On the Evolution of the Human Self: A Data-Driven Review and Reconsideration

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Abstract

We revisit the thesis we first offered in 1997, namely, that the human capacity called "the self" is the product of evolutionary pressures. A review of the literature accumulated in the 20 years prompted three changes to the original thesis. First, we expanded our 1997 conception of the self. We argue that the self consists of a multiplicity of cognitions, each of which may reflect the action of a different neural system. Second, we revised the timeline for the evolution of the human self. At least some components of the human self were present in hominids earlier than the 100,000 years-old date that we speculated served as the oldest-age boundary for the emergence of the self. Third, we supplemented the evidentiary basis by relying on advances in brain structure, brain function, and the genetic underpinnings of the brain. In comparison to the state of knowledge in 1997, there is more reason to assert in 2017 that humans have the capacity to experience a self because this trait was selected via evolution.

Keywords: self, self-concept, evolution

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Beginning late in the 20th century, we published a series of works (Sedikides & Skowronski, 1997, 2000, 2003; Sedikides, Skowronski, & Gaertner, 2004; Sedikides, Skowronski, & Dunbar, 2006; Skowronski & Sedikides, 1999, 2007) in which we argued that the human capacity called "the self" is the product of evolution. This core assertion remains unchanged. However, progress has been made on many fronts in the 20 years since we published our first treatise and in the 11 years since we published our last one. Here, we review the literature and update our thinking accordingly.

A Look Ahead: The Roadmap to the Article

Our updating proceeds along several pathways. The first concerns the nature of the self. We argue that our original conception of the self was overly restrictive. In our original work, we focused on the human ability to engage in symbolic thought about the self (which we termed the *symbolic self*). We continue to assert that the ability to engage in symbolic thought about the self is a hallmark of the human self. However, recent scholarship has induced us to think about the self in terms of a wider range of knowledge, capacities, and experiences. Reflecting this change, in the opening section of this article, we provide an overview of some of the additional knowledge, capacities, and experiences that we now think contribute to an individual's "sense of self."

In the second section of the article, we revisit the notion that the self is evolutionarily functional. It is easy to tell stories about the supposed functionality of a given human characteristic, but theorists can run the risk of not backing their speculation with sufficient evidence. We try to avoid this risk by first discussing evidence suggesting that possession of a well-regulated self is indeed a functional human trait in that it facilitates adaptive behavior (broadly defined). However, adaptiveness should also be reflected in physical manifestations. That is, one ought to be able to observe physical attributes (in brain anatomy, in the human genome, in the processes by which genes regulate physiology) that correspond to the selection of a well-functioning self in the human species. In pursuit of this latter idea, we

consider some of the self-related adaptations that characterize the human species from the perspectives of (1) human physical anthropology and (2) cross-species comparisons of animal brains and bodies to human brains and bodies.

In the third main section of the article, we turn to cross-species comparisons to examine three domains of cognition as they relate to the self. One of these is the capacity for self-recognition. Although we treated this capacity in our original articles (labeling it the *objectified self*), fascinating research has emerged that warrants consideration. A second domain of self-relevant cognition that was untreated by our earlier work is sensitivity to time – the ability to remember when something happened. Recent evidences suggests that sensitivity to time (e.g., via episodic memories) is one of the constellation of abilities that contributes to the experience of self. We discuss this ability in humans and in a cross-species context. The third self-ability, also one that we omitted in our earlier work, is the sense of agency: the inference that "I did this." We elaborate on this ability in terms of both its contribution to human functionality and in its cross-species context.

In the fourth and final main section of the article, we review the emergence of the self on the basis of recent evidence about the timeline of human evolution. We now revise our timeline for human evolution, proposing that human-like species have existed for much longer and in much more varied circumstances than originally proposed. The human self may not have emerged with rapidity (as is often assumed by those who cite the "explosion" in indicators of human artistic expression dating approximately 50,000 years ago), but instead may have had ample time to emerge gradually in hominid species. We review some of the evidence (e.g., from archaeological artifacts) that point to the possibility that the self may have an even older origin than we suggested in our earlier works.

We conclude by asserting that, even though we may have had a few details wrong, in the years since our original thesis was published, that thesis has been increasingly supported. That is, new evidence continues to fit with the assertion that the self has evolved due to

natural selection. None of the evidentiary sources is by itself conclusive, but their convergence across domains has become increasingly persuasive.

Just What Is This "Self," Anyway?

Our original article (Sedikides & Skowronski, 1997) addressed the evolutionary emergence of the *symbolic self*. Grounded in abstract self-knowledge, the symbolic self constitutes knowledge that can be represented and reported linguistically (e.g., "I was born in Chicago"). We continue to assert that this form of knowledge plays a key role in the human self and helps to distinguish the human from the non-human self. However, with the hindsight afforded by 20 years of empirical progress and theoretical progress, we realize that our focus on the symbolic self was somewhat narrow.

