Self-Recognition in Animals: Where Do We Stand 50 Years Later? Lessons From Cleaner Wrasse and Other Species

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Claims for mirror self-recognition have been made for numerous species ranging from dolphins and elephants to fish and ants. But based on rigorous, reproducible experimental evidence only some great apes and humans have shown clear, consistent and convincing evidence that they are capable of correctly deciphering mirrored information about themselves. In this article we critique some of the recent claims for self-recognition in other species and summarize some of the cognitive implications of the capacity to become the object of your own attention. Recent neurobiological evidence now appears to validate the connection between self-recognition and self-awareness.

Keywords: mirror self-recognition, species differences, self-awareness, experimental design, theory of mind

It is important to acknowledge at the outset that there is less than complete consensus about the meaning of the term "self-awareness" (see Gallagher, 2011 for different interpretations). For the purposes of this article we define self-awareness as an object rather than a subject, and as such self-awareness in our view is the capacity to become the object of your own attention, in the sense that you can begin to think about yourself and use your experience to make inferences about comparable experiences in others. When an animal is confronted with its reflection in a mirror it has literally become the object of its own attention, but the question is whether it is capable of realizing that its own behavior is the source of the behavior being depicted in a mirror, that is, visual self-recognition.

Most visually capable species initially react to seeing themselves in mirrors as if there were seeing another animal, but even after extended periods of exposure to mirrors seem incapable of correctly deciphering mirrored information about themselves. In this article we critique a number of recent high-profile claims for self-recognition in other species, including a study of cleaner wrasse, a small fish that evolved to remove parasites from other fish, in which the authors conclude that even though cleaner wrasse ostensibly pass the mark test it undermines the cognitive implications of mirror self-recognition as legitimate test of self-awareness (Kohda et al., 2019). Many of these claims fail to take into account the existing literature, lack appropriate experimental procedures and controls, offer less than parsimonious interpretations of the evidence, and are in need of independent replication.

Knowledge of the Literature

The mark test was originally devised to confirm instances of chimpanzees acting as if they realized that their behavior was the source of the behavior depicted in a mirror; that is, once they began to use mirrors to investigate and manip-

ulate features of themselves, also referred to as self-directed behavior (Gallup, 1970). We stress the importance of a thorough knowledge of the findings on mirror-image responses and self-recognition to avoid misinterpreting published reports of animals' reactions to mirrors. For example, because they may not be sufficiently familiar with the literature, in addition to applying marks that can only be seen in the mirror most investigators do not incorporate the use of control marks applied to body parts that can be seen directly, a control procedure introduced by Gallup, Wallnau, and Suarez, (1980; also Suarez & Gallup, 1981). The advantage of such marks is that they can be used to independently assess the animal's interest in the marks, thereby effectively countering the argument that the reason they fail the mark test is because they do not care about the marks on their faces and simply lack the interest or motivation to touch and investigate such marks (see Eglash & Snowdon, 1983).

A frequently offered explanation offered for the lack of mirror self-recognition (MSR) in many species is that gaze aversion prevents them from looking directly at their image in a mirror for enough time to learn to self-recognize (e.g., Hauser, Kralik, Botto-Mahan, Garrett, & Oser, 1995; Nielsen, Suddendorf, & Slaughter, 2006; Ristau, 1992). Again, however, this problem was resolved 30 years ago by Anderson and Roeder (1989) who presented capuchin monkeys with angled mirrors that precluded making eye contact with the image in a mirror. The monkeys showed interest in their reflection in the angled mirrors, but no signs of self-recognition. Two western lowland gorillas, which are notorious for showing gaze aversion, also failed to use their reflection from angled mirrors to investigate foreign marks on their faces, although they avidly attended to comparable marks on their wrist (Shillito, Gallup, & Beck, 1999).

