory bulb (hereafter

112 olfactory bulb) serves as its own relay station, sending inputs to the olfactory cortex, i.e., the

piriform cortex. This structure also receives inputs from taste, visual, auditory and

114   somatosensory systems. The olfactory bulb thus uniquely projects directly to this multisensory

cortical structure (Kay & Sherman, 2007).

116   This privileged neural circuit may explain why untrained human participants find the

conscious recall of a remembered odor difficult or impossible to perform, compared to the

118   accurate performance of the same task using visual stimuli (Herz & Engen, 1996). The

presentation of an odor even modulates object visibility, both the identity and the duration of a

120   visual stimulus (Zhou et al., 2017). Thus odors are not only difficult to recall or label

consciously, they also distort inputs from other sensory modalities and even compete with

122   language processing (Herz, 2020, pp. 472–482).

In addition to the lack of thalamic modulation, the olfactory system has robust, reciprocal

124   projections to the amygdala, a limbic structure that subserves emotional learning and memory.

This neural architecture may explain why odors are inherently emotional (hedonic). For example,

126   the memory of the odor of a stimulus, such as popcorn, is encoded with greater emotional

valency than the visual appearance or sound associated with the same stimulus (Herz, 2012,

128   2016; Herz & Cupchik, 1995; Herz & Schooler, 2002; Kontaris et al., 2020).

The absence of a thalamic projection, combined with the important projections to emotional

130   circuits, may explain why verbal encoding of odors is highly inefficient, yet odor learning and

memory are remarkably resistant to decay. In a classic study, the accuracy to identify an odor

132   decreased significantly after a 30 second retention interval. But after 30 seconds, there was only

a 3% decrease in accuracy of recall after subsequent delays of three days, one month and even

134   one year (Engen & Ross, 1973). Such studies fuel a serious, ongoing debate whether olfaction is

in itself a separate memory system, one with no distinction between short- and long-term

136   memory (Herz & Engen, 1996).

One reason why such questions remain unanswered is that we still lack a standard model of

138   odor perception. We even lack a fundamental model of the neural code by which the olfactory

brain identifies an odor, as current data support two competing theories, the pattern model and

140   the vibration model (Herz, 2020, pp. 464–468). Yet another question which has not been

definitely answered is how the brain encodes the odors it has identified, whether as the elements

142   in a mixture or the mixture as a single synthesis (Barwich, 2019; Herz, 2020, pp. 468–470;

Wilson & Stevenson, 2010). In short, the olfactory system is a sophisticated cognitive system

144   that exhibits unusual characteristics, including the difficulty of conscious representation. Instead

the olfactory system may be a uniquely emotional and unconscious learning and memory system

146   (Wilson & Stevenson, 2003; Zucco, 2003, 2007). It is small wonder that olfaction was shunned

for centuries by philosophers modeling the human mind as conscious and rational (LeGuérer,

148   2002) and is only now being taken up by a new generation of philosophers (Barwich, 2019;

Batty, 2010).

150   **The utility of olfaction**

Yet the majority of research in olfactory cognition, whether in humans or other species, is

152   designed to study how the brain identifies and assigns valency to an odor, what could be called

diagnostic olfaction. But this downplays or ignores a critical function of olfactory cognition, its

154   role in spatial orientation, i.e., *directional olfaction* (Jacobs, 2019). This is an important

distinction because many paradoxes of olfactory anatomy and psychophysics can only be

156   explained in terms of directional olfaction functions (Jacobs, 2012, 2022; Marin et al., 2021). In

the *olfactory spatial hypothesis* (Jacobs, 2012), I discuss how unique patterns of allometry and

158   neuroplasticity in the vertebrate olfactory system play a role in directional olfaction. For

example, the relative size of the olfactory system can be explained by a species's ability to orient

160   using odors. Hence it follows that directional olfaction could be a primary selective force acting

on the evolution of the olfactory system (Jacobs, 2012).

162   This insight arose from a prior consideration that distributed gradients, such as odor plumes,

had been missing from models of hippocampal function, a limbic brain structure critical for

164   spatial navigation. Françoise Schenk and I addressed this in the *parallel map theory* of

navigation (Jacobs & Schenk, 2003). It was the first model of the hippocampus to incorporate

166   olfactory gradients as orientation cues. We also proposed that orientation to such *directional cues*

was the ancestral function of hippocampal homologues (e.g., medial pallium, medial cortex) in

168   vertebrates (Jacobs, 2003). More recently, I have proposed that it was the evolution of air

breathing in lobe-finned fish, and their subsequent move to land as the first tetrapods, that led to

170   directional olfaction becoming a primary function of the olfactory system in terrestrial

vertebrates (Jacobs, 2022).