Self-knowledge can take on multiple forms. Cautioning that their list is not inclusive, Klein and Lax (2010) noted seven of them.

1. Episodic memories of one's life events.

2. Semantic summary representations of one's personality traits.

3. Semantic knowledge of facts about one's life.

4. An experience of continuity through time: The ''I'' experienced now is connected to the ''I'' experienced at previous points.

5. A sense of personal agency and ownership: The belief or experience that ''I'' (agency) am the cause of ''my own'' (ownership) thoughts and actions.

6. The ability to self-reflect: Forming meta-representations where the agent is the self and where the agent makes inferences on the basis of those representations.

7. The physical self: Represent and recognizing (e.g., in mirrors, photographs) one's body.

Of these, only two (#2 and #3) reflect the self-knowledge that we emphasized in our discussion of the symbolic self (Sedikides & Skowronski, 1997). Although the other multiple forms of self-cognitions described by Klein and Lax (2010) may at some point be linked to semantic knowledge, they also have origins in elements that go beyond it. This is not to say

that semantic knowledge is unimportant to the human self. Rather, we now suggest that semantic knowledge is one type of knowledge – among multiple cognitive contributors – to the human self. Klein (2010, p. 172) summarized this "multiplicity of self" view as follows: "there is no single, unified 'I' to be found. Rather, I argue 'the' self may best be construed as a set of interrelated, functionally independent systems."

We are inclined towards Klein's multiplicity view, in part, because of the evidence that researchers of human consciousness and the brain have generated (Damasio, 2010; Edelman, 2006). One relevant conclusion is that the evolution of the primate brain involved architecture that allowed the brain to move beyond its primary role as a processor of information. We argue that, during human evolution, brain architecture evolved in a manner that allowed the brain to be a sensory organ that could monitor its own state. Edelman (2006, p. 27) referred to this architecture as reflecting the evolution of "re-entrant connections" that form processing loops. There are areas of the brain where processing loops, many of which are primarily linked to different kinds of information, make contact with each other. Damasio (2010) described this architecture using the metaphor of hubs on an airline map. These hubs resemble major airports (O'Hare, Atlanta) that receive flights from many geographical areas and send them back to those areas. Damasio calls these hubs in the brain convergence-divergence regions, and evidence suggests that such regions play a key role in organizing the experience of self.

Crucially, these convergence-divergence areas link input that originates from various sensory systems and brain regions. Examples include input from evolutionarily older brain regions, such as the basal forebrain, thalamus, and brain stem, as well as from many higher-order brain regions. We speculate that the conscious experience of self, then, emerges from the processing loops within regions of the brain and from reciprocal interactions among these regions. This is why Klein's (2010) multiplicity of self view is relevant: The architecture of the brain similarly suggests that the experience of self incorporates a great deal of seemingly

disparate input, ranging from semantic knowledge to a sense of agency over actions to self-recognition.

In our prior works (Sedikides & Skowronski, 1997, 2003; Sedikides et al., 2006), we emphasized how the human experience of self would be affected by semantically represented self-knowledge. However, we did not consider in depth how such knowledge would *add* to the experience of self that might be present in non-human animals (e.g., via the *objectified self*). As a consequence, in emphasizing the symbolic self, we did not sufficiently cover elements of self that may have derived from the non-hominid evolution. Indeed, the view of self as a multiplicity presumes that the human experience of self might not be entirely unique from the self experienced by non-human species. This possibility is supported by the observation that the neural architecture of non-human primate brains exhibits some patterns of re-entrant connectivity that resemble those of the human brains. Hence, though primates may not experience a self identical to the human one (because their brain architecture may not allow the representation of the same highly sophisticated knowledge), the similar patterns of re-entrant connectivity in primate and human brains suggests that primates manifest elements of self that are similar to those exhibited by humans. An example of this similarity is behaviorally exemplified by the mirror recognition task: Chimpanzees react to their mirror image as if they are seeing *themselves* rather than a conspecific (Gallup, 1970).

Revisiting the Evolutionary Perspective on the Self

The possibility that elements of the self are widely shared across various organisms may appear more plausible when it is considered in evolutionary context. An evolutionary perspective on the characteristics of a target organism reflects several assumptions: (1) some of an organism's characteristics are rooted in genetics; (2) these genetically-influenced characteristics will spontaneously vary across organisms in a population; (3) some characteristics are a better fit to an organism's environment than are others; (4) those individuals who possess the advantageous characteristics will be especially successful in the organism's environment, which will cause the organism to be particularly successful in

reproductive activities; (5) reproductive success will lead to a subsequent species increase in the extent to which the advantageous characteristics occur in the population; and (6) this shift in characteristics will be accompanied by continuing variability among individuals in the population (such variability is a preconditions for continuing evolution).