Other investigators take the view that absence of evidence for visual self-recognition does not preclude self-recognition in other modalities, appealing to an auditory or olfactory sense of self (e.g., Bekoff, 2001; Cazzolla Gatti, 2016; Horowitz, 2017). However, Platek, Thomson, and Gallup (2004) demonstrated that the sense of self in humans is used to integrate information about the self from different sensory modalities: priming with one's own odor, and read-

ing or hearing one's own name led to shorter visual self-face identification latencies. While there is evidence for cross-modal integration of social sensory information in a wide range of nonhuman animals (Seyfarth & Cheney, 2009), including dogs (Adachi, Kuwahata, & Fujita, 2007), there is no evidence that they integrate different types of self-related stimuli. Differential responses to odor cues alone, as in studies of dogs, are far removed from spontaneous mirror-guided self-exploration and mirror use to investigate foreign facial marks as seen in great apes and humans. Nonetheless, as an olfactory parallel to the mirror mark test, dogs that sample a container of their own odor which has been tainted with a strange odor fail to show signs of attempting to then investigate their own body odor directly, in stark contrast to the way chimpanzees react when they see strange marks on their faces (Gallup & Anderson, 2018).

Another common methodological mistake that stems from an ignorance of the literature is to give subjects repeated exposure to body marks on themselves and/or other cage mates that leads to habituation to such marks (for an egregious instance see Swartz & Evans, 1991). In chimpanzees, for example, the interest in such marks rapidly wanes once they discover that the marks are inconsequential (Povinelli et al., 1997) and when this happens the mark test is no longer a valid test of mirror self-recognition. The single elephant described as passing the mark test by Plotnik, de Waal, and Reiss (2006) notably failed on two subsequent mark tests, plausibly for this very reason.

Regardless of the species being studied, it is also important to acknowledge relevant previous work. In a recently published claim that a tiny fish (cleaner wrasse) exhibit mirror self-recognition, although they list many articles purporting to show that various fish species cognitively match or outperform vertebrates, despite a voluminous literature on the topic Kohda et al. (2019) cite only two other reports (in their supporting information) of differences in fishes' reactions toward their own reflection versus a live conspecific. Unlike Kohda et al. (2019), however, none of the authors of those studies interpreted the differences in terms of any form of self-recognition.

Using primate examples, we have pointed out researchers should also have sufficient knowledge about their subject species' behavioral rep-

ertoire to avoid misinterpreting what the animals are doing in front of a mirror; in some cases behaviors too often described as evidence of self-recognition are in fact probably either social or abnormal behaviors (see Anderson & Gallup, 2011, 2015). As an example in another species, the claim has been made that manta rays recognize themselves in mirrors based on cephalic lobe and swimming movements not shown in the absence of mirrors (Ari & D'Agostino, 2016), but Stewart, Stevens, Marshall, and Abernathy (2017) counter that such movements are commonly observed instances of social behavior among mantas in the wild.

Both Kohda et al. (2019) and de Waal (2019; de Waal, Dindo, Freeman, & Hall, 2005) argue that certain different behavioral and physiological reactions to a mirror versus a live conspecific are somehow related to self-recognition. de Waal attributes importance to the rapid onset of such differences in capuchin monkeys, but if these are indicative of self-recognition then they should also emerge in response to static photographs of another individual versus self. If no relevant differences occur with still photographs, then movement cues may be the reason for differences toward a live conspecific and a mirror: the reflection perfectly mimics the observer, and monkeys are known to be especially attentive to individuals who imitate their movements (Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005; Paukner, Suomi, Visalberghi, & Ferrari, 2009). Note also that even if behavioral or physiological differences to visual images of self versus other are found, this can be more parsimoniously interpreted as the result of a phenotypic matching process, with no requirement for self-awareness (see, e.g., Hesse, Bakker, Baldauf, & Thünken, 2012).