172   But the data on directional olfaction in mammals is surprisingly sparse, apparently because of

the assumption that the olfactory system is not spatial, but only diagnostic. Even studies of

174   spatial orientation in highly olfactory species (e.g., laboratory rat and mouse, Order Rodentia,

Family Muridae, Subfamily Murinae) actively eliminate odors and odor plumes as orientation cues (Jacobs, 2022). This is partly due to the technical challenge of controlling such stimuli, but as a result we have a poor understanding of the relationship between olfaction, space and the hippocampus (Jacobs, 2012, 2022), despite Françoise Schenk's early work in this area (Lavenex & Schenk, 1997, 1998). This is changing, however, with studies of hippocampal function that explicitly build on the parallel map theory (Hagena & Manahan-Vaughan, 2011; Kemp & Manahan-Vaughan, 2007a, 2007b) and the olfactory spatial hypothesis (Dahmani et al., 2018; Jacobs et al., 2015; Zhang & Manahan-Vaughan, 2015). The impact of the olfactory spatial hypothesis has now reached beyond the hippocampus, with the discovery that the piriform cortex actively encodes the spatial location of odors (Poo et al., 2021). In short, there is increasing evidence that a primary function of the olfactory system is spatial orientation (Jacobs, 2022).

In contrast to mammals, there is a rich literature of orientation to odors in insects (Baker et al., 2018; Vickers, 2000; Vickers et al., 2001; Willis et al., 2013) and birds (Gagliardo, 2013; Wallraff, 2005). In birds, trained homing pigeons, as well as wild sea gulls and migrating songbirds, orient more accurately over long distances when their olfactory system is intact and functioning (Thorup et al., 2007; Wikelski et al., 2015). Recent studies of hippocampal place cells in food-storing and non-food-storing songbirds have demonstrated remarkable homologies with hippocampal function in mammals (Payne et al., 2021).

Many of these results in birds are concordant with an interpretation of avian navigation based on the parallel map theory (Jacobs & Menzel, 2014). A navigator that moves over larger distances, such as flying birds or flying insects, is able to orient to the pattern of larger stimuli. In the case of olfactory landscapes, these could be based on the association of cardinal directions to known locations. This could include orientation to localized concentrations of odors, as in the mosaic map model of Floriano Papi, or gradients of atmospheric odors, as in the olfactory navigation model of Hans Wallraff (Gagliardo, 2013). Although we lack evidence for this in birds, based on studies of plume orientation in flying insects, a larger scale of stimulus distribution should facilitate the ability to sample and orient to odor plumes. Whether odors are concentrated locally or distributed in gradients, it follows that using odors to orient will be more useful for species that navigate over larger distances. This may be one reason why mapping of space using odors is influenced by scale and why olfactory inputs are critical for accurate long-distance homing in displaced birds (Jacobs & Menzel, 2014).

206   **The PROUST Hypothesis**

In his famous passage in the first volume of the novel, "In Search of Lost Time", Marcel
208   Proust offers perhaps the finest description of the recall of a flavor memory (Proust,
2002)(Proust, 2000). Now known as a 'Proustian memory', the passage describes how the flavor
210   of a specific cookie dipped in a specific tea sparked the recall of a childhood memory. The
passage illustrates key characteristics of olfactory memory: how an odor first activates an
212   emotion which then triggers the effortful reconstruction of a spatio-temporal memory. The
precision of Proust's observations in this passage have inspired the design of studies in olfactory
214   cognition (Herz, 2016; Herz et al., 2004; Jellinek, 2004). Jellinek has deconstructed the passage
into no fewer than than eleven hypotheses about olfactory memory, many of which have been
216   confirmed empirically (Jellinek, 2004). Here are selections from Proust's iconic passage:

"But at the very instant when the mouthful of tea mixed with cake crumbs touched my palate, I
218   quivered, attentive to the extraordinary thing that was happening inside me." (Proust, 2002, p. 45).
"Where could it have come to me from — this powerful joy? I sensed that it was connected to the
220   taste of the tea and the cake, but that it went infinitely far beyond it, could not be of the same nature.
Where did it come from? What did it mean? How could I grasp it?" (Proust, 2002, p. 45).
222   "Seek? Not only that: create. It is face-to-face with something that does not yet exist and that only it
can accomplish, then bring into its light.
224   And I begin asking myself again what it could be, this unknown state which brought with it no logical
proof, but only the evidence of its felicity, its reality, and in whose presence the other states of
226   consciousness faded away. I want to try to make it reappear. I return in my thoughts to the moment that I
took the first spoonful of tea. I find the same state again, without any new clarity. I ask my mind to make
228   another effort, to bring back once more the sensation that is slipping away. And, so that nothing may
interrupt the thrust with which it will try to grasp it again, I clear away every obstacle, every foreign idea,
230   I protect my ears and my attention from the noises in the next room. But feeling my mind grow tired
without succeeding, I now compel it to accept the very distraction I was denying it, to think of something
232   else, to recover its strength before a supreme attempt. Then for a second time I create an empty space
before it, I confront it again with the still recent taste of that first mouthful, and I feel something quiver in
234   me, shift, try to rise, something that seems to have been unanchored at a great depth; I do not know what
it is, but it comes up slowly; I feel the resistance and I hear the murmur of the distances traversed."
236   (Proust, 2002, p. 46).
"Ten times I must begin again, lean down toward it. And each time, the laziness that deters us from
238   every difficult talk, every work of importance, has counseled me to leave it, to drink my tea and think
only about my worries of today, my desires for tomorrow, upon which I may ruminate effortlessly.
240   And suddenly the memory appeared. That taste was the taste of the little piece of madeleine which on
Sunday mornings at Combray (because that day I did not go out before it was time for Mass), when I went
242   to say good morning to her in her bedroom, my aunt Léonie would give me after dipping it in her infusion
of tea or lime blossom. The sight of the little madeleine had not reminded me of anything before I tasted
244   it […]." (Proust, 2002, p. 47).