These ideas have been commonly applied to understanding the physical characteristics of an organism (e.g., bacterial resistance to antibiotics). However, they can also be applied to understanding the psychological characteristics of an organism. Specifically, in regards to the self, we argue that: (1) at least some part of the human experience of self is rooted in genetics; (2) in ancestral human populations, there were individual differences across individuals in their capacity to evolve a self; (3) those individuals who were better able to evolve a self were a more optimal fit to their environment than those who did not; (4) those individuals who evolved a self were especially successful in their environment, which caused them to be particularly successful in reproductive activities, (5) reproductive success led to a subsequent increase in the species in terms of individuals' tendency to manifest a self; (6) this shift in the population mean was accompanied by continuing variability in the capacity to evolve a self among individuals in the population.

The Functionality Argument

We rely on several lines of scholarship to support the idea that the self was evolutionarily selected for in humans. One line concerns the functionality of the self. As would be expected from an evolutionary standpoint, in human populations there is variability among individuals in terms of their ability to experience a self. Moreover, humans who have a well-formed self do better than those who do not. For example, the ability to experience a self may be diminished in persons with schizophrenic disorder (Cicero, Martin, Becker, & Kerns, 2016) and persons with autistic spectrum disorder (Lind, 2010; Lyons & Fitzgerald, 2013; for a review, see Molnar-Szakacs & Uddin, 2016). Clearly, these individuals do not function as well as those whose self system is relatively intact.

However, we also urge caution when making the functionality argument. Although functionality is consistent with an evolutionary perspective, it does not constitute sufficient evidence for it. A trait can be functional in a given environment, but can still be solely derived from experience (e.g., pathogen exposure). Moreover, even when rooted in natural selection, trait functionality can shift across the evolutionary time scale. A trait may have initially evolved in response to a given set of environmental selection pressures, but, as time progresses, selection of the trait might be governed by a set of environmental pressures that are entirely different from the ones that were originally responsible for its selection.

Equally relevant is the realization that the presence of a biologically-influenced trait in a species does not imply that the trait is (or ever was) evolutionarily adaptive. Sometimes, traits of a species are simply side effects that emerge from the process of selection, but they are not themselves a focus of those selection pressures. The presence of nipples in male humans is an example. Nipples exist because they are part of the basic mammalian body plan, but to our knowledge their presence is not selected for in males. In biological (and prosaic) terms, it is likely easy to produce a male human by taking the female body plan and tweaking it a bit to produce a male. Though the male nipples seem to serve no function, there is no evolutionary pressure to remove them, and so they remain. Similar reasoning may apply to the presence of the human self. If one collects enough neurons, if the neurons are of the correct type, and if the neurons are interconnected in the right way, then the sense of self may spontaneously emerge from the resulting system. Evolution may have selected for the number, type, and connection patterns of the neurons, not for the sense of self produced from these neurons. Thus, even if humans can be shown to have a biologically-influenced sense of self that enhances functioning, it may not be true that evolution specifically selected for this trait.

Brains, Genes, and the Self

It is also the case, though, that, if evolution worked to shape the brain for enhancing its ability to experience the self and to use this experience when thinking about the world, the

traces of that selection must be reflected in the human physical system. These traces should be left in the human genome and in the products of that genome, such as the human brain.

When addressing traits that leave physical traces of change in a species (e.g., bipedalism), it ought to be possible to link changes in the genome and changes in the brain to the altered trait. However, given that the focus of our inquiry is the emergence of a human-like self, which leaves no direct products in an individual, the task becomes challenging. A potential route to our inquiry is to search for evidence among modern humans of a distorted or non-functional self, and then to examine the brains or genomes of these individuals for the physical correlates of the disorders. One could subsequently link these discoveries to possible changes in the human genome across time. This task is complicated enough, but may be especially daunting because of the multiple systems that contribute to the modern sense of self in humans. Thus, one would need to search not just for a single change, but for multiple sets of changes likely to correspond to alterations in each self aspect. Although these paths to knowledge might appear at first glance as belonging to the domain of science fiction, scholars have taken preliminary steps in that direction.

One source of evidence pertaining to the different kinds of knowledge that contribute to the self originates in anthropology and comparative biology. Though the brain tissue of the dead decomposes quickly, evidence about changes in the brain can derive from examination of the braincases of the long dead, as the brain leaves traces of organization on the inside of the skull. One can also acquire information about human brain evolution by comparing the brains of humans and non-human primates. This latter method needs to be exercised with caution: The brains of non-human primates have likely themselves changed across time via evolution. However, one can still acquire a sense of how the human brain may have changed by comparing the structure of human brains to the structure of various primate species in the context of the evolutionary timeline.