The Use of Appropriate Experimental Procedures and Controls

Better knowledge of the literature would lead to stronger studies, but many authors continue to allude to and by implication endorse tentative/preliminary claims for self-recognition (e.g., in elephants, cetaceans, and magpies; see, e.g., Baragli, Demuru, Scopa, & Palagi, 2017; Morrison & Reiss, 2018) while declining to acknowledge important experimental/procedural questions about these claims, perhaps to avoid being seen as taking sides. However, it is important to stress that critical evaluation of a claim for self-recognition in any species is not a matter of taking sides or a simple matter of dialogue and debate. Ultimately such claims are a matter of evidence, and to avoid false claims becoming widely accepted as true the evidence must be based on rigorous and appropriate methods (Gallup & Anderson, 2018).

Nowadays investigators often use video recordings to document apparent instances of mirror self-directed behaviors and the results of mark tests. Unfortunately, the content of such recordings often fails to be consistent with the claims being made and depict such ambiguous instances of behavior that they approximate Rorschach inkblots where anyone can see whatever they want to see. Recent examples of unconvincing video clips include manta rays (Ari & D'Agostino, 2016) and horses (Baragli et al., 2017). For video records to be taken seriously as evidence it is essential that they be independently rated by observers who do not know the purpose of the study. Furthermore, authors should be prepared to make all video recordings available to other investigators to examine as well.

Parsimony of Interpretation

An increasing number of articles on MSR include claims for so-called "contingency testing" or "contingency checking." The article that asserts to have demonstrated that cleaner wrasse pass the mark test is a case in point. In the second phase of Kohda et al. (2019) the authors claim that instances of idiosyncratic behavior toward the mirror constitute contingency testing but they fail to provide adequate evidence to support this claim. Unlike with another animal, an animal's interaction with its own image in a mirror is atypical. The reflection never responds independent of the observer, nor does it ever reciprocate in ways that would approximate a normal social exchange. The image in the mirror appears to represent another animal, but it merely mimics the behavior of the observer. Therefore engaging in atypical, idiosyncratic behaviors toward mirrors may simply represent attempts to engage the "other" animal in a normal exchange.

The same applies to instances of apparent mark-directed behavior. Unlike chimpanzees that attempt to touch and investigate strange

colored marks on their faces that can only be seen in mirror, cleaner wrasse have been programmed by their evolutionary history to be preoccupied with removing ectoparasites from themselves and other fish. So it should come as no surprise that when they have been marked they show longer viewing times to marks that resemble ectoparasites on what appears to be another fish that can only be seen in a mirror. The fact that marked fish assume peculiar postures in front of the mirror fails to rise to the level of self-directed behavior because this may simply be a consequence of the fact that the fish have learned that by assuming such postures they can get the image of the other fish in the mirror to move in ways that enable them to see these highly sought after marks more clearly. As is also true of our interpretation of contingency testing, this is a far more parsimonious account of the evidence.

Another possibility is that seeing the image of a cleaner wrasse in the mirror with an ectoparasite on its throat might trigger generalized scraping, similar to contagious yawning, vigilance, or self-scratching in other species, that is, a kind of social facilitation effect. Although Kohda et al. (2019) dismiss this possibility in their supporting information, they do so based on observations of only four fish. Furthermore, it is possible that repeated throat scraping may be influenced by residual irritating side effects of the injections that were used to create those marks. Indeed, as evidence that was the case, the authors acknowledge that occasional scraping of marked body flanks occurred without the mirror present. A combination of visual and tactile (irritation) cues was also the likely reason for misinterpreted instances of head-manipulation by head-implant-prepared rhesus monkeys while they looked in a mirror (Anderson & Gallup, 2011; de Waal, 2019), and by magpies that have been tested for self-recognition using stickers applied to their feathers (see below).

We also find serious design flaws in the cleaner wrasse study. First, it lacks an important control condition. In the original study of mirror self-recognition in chimpanzees Gallup (1970) used the presence or absence of mirror exposure as the independent variable. Two groups of chimpanzees were tested for mirror self-recognition, one with several days of prior mirror exposure and the other group without. Those with previous mirror experience used the mirror

to touch and investigate the marks on their faces as the dependent variable. But chimpanzees who were also marked on their faces but lacked prior mirror exposure, failed to find the marks on their faces during the test trial and acted as if they had been confronted with another unfamiliar chimpanzee.