246

248   The PROUST hypothesis (*perceiving and reconstructing odor utility in space and time*) evokes Proust's insight that olfactory cognition can evoke the reconstruction of an experience in

250   distant space and time. These cognitive mechanisms can only be understood by retracing their evolutionary history, as with the hippocampus (Jacobs & Schenk, 2003), main olfactory system

252   (Jacobs, 2012) and vomeronasal system (Jacobs, 2022). If complex cognition first emerged in highly chemosensory animals, then the answer to many questions about 4E cognition may lie in understanding how this plays out in the olfactory cognition of species today.

254   **Defining the boundaries**

To recapitulate the 4E framework (Shapiro & Spaulding, 2021): the *embodiment* of cognition

256   is its constraint by the morphology and competencies of the body. The *embedding* of cognition is how the physical environment in which that body is located shapes cognitive load; the more

258   appropriate the environment, the smaller the cognitive load. The next level is *enactivism*, where cognition emerges as the mutual interactions of a sensorimotor system with its physical and

260   social environments. Finally, these actions, which are both embedded and embodied, change and shape the *extended* social and physical environment, as "… the environmental and social

262   resources that enhance the cognitive capacities of an agent are in fact *constituents* of a larger cognitive system, rather than merely useful tools for a cognitive system that retains its traditional

264   location wholly within an agent's nervous system…." (emphasis in the original) (Shapiro & Spaulding, 2021, sec. 2.3).

266   Of course, the problem with such a framework is "cognitive bloat", where everything and hence nothing is cognition (Kaplan, 2012). An accepted solution to this has been the concept of

268   "mutual manipulability" (Craver, 2009; Kaplan, 2012). As defined in comparative cognition, "systematic manipulations of the object must affect the animal's cognition, and changes in the

270   animal's cognition must affect the object, via some causal chain. Only when this two-way flow has been established can the object be considered part of the animal's extended

272   cognition."(Cheng, 2018, p. 6).

One such example is the analysis of orb-weaving in spiders as *extended cognition* (here used

274   to represent all levels of embodied cognition) (Japyassú & Laland, 2017). As a spider tightens the threads of a web, this creates a new environment where smaller insect prey can be detected.

276   This change in prey detection feeds back on the attentional system of the spider. Thus the spider's cognition (attention and perception) is extended into its environment, i.e., its web

278   (Cheng, 2018; Japyassú & Laland, 2017).

Cheng explains the mutual manipulability criterion more broadly as follows: "In general,

280   information-seeking behavior that supports a cognitive enterprise often satisfies the mutual

manipulability criterion. Kaplan (2012) gave the example of saccadic eye movements in humans

282   to look repeatedly at a target to support working memory. To satisfy the mutual manipulability

criterion, certain cognitive states must cause more or different kinds of information seeking, and

284   the information seeking must help the enterprise." (Cheng, 2018, p. 11). He describes the

example of a specific movement (a pirouette) made by a navigating ant when it reaches an

286   ambiguous choice point. The pirouette does not enhance locomotion but instead functions to

gather additional information. Thus, like the saccade, the ambiguity of the location (a cognitive

288   state) leads to the information seeking of an action (the pirouette), which then changes the

cognitive state and thereby satisfies the mutual manipulability criterion.

290   Yet once again, these examples from ants and humans are derived from visual cognition. My

goal here, given the importance of chemosensation in animal behavior, is to explore what we can

292   learn by placing olfactory cognition in the 4E framework and adding *evolved* as a fifth level of

analysis.

294   **Embodied cognition**

As in the examples from ant and human vision, the act of an olfactory sample satisfies the

296   mutual manipulability criterion, as a cognitive state that causes useful information seeking. In

air-breathing terrestrial vertebrates using nasal respiration, this sample is embodied in the sniff.

298   Air is inhaled through the nostril and moves through the nasal cavity to reach the olfactory

epithelium, where odorants contact the olfactory receptors. The inspired air then continues

300   through the pharynx, carrying oxygen to the lungs (Mainland & Sobel, 2006). There are two

forms of sampling in mammals and this is called orthonasal olfaction – inhalation through the

302   nose. The other form is retronasal olfaction in mammals, where odors in the mouth are carried

via expiration to the olfactory epithelium before being exhaled (Ni et al., 2015; Small et al.,

304   2005).

An orthonasal sniff has two functions, olfaction and respiration, and thus respiration is an

306   integral component of olfactory cognition (Mainland & Sobel, 2006). As in vision, the sniff itself

is necessary and sufficient to activate the olfactory brain in mammals. If the eye is kept

308   motionless, a visual image is not detected, despite the photons hitting the retina. In human

olfaction, if the odorant is experimentally placed in contact with the epithelial olfactory receptors

310   but in the absence of a sniff, the odorant is also not perceived. Yet a sniff, even in the absence of

an odorant, activates the oscillation frequencies (e.g., theta) that are normally associated with

312   odors during sniffing (Mainland & Sobel, 2006).

Humans modulate their sniff when asked to imagine odors, increasing the volume of the sniff

314   for pleasant odors and decreasing the volume for unpleasant odors (Mainland & Sobel, 2006) .