The conclusions from anthropological and comparative biology sources converge (Sherwood, Subiaul, & Zawidzki, 2008). The modern human mind may be conceived as a

mosaic of traits inherited from a common ancestry with our close relatives. That is, the human brain is generally organized in a fashion similar to that of primate species, and the closer to humans the species become, the more similar the organization. For example, the left hemisphere dominance in humans is commonly associated with the proclivity for language. However, the *planum temporale*, a surface feature of the cerebral cortex in the region of Wernicke's area, displays left hemisphere dominance in humans, bonobos, chimpanzees, gorillas, and orangutans.

Unique among humans, though, these ancestral traits have been likely supplemented by evolutionary specializations within particular domains (e.g., language). These modern human-specific cognitive adaptations and linguistic adaptations appear to be correlated with enlargement of the neocortex and related structures. Moreover, several anatomical and molecular changes have occurred that might reflect the high metabolic demand and enhanced synaptic plasticity of modern human brains. Accompanying these trends is that some higher-order unimodal and multimodal cortical areas have grown disproportionately relative to primary cortical areas. For example, when comparing human brains with the brains of other higher order primates, Wey et al. (2014) observed that only humans have multi-region lateralized networks, which provide fronto-parietal connectivity. According to these authors, this pattern of within-hemisphere connectivity distinguishes human brains from the brains of nonhuman primates. These observations echo and emphasize the Damasio (2010) convergence/divergence areas mentioned earlier in this article.

In theory, evidence about changes in the human genome can come directly from DNA comparisons of the genes of modern humans with both the genes of deceased archaic humans and deceased non-*Homo sapiens* species members. This is not pie-in the sky thinking. In recent years, researchers have reportedly produced a complete genomic sequence of a Neanderthal woman (Prufer et al., 2015). They concluded that there is only a small list of simple DNA sequence changes distinguishing modern humans from Neanderthals. Many of these differences are linked to the biology of the neocortex. This finding pertains to other

areas of research that have implications for the human self. For example, as we note later in this article, the genetics of the neocortex may be related to the evolution of various psychopathologies, many of which include alterations in the sense of self.

This is indeed a highly active area of research (Northoff, 2014; Zhao, Luo, Li, & Kendrick, 2013). Four of the most studied disorders involving self distortions are schizophrenia, autism spectrum disorder, major depression, and borderline personality disorder. Zhao et al. (2013; see also Northoff, 2014) suggested that distortions of the sense of self in psychological disorders are associated with alterations in the brain's cortical midline system (including the perigenual anterior cingulate, inferior frontal gyrus, and insula) and the mirror neuron system (including the fronto-parietal region [precentral gyrus, precuneus, supramarginal gyrus, inferior parietal lobule] as well as the limbic system [anterior insula and anterior mesial frontal cortex]). This last putative association fits with the observation that the insula is activated during self-reflection (Modinos, Ormel, & Aleman, 2009).

Zhao et al. (2013) also suggested that heightened inter-hemispheric connectivity is related to alterations in the sense of self. In a convergent manner, Wey et al. (2014) concluded that such within-hemisphere connectivity serves to distinguish human brains from the brains of other higher primates. It is this kind of connectivity that Damasio (2010) emphasized in his theorizing about the genesis of the human ability to engage in self-reflective thought.

Research linking genetics to brain structure and brain function in individuals with various psychopathologies is underway. For example, Won et al. (2016) explored activity in regulatory regions of genes on the human genome that may be related to schizophrenia. These regions work like rheostats, increasing or decreasing a target gene's activities. Such rheostat-like loci may regulate genes known to be crucial to brain development, and are very active early in brain development. It follows that disorders such as schizophrenia (and, by extension, the self-distortions that are symptomatic of schizophrenia) may have a basis in the genetics that control brain development.

Researchers also have compared the genetics of non-human primate species to the human genome in order to gain insight into brain alterations that may have occurred during evolution (Reilly et al., 2015). Relevant studies have examined corticogenesis (the process in which the cortex of the brain is created during neurodevelopment), and again have focused on those gene regions that regulate the expression of genes. Consistent with an evolutionary perspective, Reilly et al. (2015) concluded that many human lineage changes reflect alterations in gene regulation. That is, these alterations operate within older regulatory mechanisms and evolutionary processes essential for building the mammalian cortex, but they appear in modified form in humans. Saphire-Bernstein, Way, Kim, Sherman, and Taylor (2011) have forged a link among elements of the self, the brain, and genetics. They reported that varying genetic forms of the oxytocin receptor are associated with varying levels of self-esteem and depression.

Clearly, there is a long way to go from integrating the information needed to understand whether, and how, evolution may have produced variations that led to the human brain. Nevertheless, this research theme has bloomed since our initial work (Sedikides & Skowronski, 1997). As illustrated by our all-too-brief review, early returns are encouraging for establishing the anatomical and genetic underpinnings of the self. This biological evidence is not definitive to the thesis that evolutionary pressures selected for a self in humans, as noted earlier. However, the evidence that researchers generate about genes and the brain is a prerequisite for concluding that evolution has influenced the emergence of the human self, and so such evidence supports the evolutionary thesis.