How would fish without prior exposure to mirrors respond on the mark test? We do not know, because Kohda et al. (2019) did not include this important control condition. If fish that were naïve to mirrors also engaged in throat scraping during the test, the results would invalidate the claims by Kohda et al. (2019) because such fish would not have had the opportunity to learn that their behavior was the source of the behavior being depicted in the mirror. In other words, just like chimpanzees, fish without prior experience with mirrors would not have been able to learn to use a mirror to become the object of their own attention; any instances of throat scraping would therefore likely be another peculiar artifact of their evolved preoccupation with ectoparasites.

Second, on the mark test, fish were first sham-marked and exposed to the mirror (to which they were by now thoroughly habituated), followed by color-marking when the mirror was absent, and then finally color-marked when the mirror was reintroduced. This order of testing inadvertently entails removing and then reinstating the "other" fish in the mirror, likely resulting in a dishabituation effect shown in a resumption of social and other responses, reported previously in fish (e.g., Baenninger & Mattleman, 1973) and in monkeys (Bayart & Anderson, 1985; Eglash & Snowdon, 1983; Gallup & Suarez, 1991; Suarez & Gallup, 1986). In the case of the cleaner wrasse the sudden reappearance of the reflection might be responsible for the generalized increase in activity during this phase. It is also important to realize that the continued occurrence of albeit brief and intermittent instances of social or aggressive behavior directed toward the mirror, for example in rhesus monkeys (Rajala, Reininger, Lancaster, & Populin, 2010), pigtailed macaques (Thompson & Boatright-Horowitz, 1994), capuchins (de Waal et al., 2005), or cleaner wrasse (Kohda et al., 2019) undermines apparent instances of mirror self-recognition.

We agree with Kohda et al. (2019) that cleaner wrasse fail to show any evidence of

self-awareness. But we part company with them about whether cleaner wrasse pass the mark test.

Similar problems of interpretation apply to claims that dolphins can recognize themselves in mirrors (Reiss & Marino, 2001). While widely acclaimed and uncritically cited as evidence for self-recognition in dolphins, the two dolphins that were tested showed an increase in viewing time after being marked with black dye. But monkeys with extensive exposure to mirrors also show an increase in attention to their image in a mirror following the application of facial marks yet fail to locate the source of those marks. Another problematic feature of the study with dolphins was that their interest in the marks seemed almost obsessive. In contrast, when chimpanzees discover that the strange red marks on their faces in the mirror are inconsequential, they rapidly lose interest in and ignore the marks. The dolphins, however, spent extended periods of time looking at these equally inconsequential black marks in the mirror, yet again unlike primates they show no interest in such marks on other dolphins. How can an animal that is not smart enough to learn to ignore an inconsequential body mark learn to recognize itself in a mirror? Clearly, such a preoccupation would be highly maladaptive under natural conditions. What was missing in the dolphin study was a control condition in which marks were applied to body parts that could be seen directly without a mirror. Would dolphins be equally preoccupied with such marks? If not, the Reiss and Marino (2001) findings may be an artifact of the testing procedure that was used. More recent mark tests on dolphins (Morrison & Reiss, 2018) also remain challenged by these animals' inability to show true mirror-guided self-exploration of the marks as seen in humans and great apes.

Results Must Be Replicated

Replication is the corner stone of science. Strictly speaking, the results of any research project do not rise to the level of scientific facts until they have been independently replicated by other competent scientists.

The study of mirror self-recognition in elephants (Plotnik et al., 2006) can be used to illustrate this point. Out of three elephants that were tested only one showed evidence of using the mirror to inspect marks on itself that could only be seen in the mirror. However when the same individual was retested, it failed the mark test, twice. As per our discussion of knowing the literature and experimental design, the failure to replicate the earlier results with this elephant may have been a consequence of habituation and resulting diminished mark salience. These findings with elephants also need to be tempered in light of previous research using the mark test that failed to find evidence for mirror self-recognition in elephants (Povinelli, 1989). Therefore, even though the Plotnik et al. (2006) study is widely cited as evidence for self-recognition in elephants, the evidence is not based on elephants, that evidence is based on a single elephant; no report of a replication of the positive result has been published, which makes the conclusion tentative and suggestive at this point.