There is also a 'dialogue' between cortex and olfactory bulb, that has been well documented in

316   laboratory murines. When a laboratory rat is preparing to enact a sniff to earn a reward, its

entorhinal cortex (a higher sensory integration structure that funnels information to the

318   hippocampus), activates before the sniff and hence before the activation of the olfactory bulb.

This top-down modulation of olfaction is driven by an expectation based on the rat's prior

320   learning experiences (Kay & Freeman, 1998). There is also a 'language' for this dialogue, in the

form of oscillatory dynamics, which are convergent in form and function between mammals and

322   insects (Ache & Young, 2005; Kay, 2015; Laurent, 2002).

The importance of the sniff for cognition goes beyond olfactory tasks: orthonasal respiration

324   is not only necessary for olfactory perception but also for the consolidation of learning. It has

been recently demonstrated that nasal respiration synchronizes disparate brain regions,

326   enhancing the consolidation of learning, even in non-olfactory structures and in non-olfactory

tasks (Heck et al., 2017, 2019; Sheriff et al., 2021; Tort et al., 2021). This effect has been

328   demonstrated in humans: respiration through the nose, but not the mouth, facilitates memory

consolidation (Arshamian et al., 2018). In laboratory mice, these appear to be top-down

330   influences on nasal respiration (not vice versa) and occur even during REM sleep (Tort et al.,

2021). I have proposed that these effects can be explained by the evolutionary history of air

332   breathing in vertebrates (Jacobs, 2021).

The act of odor sampling is also highly purposeful and dynamic. A sniff is 'focused' by

334   changing its duration, intensity, volume and temporal pattern (Schoenfeld & Cleland, 2006) .

The sniff is therefore active information seeking, not simply respiration (Jacobs, 2019), and its

336   structure is fine-tuned for this purpose, as in a visual saccade. This behavioral modulation of

sniffing focuses the information seeking via the specialized structure of the inner nasal skeleton,

338   which varies significantly among mammalian species (Valkenburgh et al., 2014; Zwicker et al.,

2018). The focusing of the sniff further exploits the chromatographic function of the nasal

340   epithelium, a function first proposed by Mozell and Jagodowicz (Mozell & Jagodowicz, 1973).

The chromatograph organization of the epithelium was proposed to emerge due to the molecular

342   properties of an odorant, which cause it to be absorbed in different zones along the olfactory

epithelium; this later led to the theory of zonation (Schoenfeld & Cleland, 2006). Both the

344   chromatograph and zonation hypotheses have received empirical support. As predicted,

laboratory rats adapt their sniff characteristics to the chemical structure of the odorant they are

346   sniffing (Rojas-Líbano & Kay, 2012).

This fine control of sniffing also modulates the perceived difference between the target odor

348   and the background odor. Laboratory rats increase this difference by increasing the frequency of

sniffing, thus creating an adaptive filter (Verhagen et al., 2007). Similarly, trained search dogs

350   increase the frequency of their sniffing at decision points, at locations where they must make

finer odor discriminations (Thesen et al., 1993).

352   The speed of the sniff also changes the spatial location of the samples being collected. In

physics, the faster a fluid is transported through a tube, the greater is the area from which the

354   sample is collected. The catchment areas are separated even farther if the tube is lengthened

(True & Crimaldi, 2017). Thus rapid sniffing through two external nostrils should theoretically

356   increase the spatial separation of the odor samples, thus enhancing stereo olfaction (Jacobs,

2019). Stereo olfaction has been demonstrated to increase the accuracy of directional olfaction,

358   both empirically (Catania, 2013; Martin, 1965; Wu et al., 2020) and in a computational analysis

of real world odor plumes (Boie et al., 2018). Increasing the spatial separation between the input

360   locations enhances directional olfaction even farther: in sharks, the further apart in space and

thus in time that two odor samples are collected, the greater accuracy of determining the

362   direction of the odor source (Gardiner & Atema, 2010). The physical properties of how fluids

move through tubes could explain the evolution of the mammalian external nose and why tube-

364   shaped nostrils are found in certain olfactory navigating species in birds (e.g., tube-nosed

seabirds, Order Procellariiformes) and mammals, including the evolution of the external nose in

366   the genus *Homo* (Jacobs, 2019).

Finally, a sniff, like a visual saccade, fulfills the mutual manipulability criterion, because the

368   new information changes the cognitive state. But unlike vision, the act of sampling odors also

disturbs the stimuli that are being sampled. The movement of sampling (sniffing, movement of

370   antenna or other antenniform structures such as tentacles or antennules, movement of the head,

casting of the body and other forms of locomotion) distorts the fluid dynamics of the air and

372   hence the geometry of the plume. Also, when an odorant is sampled, it is absorbed into the

olfactory epithelium. Molecules that are not absorbed by the olfactory epithelium are mostly

374   captured in the mucosal lining of the inner nose. In the bullfrog, this lining absorbed 78% of odor

molecules that were not absorbed by the olfactory epithelium (Hornung & Mozell, 1977). The

376   act of olfactory sampling thus permanently removes a stimulus from the surrounding

environment. The physical movements of sampling are no doubt more significant than the

378   removal of odorants from the transport vehicle (air or water). Yet from first principles, it is

nonetheless possible that this unique aspect of olfaction, compared to vision or audition, could be

380   important for modeling its embodiment.