Cross-Species Behavioral and Cognitive Evidence

One other key evidentiary source linking the self to evolution lies in cross-species comparisons of behavioral characteristics and cognitive characteristics (Terrace & Metcalfe, 2005). This source is especially relevant, because evolution does not create something from nothing – it merely selects from what is already available. According to this principle, if a biological basis underlies the human capacity to experience a self, then that same

biologically-based capacity (or precursors of, or variants of, that capacity) ought to be present in other species. Moreover, if the human experience of self is produced by a multiplicity of components, some of which likely have a biological basis, then these components may have emerged in evolution in different species and at different times. Hence, different species may each display only one, or a few, of the multiplicity of human self-components described by Klein and Lax (2010). As a reminder, the Klein and Lax list is not exhaustive; self-related cognitions may extend beyond it.

Self-Recognition

Cross-species studies continue to lend credence to the view that components of the self are biologically grounded and were subject to evolution. Non-human species exhibit behaviors indicating that these species have at least some capabilities (e.g., an objectified self) that resemble the components of the human self (Bekoff, 2002). From an evolutionary standpoint, these self components ought to be observed in species that are, in genetic terms, highly related to the human species (e.g., bonobos, chimpanzees). Indeed, findings we reviewed in 1997 were consistent with his idea. For example, chimpanzees are capable of noting that an image in the mirror was their own image (Gallup, 1970), and this is a capacity that is shared among other great apes (bonobos, gorillas, orangutans). Recent evidence, though tenuous, suggests that this self-recognition capacity extends to primates who are not as similar to humans as are the great apes, such as rhesus monkeys (Chang, Fang, Zhang, Poo, & Gong, 2015; Rajala, Reininger, Lancaster, & Populin, 2010).

Further, mirror self-recognition even appears in animals that are less genetically closely related to humans than are other primates. Non-primate animals who are thought to pass this test include dolphins (Marten & Psarakos, 1994; Reiss & Marino, 2001), elephants (Plotnik, de Waal, & Reiss, 2006), orcas (Delfour & Marten, 2001), and the Eurasian magpie (Prior, Schwarz, & Güntürkün, 2008). One reason why evidence for the presence of this self-component might occur in animals that are not part of the primate line is that evolution often solves similar problems in similar ways. Thus, if a non-human species occupies an

environmental niche similar to the niche occupied by the species in the evolutionary line that led to the human species, then non-human species might be expected to exhibit characteristics similar to the human species. For example, the evolutionary line that led to humans has included relatively large-brained individuals whose food sources were widely dispersed in time and space. Elephants pass the mirror test, and are a relatively large-brained species whose food sources are widely dispersed in space and time. Similarly, though they live in an aquatic environment, dolphins manifest self-recognition, and they too are large-brained species whose food supplies are often widely dispersed.

In this regard, Hills and Butterfill (2015) proposed behavioral and biological commonalities between external foraging in space and internal foraging over environments specified by cognitive representations, and they explored the implications of these commonalities for understanding the origins of the self. According to these authors, the cognitive systems that use embodied prospective foraging require a primitive sense of self, which is needed to distinguish actual from simulated action. This perspective, which echoes some of the arguments offered in the original Sedikides and Skowronski (1997) article, again implies that the emergence of some elements of the capacity for self-thought, in evolutionary terms, are relatively old. This implication is backed by the fact that some of the components of self-thought are shared across widely divergent species.

However, in addition to problems posed by food procurement, species that exhibit self-recognition also maintain a social habit. Part of the evolutionary benefit of having self-recognition capacities may be to enhance one's functionality in a highly social context. Indeed, we regard this social component as crucial to the evolution of a complex, multifaceted self. This certainly fits with the emerging view of primates in general: It has been suggested that primate brains are "built to be social" (De Waal & Ferrari, 2012). However, the more general point is that the possession of a self (as indexed in self-recognition ability) may fit the biological concept of convergent evolution. Via evolution, and in particular the capacity for self, nature may have found a way to tune big-brained social

organisms so that they be well suited to survival in environments which present difficulties in food procurement.

Sensitivity to Time

Similar evidence continues to accumulate in other domains. For example, one of the facets of the self highlighted by Klein and Lax (2010) is the ability for mental time travel. Tulving (1985) suggested that such an ability reflects autonoetic consciousness. Autonoetic consciousness refers to mentally placing the self in the past, in the future, or in counterfactual situations, and thus being able to examine one's thoughts. Klein and Lax (2010) propose that this kind of consciousness is a member of the self multiplex.