We are not arguing that elephants and dolphins are incapable of recognizing themselves in mirrors. But until these findings have been independently replicated (using more rigorous methodology in the case of dolphins) the existing evidence is suggestive but not conclusive, and therefore the jury is still out.

Another way to look at the problem posed by evidence that is restricted to a single animal is to apply statistical logic. In the case of inferential statistics where the objective is to make inferences about a population, the degrees of freedom are represented by the sample size minus one. If $N = 1$, then $N - 1 = 0$ which means that in the case of only one animal you have no degrees of freedom and therefore no basis for making inferences. The other way to think about this is with inductive logic where the attempt is made to use individual cases to generalize to a population. Other things being equal, the accuracy of inductive logic is proportional to the sample size and a sample of one is inadequate.

In the case of birds, only one out of 17 Clark's nutcrackers exhibited any evidence for mirror self-recognition (Clary & Kelly, 2016). Moreover, the often-cited claim by Prior, Schwarz, and Güntürkün (2008) for self-recognition in two out of five magpies has received no support from studies of other corvids: New Caledonian crows, jackdaws, and jungle crows have all failed to show evidence of self-recognition (Kusayama, Bischof, & Watnabe,

2000; Medina, Taylor, Hunt, & Gray, 2011; Soler, Pérez-Contreras, & Peralta-Sánchez, 2014). To add to the discussion of failures to find mirror self-recognition in other corvid species, recent evidence shows that carrion crows and hooded crows also fail to exhibit mirror guided self-directed behavior and fail the mark test (Vanhooland, Bugnyar, & Massen, in press). In addition, the work by Soler, Pérez-Contreras, and Peralta-Sánchez (2014) with Jackdaws raises the possibility that the results reported by Prior et al. (2008) may have been compromised and confounded by tactile cues associated with the marks.

How Little Most Animals Know About Mirrors

Pigeons can be used to illustrate how limited the understanding of mirrors is by some birds. Many species that fail to show evidence of recognizing themselves in mirrors (e.g., monkeys, also elephants) can nonetheless learn to use mirrors to find and locate hidden food (Anderson, 1986; Povinelli, 1989). Pigeons can also be trained to use mirrors to locate hidden food, but it was recently discovered that after such training when pigeons were given the option they preferred to use peripheral vision instead of mirrors to find hidden food (Ünver, Garland, Tabrik, & Güntürkün, 2017). These researchers also discovered that when the same pigeons were tested under monocular conditions they attempted to walk through the mirror in a futile attempt to access food as if the mirrored space was real, reminiscent of how some humans with mirror agnosia try to reach directly for objects visible only in a mirror (Ramachandran, Altschuler, & Hillyer, 1997). This raises additional serious questions about claims by Epstein, Lanza, and Skinner (1981) for mirror self-recognition in pigeons. Indeed, it appears possible that pigeons and perhaps many other animals cannot even begin to fathom the reflective properties of mirrors, let alone recognize themselves in mirrors.

To illustrate just how little monkeys, appreciate what they see when they confront themselves in mirrors, a pair of rhesus monkeys were raised together in front of a full-length mirror where they were given 14 hr of mirror exposure every day. The rationale for this study was driven by the assumption that among primates,

species differences on traditional tests of learning and problem solving are a matter of degree rather than a matter of kind. Chimpanzees, for example, often solve a variety of cognitive problems faster than monkeys but if given enough time monkeys reach the same level of performance. Therefore, the decision was made to give a pair of rhesus monkeys an extended opportunity to earn to recognize themselves in mirrors. Would a week, a month, or even a year of mirror exposure be enough? As we show below even a lifetime will not suffice.