Olfactory cognition thus demands intricate and purposeful sampling, with high dimensional

382   dynamic sniffing, adapted to focus the deposition of odorant molecules in specific zones within

an aerodynamic nasal environment. Olfactory sampling clearly fulfills the mutual manipulability

384   criterion: the cognitive state leads to a movement which changes the environment, and this

changed state in turn changes the cognitive state of the agent. In summary, from the morphology

386   of the nose to the mode of respiration, olfactory cognition is embodied in structures outside the

brain.

388   **Embedded cognition**

Because of its unique properties, olfactory cognition is also deeply embedded in the physical

390   affordances of the external odor landscape. Any significant movement of an odorant, whether in

air or water, occurs not by diffusion, which is too slow to be biologically useful to an animal

392   orienting in space, but by advection, transportation in a fluid (Koehl et al., 2001; Moore &

Crimaldi, 2004). Directional olfaction thus demands an integration of chemosensory and other

394   embodied inputs to measure the movement of the transport vehicle, such as its speed or

turbulence. Combined, these inputs allow the navigator to construct a movement strategy that

396   allows it to orient even within a turbulent odor plume (Baker et al., 2018; Weissburg, 2010).

This necessitates estimating hydrodynamic forces by aquatic species and aerodynamic forces

398   in terrestrial species. Plumes differ in air and water, which constrain how odors can be sampled,

e.g., the antennule flick of a crustacean (Koehl et al., 2001), versus the olfactory organ sampling

400   of a fish. Extremely large odorants can be transported in water and useful to an aquatic species

(fish can smell peptides using their olfactory system) but the chemicals must dissolve in water

402	(Kishida, 2021). This adds a different constraint on the makeup of a odor landscape for an
aquatic animal. In contrast, odorants borne in air must be volatile, with small molecular weights.

404	The affordance of a light volatile can be spatial orientation: the long-range detection of odors
associated with a cardinal direction after long-distance spatial displacement, as in homing

406	pigeons (Gagliardo, 2013). House mice can safely identify the species and gender of an unknown
mouse at a distance by sampling volatile odors, but need to have direct contact to identify the

408	individual (Hurst & Beynon, 2004). Thus how odors are embedded in the physical environment
constrains the kind of information that can be extracted from them.

410	This embedding of olfactory cognition means that the olfactory agent must have mechanisms
in place to decode the movement of fluids (Baker et al., 2018; Vickers et al., 2001; Weissburg &

412	Zimmer-Faust, 1994) , whether air (anemosensory) or water (hydrodynamics). Terrestrial
mammals accomplish this 'anemo-chemo cognition' by integrating respiration, olfaction and

414	aerodynamics in remarkable synchrony. In the laboratory murines, there is an orofacial system of
neural control for dynamic sniffing. This synchronizes the sniff (respiration and olfaction),

416	hippocampal oscillations associated with spatial learning (at the theta frequency) and the
whisking movement of the vibrissae (Kleinfeld et al., 2014). Laboratory rats can encode wind

418	direction using their vibrissae (Yu et al., 2016), which suggests that this finely tuned orofacial
system is adapted for directional olfaction.

420	A final factor that influences embedded olfaction is the geometry of the physical landscape.
This also changes the information content of odors. A southern facing slope, for example,

422	increases in temperature more rapidly than a northern facing slope (Conover, 2007a). The
atmosphere, shape and texture of the terrain also influences the movement of odors and hence

424	should also influence the behavior and cognitive states of predators and prey. Prey animals
should theoretically exploit the odor landscape by using hot, dry locations as a temporary refuge

426	from olfactory predators(Conover, 2007b) . The movements of individuals in such a landscape
would in turn alter the distribution of their odors in the environment, which would in turn change

428	the cognitive state of the individuals attempting to locate them, either predators or prey.

Enacted cognition

430	Enactivism can be described as the hypothesis that as an agent acts, it creates a perception of
its world. "The key point, then, is that the species brings forth and specifies its own domain of

432	problems ...this domain does not exist "out there" in an environment that acts as a landing pad for

organisms that somehow drop or parachute into the world. Instead, living beings and their
environments stand in relation to each other through mutual specification or codetermination."
(Varela et al., 1991, p. 198). Much of what has already been reviewed supports this in olfactory
cognition: the necessity of the sniff for an odorant to be perceived, the focusing of the sniff to the
molecular structure of the target odorant, creating an adaptive filter by changing sniff frequency
or increasing stereo olfaction by casting and/or sniff frequency, and finally integrating these
inputs with the fluid mechanics of air or water.

Real-world examples can be seen in the directional olfaction of trained search dogs. Search
dogs increase sniff rate at choice points, where they must make fine diagnostic decisions to
determine the direction of travel of the human whose footprints they are tracking. Once the
direction has been diagnosed, sniff frequency declines and speed of movement increases (Thesen
et al., 1993). Dogs can determine the direction of travel by sampling five or more successive
human footprints. The interpretation is that the complex odor mixture of human scent is a
mixture of small and large molecules. Light volatiles disperse sooner after deposition of the
mixture and hence their presence is evidence that the mark was made more recently in time
(Alberts, 1992; Baeckens et al., 2017; Scordato et al., 2007). A footprint that still retains light
volatiles must have been made more recently than a footprint with a lower concentration of such
molecules, and must indicate the most recent sample and hence the human's direction of travel
(Hepper & Wells, 2005; Wells & Hepper, 2003). Thus diagnostic olfaction is enhanced to solve a
problem in directional olfaction.