Tulving (1985) further suggested that episodic memory is a correlate of the presence of autonoetic consciousness (see also Vandekerckhove, Bulnes, & Panksepp, 2014). Episodic memories involve subjective event re-experiencing (including images, sights, smells, and feelings), as well as the knowledge that these events occurred in an earlier time. In particular, Tulving (p. 581) wrote that autonoetic consciousness is:

> correlated with episodic memory. It is necessary for the remembering of personally experienced events. When a person remembers such an event, he is aware of the event as a veridical part of his own past existence. It is autonoetic consciousness that confers the special phenomenal flavour to the remembering of past events, the flavour that distinguishes remembering from other kinds of awareness, such as those characterizing perceiving, thinking, imagining, or dreaming.

Other researchers have taken these ideas farther. Lou et al. (2004), for example, reasoned that autonoetic consciousness emerges via retrieval of episodic memories, and that such retrieval affects conscious self-representation, which is mandatory to the perception of a coherent and meaningful life. This capability would seem to be quite functional. Without the ability to recall experiences and reflect on them, humans would be stuck in a state of constant awakening, without a past and therefore unable to prepare for the future.

Given its link to autonoetic consciousness, episodic memory – the "what-where-when" re-experiencing form of memory - was thought to be unique to humans (Tulving, 2005). Recent evidence, though hotly contested, has challenged this assumption (Cheng, Werning, & Suddendorf, 2015; Corballis, 2013; Klein, 2013, 2014). Much of the debate about the presence of episodic memories in non-human species lies in data showing that animals can act as if they remember time (Chang et al., 2015). As would be expected from an evolutionary perspective, such a tendency can be seen in species that are, in evolutionary terms, relatively close to humans. These include non-human primates, such as chimpanzees and bonobos (Martin-Ordas, Haun, Colmenares, & Call, 2010), baboons (Noser & Byrne, 2015), and rhesus monkeys (Hoffman, Beran, & Washburn, 2009). The research conducted by Martin-Ordas et al. (2010) is illustrative. In one study, preferred perishable food (frozen juice) and less preferred but non-perishable food (grape) were hidden from primate subjects. Primates could choose one of the foods either after 5 minutes or 1 hour. The frozen juice was still available after 5 minutes, but melted after 1 hour, becoming unobtainable. Apes chose the frozen juice to a significantly greater extent after 5 minutes and the grape after 1 hour, suggesting that they could remember how the passage of time affected the results of their foraging episodes.

Similar findings have been reported in regards to non-primate species, such as birds (pigeons, black-capped chickadees, magpies) and mammals (rats, meadow voles, Yucatan minipigs, dogs). The research conducted by Clayton and Dickinson (1998; see also Dally et al., 2006) is illustrative. One set of studies showed that scrub jays (*Aphelocoma coerulescens*) acted as if they remembered when they cached food. Jays were allowed to search for highly perishable 'wax worms' and less perishable peanuts that they had previously cached. The birds learned to avoid searching for the wax worms after long delays between cache and search, suggesting that they 'remembered' the delay.

Given these findings, that animal behavior can be sensitive to time is not in much doubt. At issue is whether an animals' ability to use time reflects the presence of an episodic

memory system and/or autonoetic consciousness. Some (Corballis, 2013) are willing to make such a leap. Others are not. Klein (2014), for example, argues that, without the presence of independent evidence for autonoetic consciousness in animals, one cannot attribute episodic memory to them, even if their behaviors may indicate some level of sensitivity to time. In this view, it is the subjective experience that occurs during retrieval that constitutes an essential property of episodic memory. Chang et al. (2015) separates autonoetic consciousness from episodic memory (as does Klein, 2016), suggesting that autonoetic consciousness may require cognitive components that go beyond an episodic memory system, but that episodic memory does not require autonoetic consciousness.

The reliance on subjective experience as an indicator of episodic memory in humans complicates data interpretation: It is controversial to consider non-human species' sensitivity to time as indicative of the ability to experience episodic memory. Neuroimaging and neuroanatomy studies provide one resolution to this dilemma (Eichenbaum, 2013; Templer & Hampton, 2013). For example, in comparison to non-episodic memories, episodic memories in humans are particularly dependent on the integrity of the hippocampus and related structures. Some studies have examined whether non-human animals have episodic memories by testing if memories of non-human animals are similarly dependent on this hippocampal system. This seems to be the case. For example, after encountering a sequence of five odors, the behavior of rats with hippocampal lesions was inconsistent with the idea that they could recall odor order. This insensitivity to order occurred despite the rats acting as if each odor was familiar (Eichenbaum, 2013). A similar conclusion has been reached from hippocampal system lesion studies conducted in monkeys. For example, monkeys with fornix lesions, which disrupt the hippocampal system, were unable to make accurate recency judgments (Charles, Gaffan, & Buckley, 2004).