Initially these monkeys reacted to seeing themselves in the mirror by threatening and attempting to attack the reflection. While over time these social and aggressive responses began to wane and eventually disappeared, both monkeys failed formal marks tests of self-recognition and never used the mirror to inspect features of themselves that could only be seen in the mirror. After over 10 years of such exposure to the mirror, when the mirror was simply moved from one side of the cage to the other it produced a dramatic but short-lived reinstatement of social behavior including threats and attempts to attack the reflected image (Suarez & Gallup, 1986). Several years later it was discovered that merely removing the mirror produced the same effect, that is, when it was shown to the monkeys again in the same location 5 days later they acted as if they were seeing monkeys they had never seen before and responded to it aggressively (Gallup & Suarez, 1991).

Gallup et al. (1980) also studied these monkeys that were reared together by providing them with more explicit information about their identity in a mirror. Rhesus monkeys, just like many other animals can easily learn to identify and respond differentially to other monkeys. Therefore, it was reasoned that when two familiar monkeys were exposed to the same mirror, they should be able to easily recognize the reflection of their familiar companion, and by implication this ought to raise the question of who the other monkey in the mirror is; that is, "If that is the same monkey sitting right next to me, then who is that other monkey?" The fact that this arrangement did not lead to mirror self-recognition means that either rhesus monkeys do not realize that another monkey cannot be at two different places at the same time, or they do not know who they are in the first place.

Menzel, Savage-Rumbaugh, and Lawson (1985) devised a task that required both rhesus monkeys and chimpanzees with prior experience with mirrors to learn to reach through a hole in an opaque barrier to find food incentives positioned at different locations on the other side. While the animals could not directly see where the incentives were hidden, there was a mirror placed directly facing the hole that could be used to locate the incentive and to monitor and guide the position and movement of their hand to where the food was. Whereas chimpanzees solved the problem almost immediately, rhesus monkeys with extensive prior experience with mirrors consistently failed to locate the food by watching the movement of their own hand in the mirror. Indeed, during the trials the monkeys sometimes vocalized and threatened the image in the mirror when they saw their hand move toward the food, almost as if it represented the hand of another competing monkey. This phenomenon calls to mind reports of a condition known as asomatognosia, where schizophrenic patients treat the reflection of their hand in a mirror as if it was a stranger's hand.

There is growing evidence that schizophrenia is a self-processing disorder where a disturbed sense of body ownership coupled with an impaired sense of personal agency causes patients to misidentify the source of their own behavior (for a review see Klaver & Dijkerman, 2016). For instance when some schizophrenics see both their hand and the hand of someone else on a TV monitor in real time and they cannot distinguish which hand is theirs, if they are instructed to move their hand while watching the monitor they still cannot identify which hand is theirs because of a lack of personal agency (Daprati et al., 1997). As a further illustration of the inability to identify the source of their own behavior, a recent study found that when people with premorbid schizophrenic-like traits were asked to tickle themselves, they acted as if they were being tickled by someone else (Lemaitre, Luyat, & Lafargue, 2016).

In summary, these findings with pigeons and rhesus monkeys are dramatically out of phase with the gradualist perspective advocated by Clary and Kelly (2016), de Waal (2019), Kohda et al. (2019) and others.

Replication and Retention of Mirror Self-Recognition in Chimpanzees

In stark contrast to claims for MSR in elephants, dolphins, and birds, mirror self-recognition in chimpanzees has been replicated many times by numerous investigators all over the world (for reviews see Anderson & Gallup, 2015; Gallup, Anderson, & Shillito, 2002). Indeed there is now a study which shows that individual differences in self-recognition among chimpanzees are highly stable over time.