Because olfactory cognition depends so directly on the physics of the transport vehicle,
meteorological conditions influence the detectability of airborne odors. Olfactory discrimination
is also impacted by atmospheric conditions; detection thresholds are higher in hotter, drier
climates. Search dogs adapt their search strategy under such conditions. Dogs following a trail of
human footprints under hot and dry conditions were less accurate and increased their sampling of
the ground versus the air. This slowed their forward rate of progress, compared to a dog with its
head up, who can run and sniff at the same time. When the signal is lost, the dog must resort to
slower sampling of the heavier molecules that persist on the substrate, when the lighter
molecules, which are easier to track but more likely to degrade in hot or windy conditions, can
no longer be reliably followed (Jinn et al., 2020).

Similar issues must be faced by aquatic species tracking the hydrodynamics of odor plumes

464   underwater, as has been studied in detail in crustaceans (Weissburg & Zimmer-Faust, 1994);

understanding the cognition underlying odor tracking in aquatic vertebrates such as fish would

466   greatly increase our understanding of such enacted cognition. Seals, like rats tracking wind

plumes with their vibrissae, track the hydrodynamic plumes of their prey with input from their

468   vibrissae, although as secondarily aquatic mammals, seals have lost the ability to detect odors

dissolved in water (Adachi et al., 2022; Dehnhardt et al., 2001; Kishida, 2021). In summary,

470   anemo-chemo cognition in air-breathing terrestrial animals supplies important examples of

enacted olfactory cognition.

472   **Extended cognition**

The classic example of the extended mind in humans is a notebook, allowing the inclusion of

474   information that is stored in the environment, instead of the nervous system, and is easily

accessible (Clark & Chalmers, 1998). Scent marks are depositions of sociochemical odor

476   mixtures on substrates such as the ground surface or vegetation. These and other sociochemicals

are rich repositories of information, transmitting species, sex, age and individual identity, but

478   also changes in state over time, including reproductive, disease, stress and even nutritional states

(Kavaliers et al., 2020; Zala et al., 2004). Because these odors are repositories of information

480   stored in the environment, they also satisfy the criterion of accessibility. As in a notebook, an

individual may rely on information that is accessible in the environment (Clark & Chalmers,

482   1998). Sociochemicals thus effectively act as public records of information, not dissimilar to the

written language of humans.

484   The information is structured as a form of olfactory 'social media', a present and past record

of social encounters, acted out in public. The meaning of a mark is determined by three of its

486   characteristics: who, where and when. Just as the meaning of a human footprint to a search dog

is dictated by its location in space and time, the same is true of scent marks (Hurst & Beynon,

488   2004). To extract the full meaning of a mark, an agent will study spatial and temporal changes in

the placement and composition of odor mixtures, over periods of minutes, hours or longer

490   (Gosling & Roberts, 2001). Because scent marks undergo predictable changes in composition,

providing a unique time-stamping function, these changes can convey the competitive status of

492   the individual that left the mark (Alberts, 1992).

The control of this process is important. The main urinary protein found in the urine of male

494   house mice functions not only as a marker of individual identity but is also structured to slow the

degradation of the odor mixture. By increasing the longevity of a fresh signal, these expensive

496   metabolites enhance a male's competitive ability (Hurst et al., 1998). The spatial location is

equally critical for determining the meaning of a scent mark. A small displacement between

498   house mouse scent marks conveys important information about social competition to a

conspecific (Hurst & Beynon, 2004).

500   The dynamics of counter-marking – where a competitor places a new scent mark over or

adjacent to a prior mark – adds the further dimension of a public competition, witnessed by all.

502   The age and location of a male's countermark gives observers time-stamped evidence that a

social competition between known antagonists has occurred. The geometry of countermarks

504   (which mark is uppermost, which is broken) is a further source of information (Johnston, 2003;

Johnston et al., 1995; Tomlinson & Johnston, 1991). This record of social competition is public,

506   long-lasting and accessible to anyone tracking the competitive ability and history of the

contestants (Hurst & Beynon, 2004). A mark placed in a particular time and space can convey

508   ownership or a challenge, demonstrating that a non-territory holder has invaded and marked the

property of another. A scent mark can directly advertise physiological state (Kavaliers et al.,

510   2020; Wyatt, 2010) or indirectly, that the signaler has an energetic budget sufficient to visit and

mark widely dispersed locations (Gosling & McKay, 1990). Finally, another source of public

512   information are odors that an individual carries with them, on their bodies. Complex

sociochemicals may be emitted during social interactions, such as displays of scent glands and

514   ritual urination (Alberts, 1992; Drea, 2015). Thus as extended sources of information,

sociochemicals exist in the physical and social domains, but can occur either separate or

516   coincident in time and space from a direct social encounter.

Finally, the environment holds a wealth of information about odor utility in space and time,

518   that extends beyond a species's sociochemicals. Any state-dependent odor could yield spatio-

temporal data. The odor of ripening fruit or the decay of a predator odor in a potential nest site

520   yields information from the past (degraded odors), present (current strong odors) and future (the

extrapolation of an odor to predict a future state). Thus a cognitive agent responding to these

522   odors (eating the fruit, rebuilding the nest) changes the landscape, which then changes the agent's

cognitive state. Thus an agent's responses to changes in the location or chemical composition of

524   odors in its environment, whether sociochemical or other odors, fulfils the mutual manipulability

criterion.