Studies that use electrophysiological recordings during task performance have arrived at similar conclusions. For example, the magnitude of changes in patterns of rat hippocampal ensembles during an odor order test predicts memory performance (Manns, Howard, &

Eichenbaum, 2007). Indeed, it has been suggested that specific neuronal ensembles or pathways are linked to the encoding of specific memories and perhaps the passage of time. These ensembles or pathways include the lateral prefrontal cortex (PFC) and medial PFC. Evidence for this timekeeping function has been obtained in monkeys (Ninokura, Mushiake, & Tanji, 2004) and in rats (DeVito & Eichenbaum, 2011). According to Templer and Hampton (2013, p. 802), the non-human species studies collectively "provide strong evidence for a homologous EM (episodic memory) function of the hippocampus among humans, monkeys, and rodents."

Judging from the current state of the literature, we agree that the evidence favors the view of non-human species having an episodic-like memory subsystem. This subsystem is sensitive to time. However, we surmise that this time-sensitive memory system alone is not sufficient to infer the presence of a sophisticated autonoetic self-referential thought system that can engage in the kinds of mental time travel discussed by Tulving (1985). Knowledge of the temporal characteristics of an event does not, in and of itself, produce the event reliving experience and ownership experience that characterize autonoetic consciousness. Such experiences would require the re-entrant connection patterns and convergence zones described by the neuroanatomists, with those interconnection patterns being prominent in primates (and especially in humans).

Nevertheless, the widespread presence of a time-sensitive episodic memory-like system in non-human species fits with our general thesis: It is plausible that the human self was formed as a result of evolutionary pressures. Evolution often co-opts and reshapes traits in ancestral species and uses them in later-evolving species, and the time sensitive episodic-like memory in non-human animals fits this view. The "airline route" hub-and-spoke neural architecture of the human brain may have evolved so that one of the contributors to the sense of self was this time sensitive, episodic-like memory.

Sense of Agency

As noted by Klein and Lax (2010), one indicator of the self is a sense of agency over one's actions. The construct refers to the subjective awareness that one is initiating, executing, and controlling one's own volitional actions in the world. This sense of agency is impaired in individuals who have a disrupted self, such as those with schizophrenic disorder (Asai, Sugimori, & Tanno, 2008) or autistic disorder (Molnar-Szakacs & Uddin, 2016).

An argument for the evolution of the self would be supported, if this sense of agency was shared in other species. Indeed, this seems to be the case. Research by Kaneko and Tomonaga (2011) suggests that chimpanzees also have the capacity to experience agency (for a review, see Moore, 2016). In one study, chimpanzees were presented with two cursors on a computer display. One cursor was manipulated by a chimpanzee using a trackball, whereas the other cursor displayed motion that had been produced previously by the same chimpanzee. Chimpanzees successfully identified which cursor they were able to control. Additional studies showed that at least one chimpanzee could monitor the movement that was theirs in both the temporal dimension and the spatial dimension. Such understanding of agency may be shared by rhesus monkeys (Couchman, 2012, 2015) and may also extend beyond the primate line to dolphins (Herman, 2012).

We speculate that this sense of agency may (at least partially) be rooted in the mirror neuron system. Although this system has been implicated in one's ability to mimic others, it also seems to be involved in the monitoring of self-movements, which may contribute to the sense of agency (Maeda, Ishida, Nakajima, Inase, & Murata, 2015). Interestingly, the mirror neuron system may, in evolutionary terms, be relatively old, given that it is shared with other species, such as birds (Prather & Mooney, 2015). This may represent another example of how evolution co-opts existing traits. The mirror neuron system, which likely evolved to facilitate social learning, may have been shaped by evolutionary pressure to be a contributor to an individual's sense of self.

Revising the Timeline for the Emergence of the Human Self

The principles of evolution suggest that the human self should not have evolved all at once, but should have emerged gradually across long stretches of time as the biological makeup of the species was shaped by the environment. We proposed that the human species evolved in a challenging physical environment in which it was difficult to find/capture food or to find protection against predation (Sedikides & Skowronski, 1997). One species-wide response to these environmental pressures may have been the evolution of a social habit and a complex self. We argued that functioning in a social world can be optimized by the ability to think abstractly about oneself and about one's place in the group. In the context of our timeline examination, we also explored the available physical evidence about brain size and differentiation, and we attempted to link those changes across time to the emergence of the human capacity for self. The human self seemed to emerge as the cortex enlarged and differentiated, suggesting that the capacity to think about the self in complex ways and to use language was linked to the emergence of the self.