When retested with mirrors after an 8-year interval without any intervening exposure to their reflections, most chimpanzees that had previously shown self-recognition continued to do so, whereas those that failed to show self-recognition on the first occasion continued to show no signs of realizing that their behavior was the source of the behavior depicted in the mirror (de Veer, Gallup, Theall, van den Bos, & Povinelli, 2003). Thus, because individual differences in the capacity to recognize themselves in mirrors can be replicated in the same individuals over time and space, once self-recognition emerges in chimpanzees it appears to be a highly stable trait just as it is in humans. No such demonstrations have been reported for any nongreat ape species for which claims of mirror self-recognition exist.

Why There May Be No Evolutionary Continuity When It Comes to Mirror Self-Recognition

Adhering to the view of evolution as a continuous process, many authors think that species showing no compelling evidence for MSR may nonetheless have "intermediate" capacities for self-awareness (i.e., the gradualist or "graded" argument mentioned above). However, it is entirely conceivable that mental continuity does not fully characterize the reality of cognitive evolution; indeed it can be argued that among biological phenomena evolutionary discontinuity is the order of the day.

The definition of a species, as a population of organisms that are reproductively isolated from all other species but are capable of producing reproductively viable offspring, makes species differences a matter of kind—not degree—because speciation precludes genetic exchange of subsequent adaptations between species. No

contemporary species is ancestral to any other species. Humans did not evolve from chimpanzees. Although human and great apes share many traits, most of these are thought to derive from a now-extinct common ancestor. Once the split leading to modern chimpanzees and humans occurred any ensuing genetic adaptations in either species would be unique because at that point the ancestral forms became reproductively isolated from one another. Similar adaptations occasionally do emerge in different species (i.e., convergent evolution), but those do not qualify as instances of evolutionary continuity.

The Consequences of Self-Awareness

Consciousness is bidirectional. To be aware of the world around you is to be conscious. To be self-aware means that you can become the object of your own attention, and think about yourself in relation to past, present, and even future events. Many animals have clever brains in the sense of learning and problem solving, but blank minds in that they are incapable of using their experience and mental states to make inferences about comparable experiences and mental states in others.

Are most species self-aware? How this question is answered is often more a matter of faith than fact but answering in the affirmative carries with it the assumption that species are self-aware until proven otherwise. If it is true that you cannot prove the null hypothesis, and if the corollary is also true, namely that the absence of evidence is not evidence of absence, then the only tenable and heuristically meaningful approach is to assume that different species lack the capacity for self-awareness until proven otherwise (Gallup, 1993). The growing tendency toward uncritical acceptance of published findings that are based on inadequate or flawed procedures and subject to over- or misinterpretation of animals' reactions that have not been independently replicated, does little to promote real progress in the comparative study of self-recognition and self-awareness.

The Ontogeny of Human Self-Awareness and Mental State Attribution

Prior to 15 months of age most children react to themselves in mirrors much like other species do: They respond as if confronted with another child and often treat the reflection as a playmate. Between a year and a half and 2 years of age two thirds of children begin to recognize themselves in mirrors. At about the same time that they realize that their behavior is the source of the behavior seen in the mirror, children also begin to show evidence of being able to use their experience to make inferences about what other people know, want, or intend to do. And they begin to show some of the other hallmarks of self-awareness such as object permanence, prosocial behavior, visual perspective taking, the use of personal pronouns, and the development of autobiographical memory (see Gallup, 1998).

Evidence is accumulating for tactical deception and counterdeception, consolation, spontaneous altruism, visual perspective taking, spontaneous helping, and theory of mind in great apes (e.g., Cordoni, Palagi, & Tarli, 2006; de Waal & van Roosmalen, 1979; Krupenye, Kano, Hirata, Call, & Tomasello, 2016; Russon, 2009; Shillito, Shumaker, Gallup, & Beck, 2005; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Webb, Romero, Franks, & de Waal, 2017; Zimmermann, Zemke, Call, & Gómez, 2009; but for counter arguments see Penn, Holyoak, & Povinelli, 2008; Penn & Povinelli, 2007). Such evidence is consistent with the view that self-awareness is what underwrites the emergence of mental state attribution. In humans mental state attribution becomes more sophisticated as children get older, but there are no *bona fide* instances of humans being able to take into account what others know, want, or intend to do in the absence of being to recognize oneself (Gallup, Platek, & Spaulding, 2014). Comparable developmental work remains to be done on great apes.