526   **Evolved cognition**

If embodied cognition can be said to incorporate time scales of seconds to hours, then this

528   raises the question of whether it can also include longer time scales, such as evolutionary time

(Cheng, 2018). For example, in niche construction, over evolutionary time, the actions of

530   individuals alter their population's environment, which then alters the value of future actions

(Laland et al., 1999). Human culture is an extreme example of niche construction (Jablonka,

532   2011), but it is a general principle of evolution; the foraging decisions of scatter hoarding

squirrels results in the squirrels planting their own food trees (Robin & Jacobs, 2022). Thus

534   niche construction should fulfill the mutual manipulability criterion. And if processes such as

niche construction show that cognition is indeed embodied over evolutionary time scales, then

536   we should begin the analysis with the earliest forms of adaptive behavior, such as chemosensory

behaviors.

538   Most animals rely to some extent on chemosensory modalities — to orient in space, find

food, interact with conspecifics and avoid predators (Bargmann, 2006). Using the metric of the

540   size of gene families, animal species continue to invest more heavily in chemosensation than any

other sensory modality: the largest gene families found in animals are those that encode olfactory

542   receptors (Grus & Zhang, 2008; Nei et al., 2008). Because the gene families are so large, it is

possible to construct phylogenies for chemosensation dating back hundreds of millions of years,

544   and to identify homologous olfactory receptor genes within the phylum Chordata.

Indeed, chemosensation is arguably the only cognitive trait that can be plausibly studied over

546   the entire phylogenetic history and taxonomic breadth of animal species. For example, the

Florida lancelet (*Amphioxus*), a basal chordate species, shares over 30 olfactory receptor genes

548   with vertebrates (Niimura, 2012) and similar reconstructions have been possible with the

accessory or vomeronasal olfactory system (Grus & Zhang, 2006, 2009).

550   Convergence in olfactory structure and function is another tool for the study of embodied

cognition. Convergence has been found in the topography of neural circuitry, the structure of

552   receptors and in the form of neural architecture, such as glomeruli, among the olfactory systems

of molluscs, crustaceans, insects and vertebrates (Ache & Young, 2005; Eisthen, 2002). In

554   insects and laboratory rodents, glomeruli allow for combinatorial encoding of odor mixtures. An

odor object (e.g., 'coffee') is the perception of an object that is constructed from many, even

556   hundreds, of monomolecular odorants (Wilson & Stevenson, 2010). The odorants creating the

percept of 'coffee', for example, can vary in numerous parameters which is why flavors can be

558   so subtle, though the definition of a flavor includes input from the taste and somatosensory

       systems as well (Herz, 2009; Shepherd, 2013; Wilson & Stevenson, 2010). The combinatorial

560   nature of olfaction thus supports a massive capacity for encoding information (Kay et al., 2009;

       Laurent, 2002) .

562   The use of olfactory cognition by animals has clearly led to the construction of new

       ecological niches and shaped cognitive states over evolutionary time. Examples I have already

564   mentioned include how orienting to odors may also have shaped the evolution of the vertebrate

       brain and the vertebrate hippocampus (Jacobs, 2012; Jacobs & Menzel, 2014). The tradeoffs

566   between olfaction and respiration in lobe-finned fish that led to the first land vertebrates may

       also have shaped the evolution of the mammalian hippocampus and cognition. Air breathing led

568   to the restriction to the olfactory system of encoding only air-borne odors. This could explain the

       increase in size and complexity of the vomeronasal system in terrestrial vertebrates. With the

570   olfactory system becoming specialized for directional olfaction, the vomeronasal system could

       have taken over the role of the diagnostic olfaction of large, water-soluble signature mixtures, a

572   role formerly performed by the olfactory system in their fish ancestors (Jacobs, 2022).

           Directional olfaction may also explain patterns of olfactory bulb size in paleontology,

574   specifically the grade shifts in brain size in Jurassic mammals. Each increase in brain size during

       this geological period was preceded by an increase in the volume of the olfactory bulbs (Rowe et

576   al., 2011). This paleontological record could be evidence for the evolution of increasingly

       complex spatial navigation to odors. As species increased their space use, this could have led to

578   increases in trophic level and further abilities in spatial cognition (Jacobs, 2012). This

       interpretation may also explain a result in a Miocene cercopithecoid primate. Here, too, the fossil

580   record shows that large olfactory bulbs preceded an increase in sulci, a measure of cortical

       complexity (Gonzales et al., 2015). This could be further evidence that directional olfaction

582   preceded an increase in behavioral complexity, which could have eventually bootstrapped the

       evolution of larger and more complex brains (Jacobs, 2012).