Accordingly, we explored the hypothesized timeline of hominid evolution to ascertain that the supposed environmental pressures fit the factual knowledge that existed about our ancestral environments and hominid evolution (they did). We also searched for physical evidence (e.g., self-referential art, personal adornment, burial of the dead) in the context of that timeline, which might be construed as expression of the self-concept. Our review led us to suggest that the human capacity for self might have been evident as early as 100,000 years ago (late Pleistocene epoch). Somewhat controversial was the accompanying suggestion that a human-like self may have predated *Homo sapiens* and have emerged in an earlier species, such as *Homo erectus.* However, because of their large brain capacities, it is possible that species who predated *Homo erectus,* such as *Homo heidelbergensis* and/or *Homo antessessor* (both 1125–1450 cm^3) might also possess at least some of the elements of the modern self. Nonetheless, regardless of the exact hominid species responsible, physical traces

indicated that a human-like self may have existed outside of the *Homo sapiens* species (see also Sedikides & Skowronski, 2003; Sedikides et al., 2006).

This proposal deviated from standard views of the self's emergence, which placed that date at around 50,000 years ago—a date at which evidence (e.g., artistic figurines, bow-and-arrow technology, personal ornamentation, ritualized burials) seemed abundant (Coolidge & Wynn, 2016; Leary & Buttermore, 2003). Contradicting this view, we regarded the 100,000 years-ago dating of the emergence of a human-like self as justifiable because of the convergence of relevant environmental pressures. Moreover, brain cast data showed that the brains of some non-*Homo sapiens* species members were relatively large (*Homo heidelbergensis* and/or *Homo antessessor* range from 1125–1450 cm^3) and differentiated. These were hunting species (as opposed to merely scavenging ones). Furthermore, these species lived in stable and interdependent small groups ("bands") that were parts of larger societies and represented a form of societal structure, as indexed by the repeated use of home base areas. In our view, these factors pointed to a relatively early emergence of a human-like self in hominid species other than *Homo sapiens*.

We thought we were being daring in suggesting the emergence of a human-like self as early as 100,000 years ago. At the time we wrote the 1997 article, the evidentiary foundation in support of this assertion was relatively scarce. Since then, accumulating evidence indicates that we were timid in our estimation. For example, some research groups reported that they found beads, likely used for personal adornment, dated to about 100,000 years ago (Henshilwood et al., 2002; Jacobs, Duller, Wintle, & Henshilwoo, 2006). Archaeological sites concerned with the history of artistic expression in the human species are also relevant to the argument (Morriss-Kay, 2010). Evidence of such expression is an indicator that early human species evolved at least the beginnings of a complex self. Recent finds have broken the 100,000 years-ago barrier: Ochre, a color often associated with bodily adornment, was used by hominid species about 164,000 years ago (Marean et al., 2007; McBrearty & Stringer, 2007). Assuming that non-bodily related artistic products also index the beginnings

of a human-like self, that date may be pushed back even further. A carving of the head and torso of a woman attributed to *Homo heidelbergensis* has been dated to at least 250,000 years ago (d'Errico & Nowell, 2000). Evidence of a boost in working memory capacity—necessary for self-regulatory functions—over the last 200,000 years (Coolidge & Wynn, 2016) is also indirectly consistent with the possibility of pushing back the dating of the self's emergence.

In retrospect, we should not be surprised at such discoveries. Evolution often proceeds via the slow emergence of a trait across time. Thus, although evidence points to the presence of a modern-like self by about 50,000 years ago, it makes sense that a less well-formed self, or some of the components of the modern self, would have emerged in earlier times. This is especially probable given that recent discoveries seem to have pushed the emergence of hominid species with relatively modern human-like characteristics to as early as 300,000 years ago (Hublin et al., 2017).

Summing It All Up

Twenty years ago (Sedikides & Skowronski, 1997), we introduced the relatively novel idea that the human sense of self emerged as a function of selection pressures. This assertion remains unchanged.

However, at least three parameters have changed. One of these is our view of the self. In 1997, this view encompassed the human capacity to consider the self symbolically. We now regard the self as reflecting a multiplicity or a conglomeration of conceptually separate sources of knowledge that usually combine in normally functioning humans to produce the sense of self. The second parameter that has changed is our timeline for the emergence of the self. In 1997, we "daringly" placed a date of about 100,000 years ago as the lower boundary for trustworthy evidence indicating that hominid species exhibited some form of a self. We now think that the timeline can be stretched farther into the past. At least some elements of the human self seem to have been around a long while, perhaps even as long as 300,000 years ago. The third parameter that has changed is the evidence. In our 1997 article, we relied on observations of humans, cross-species comparisons of the behavior of animals and humans,

and archaeological reports. We enhanced these sources of evidence, but supplemented them with studies on brain structure, brain function, and the genetic underpinnings of the brain.

Gratifyingly, the new evidence continues to fit with the assertion that the self has evolved due to natural selection. None of the sources of evidence is by itself conclusive. However, the convergence of evidence across domains has become increasingly persuasive across time. Perhaps in another 20 years, when we hopefully revisit this topic, we will be able to argue that research has documented definitively our assertion.

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