At the other end of the life span as symptoms of dementia progress in elderly patients, some people eventually reach the point where they no longer recognize themselves in mirrors. It is particularly interesting that when this occurs it happens prior to the onset of prosopagnosia or the inability to recognize faces of familiar people (Biringer & Anderson, 1992). Indeed, with the loss of mirror self-recognition the more primitive social stimulus properties of mirrors have been cleverly used to manage wandering in institutionalized dementia patients by minimizing unauthorized exits from the ward

(Mayer & Darby, 1991). By placing a full-length mirror on the door to the ward, contact with the door was substantially reduced, probably because patients who walked toward the door were intimidated by the sudden approach of an apparent stranger in the mirror.

The Neurobiology of Mirror Self-Recognition and Self-Awareness

Butler and Suddendorf (2014) have done some impressive work looking at structural neurological indicators that may distinguish species that recognize themselves from those that do not. Focusing on individual rather than species differences, there is now growing evidence (Hopkins, Latzman, Mahovetz, Li, & Roberts, 2019; Mahovetz, Young, & Hopkins, 2016) for brain and genetic differences that distinguish chimpanzees that can recognize themselves in mirrors from those that cannot. For instance, individual differences among chimpanzees in cortical thickness appear to be correlated with performance on mirror tests of self-recognition (Hopkins et al., 2019).

Using functional near-infrared spectroscopy, Bulgarelli et al. (2019) recently found that children who showed MSR at 18 months of age exhibited significantly stronger frontal-temporoparietal connectivity than 18-month-old children who did not pass the mirror test. Additional evidence reviewed by Bulgarelli et al. (2019) has shown that the frontal-temporoparietal cortex, and other related brain regions in what is known as the Default Mode Network (DMN) are activated when adults engage in self-referential processing. Indeed, consistent with other points we make, the DMN has also been implicated in autobiographical memory, mental state attribution, and mental time travel. Thus, the relationship between MSR, self-awareness, and other theory of mind related phenomena has now been validated by tangible neurobiological evidence. These findings are consistent with another recent study that found increased fronto-parietal white matter connectivity among for chimpanzees that pass the mirror test (Hecht, Mahovetz, Preuss, & Hopkins, 2017).

Self-processing in humans also appears to be localized in the right cortical hemisphere of the brain (Platek, Keenan, Gallup, & Mohamed, 2004). It may be more than coincidental that the capacity to engage in mental state attribution and to exhibit autobiographical memory are also located in right frontal cortex (for a review see Gallup, Anderson, & Platek, 2011). It is also important to note that the human frontal cortex is growing more rapidly than any other part of the brain between 18 to 24 months of age, which corresponds to the age that children learn to recognize themselves in mirrors. This may be related to *infant amnesia* where no one has any memory of things that happened prior to a year and a half to 2 years of age. Thus, the emergence of consciousness and self-awareness appear to occur hand in hand.

Conclusion

Five decades of research, scores of published articles, the use of a variety of techniques, and animals ranging from panda bears to parrots and even ants, lead to the conclusion that species differences in mirror self-recognition appear to be differences in kind rather than degree. When rigorous, reproducible, experimental evidence is used to replace wishful thinking, intuition, and subjective impressions, attempts to champion an evolutionary continuity of self-awareness have not held up. The ability to become the object of your own attention and recognize yourself in a mirror appears to be a cognitive precursor to being able to make inferences about what others know, want, or intend to do. The evidence for this suite of cognitive abilities in primates is convincing for humans and suggestive for chimpanzees and orangutans. As a result, the link between self-awareness and mental state attribution may qualify as an instance of a relatively abrupt, albeit restricted cognitive change akin to what biologists have identified as *punctuated equilibrium*.

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