584   A final example that underscores the importance of olfactory cognition in evolution comes

       from cetaceans, in particular the suborder of toothed whales (Odontoceti). With the exception of

586   sea turtles, secondarily aquatic vertebrates have not regained the ability to smell odors dissolved

       in water (Kishida, 2021), though shrews and moles smell odors underwater through air bubbles

588   (Catania et al., 2008). Cetaceans (among other taxa, such as birds and catarrhine primates) have

lost the second vertebrate olfactory system, the vomeronasal system (Meisami & Bhatnagar,

590   1998). They also have reduced main olfactory systems. This loss of function is most extreme in

the toothed whales; species in the suborder of baleen whales (Suborder Mysticeti) may detect air-

592   borne odors while respiring and orient to odors associated with a local abundance of prey species

(George et al., 2010). Yet despite the sophisticated spatial orientation in three-dimensional space

594   seen in toothed whales such as dolphins, porpoises and killer whales (Marino, Connor, Fordyce,

Herman, Hof, Lefebvre, Lusseau, Nimchinsky, et al., 2007), the hippocampus is significantly

596   smaller than expected for brain size in odontocetes (Patzke et al., 2013).

What is notable in this group is the simultaneous loss of the olfactory system and the

598   reduction in hippocampus. The most parsimonious interpretation is that the hippocampus, a

structure crucially involved in spatial orientation in terrestrial species (Jacobs & Schenk, 2003),

600   is indeed specialized for the use of odors in directional olfaction. The loss of directional olfaction

would have been offset by the evolution of echolocation, an orienting mechanism suited to their

602   new environment. Echolocation in toothed whales is convergent in function, even its genetic

basis, with echolocation in bats (Order Chiroptera) (Jones & Teeling, 2006; Teeling, 2009).

604   Directional olfaction in bats is constrained by their respiratory system, which may explain why

echolocation also evolved in this group, which nonetheless retain diagnostic olfaction. All

606   suborders of bats retain the main olfactory system and the hippocampus, and some species also

retain the vomeronasal system (Bhatnagar & Meisami, 1998). At present, the only explanation

608   offered for this phylogenetic distribution of limbic structures, i.e., the hippocampus and the main

olfactory system, is the olfactory spatial hypothesis (Jacobs, 2022).

610   Because of the deep history and broad taxonomic breadth of chemosensory cognition, there

are many parallels in insects and mammals in olfactory structure and function, as already

612   discussed (Ache & Young, 2005). The loss of directional olfaction in cetaceans may also have a

parallel in insects, specifically in the secondarily aquatic water boatmen and water striders

614   (Order Hemiptera). Just as cetaceans have successfully invaded the water with new sensorimotor

adaptations, these insects have also replaced the use of olfactory signals. Instead, water striders

616   communicate using 'ripple signals' – tactile inputs from the seismic movements of the water

surface generated by an individual or its conspecifics, i.e., mates and competitors (Han &

618   Jablonski, 2019; Wilcox, 2016). In the insect brain, the multi-sensory associative structure is the

mushroom body. Because of its major inputs from the olfactory input center (the antennal lobe), the mushroom body was long assumed to be a purely olfactory structure. This was challenged by data from water striders, which have a robust mushroom body but vestigial antennal lobes (Strausfeld et al., 2009). This is similar to the history of interpretations of the mammalian hippocampus. Before its role in spatial orientation was discovered (O'Keefe & Nadel, 1978) , the mammalian hippocampus was also considered to be only a 'nose brain' (rhinencephalon), for the same reason (Silveira-Moriyama et al., 2016).

Thus, there are parallels between echolocating cetaceans and the ripple-signaling water striders. Both groups have reduced or absent olfactory systems. Yet in the dolphin, a multi-sensory associative center, e.g., the entorhinal cortex, is not reduced in size (Breathnach & Goldby, 1954; Marino, Connor, Fordyce, Herman, Hof, Lefebvre, Lusseau, McCowan, et al., 2007). Likewise in water striders, there is a loss of the olfactory structure, the antennal lobe, with no concomitant reduction in the mushroom body (Strausfeld et al., 2009).

The study of highly specialized 'champion species' have often led to the discovery of new principles of brain and behavior . As in the 'cognitive fossil' of nasal respiration modulating human memory (Jacobs, 2022), the organization of cognition in dolphins and water striders might predict the organization of nervous systems in other taxa that have lost directional olfaction. This could shed light on questions about the function and evolution of multisensory associative centers (e.g., entorhinal cortex or mushroom body) and how they have changed, relative to the ancestral, olfactory state. Terrestrial animals invading the water — evolving into new bodies, with new actions creating new perceptions (e.g., echolocation, ripple signals) in a newly embedded and extended world — could lead to identifying first principles of embodied cognition.

Conclusion

It is manifest that no theory of embodied cognition can be complete without including olfactory cognition, the common denominator of sensorimotor behaviors in living organisms. Yet studies of cognition, by psychologists, philosophers and neuroscientists, have largely overlooked the importance of this sensory modality (Barwich, 2019; Jacobs, 2022; McGann, 2017; Shepherd, 2004, 2016).

The PROUST hypothesis seeks to redress this oversight by highlighting the embodiment of the sense of smell. Far from being an old and eccentric artifact of our evolutionary history,

650   olfaction may represent the very scaffold of thought, the computation upon which complex

brains evolved (Jacobs, 2012). Recent advances in cognitive neuroscience, demonstrating the

652   importance of nasal respiration for human memory, must put to rest any thought that this is a

niche topic. Hence to understand cognition, we must face the challenge of understanding this

654   complex and understudied sensory modality, in particular directional olfaction (Jacobs, 2012,

2022). By embracing our olfactory minds, perhaps a whole new PROUSTian world will appear,

656   crossing time, space and evolutionary history.

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