Social, Machiavellian and Cultural Cognition: A Golden Age of Discovery in Comparative and Evolutionary Psychology

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Marking Machiavellian Intelligence: Contemporary Comparative Perspectives on Cognitive and Cultural Evolution
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Abstract

The years since the publication of *Machiavellian Intelligence* have witnessed a Golden Age in discoveries concerning social cognition in human and non-human primates and many other animal taxa too. Here I briefly dissect some of the variants of the social intelligence hypotheses that have evolved in this time and offer a selective overview of scientific discoveries in this field, particularly in primates, over the last 30 years.

Keywords: animal intelligence, social cognition, social intelligence, Machiavellian intelligence; cultural intelligence hypothesis

In our introduction to *Machiavellian Intelligence*, Richard Byrne and I distinguished three different forms of 'social intellect hypothesis' embedded in the landmark article of Humphrey (1976) and other foundational contributions to the embryonic field of research that we reviewed (Whiten and Byrne 1988a). Such hypotheses have further proliferated since, but our originally-proposed triad remains worth re-visiting to structure this concise invited essay concerning developments in the field in the past three decades. Editorial requests for brevity preclude an exhaustive review.

Hypothesis 1: Where social lives are as complex as those of many monkeys and apes, extensive components of cognition will have evolved as adaptations for dealing with this, yet in comparison to non-social cognition, social cognition includes rich phenomena awaiting discovery (note – this was a hypothesis of the 1970s)

Humphrey (1976) remarked that much of the testing of 'intelligence' in both human and non-human primates had, by then, been done through tests with physical objects, neglecting socially-oriented cognition. Thus if we think of intelligence/cognition as an iceberg, the suggestion was that the massive part beneath the surface represented uncharted social cognition. Perhaps calling this a 'hypothesis' over-dignifies it. However I suggest that although the two further hypotheses I describe below are more obviously regular scientific hypotheses about cause and effect in the natural world, they have proved inherently challenging to test; by contrast, this first broad 'hypothesis' stimulated a generation of researchers to achieve monumental strides in delineating the complexities of animal social cognition.

The point can be illustrated by statistics extracted from a tabulation in Whiten (2018a) of Web of Science citations, including that 'social/Machiavellian intellect/intelligence' occurred in just 21 article titles (and in 60 as 'topic') in 1991-5, whereas for 2011-2015 the figure had risen to 123 (495 as 'topic'). The corresponding figures for 'social brain' (see below) were 0 (title) and 3 (topic) in 1991-1995, but rose respectively to 146 and 537 for 2011-2015. And between these two periods 'social cognition' rose from 91 (title) and 302 (topic) to 932 and 6,281 citations respectively! A Golden Age indeed.

The behavioral and cognitive domains addressed have become comprehensive, as foundational field observations have been supplemented by rigorous and revealing experiments. For example in primates alone (the order focused on by Humphrey and in *Machiavellian Intelligence*), investigations have spanned the following (noting for each, one or more recent reviews plus a more specific illustrative example of the sophistication revealed): (i) *Social knowledge* (Seyfarth and Cheney, 2015a, 2017); for example, a baboon threatened by another individual is likely later to treat both threats and reconciliatory grunts from associates of that individual differently, indicating knowledge of third-party relationships (Wittig et al. 2007a,b; Wittig et al., 2014, for similar findings in chimpanzees); (ii) *Social computation and mindreading* (aka theory of mind) (Call and Santos, 2012; Whiten 2013); Crockford et al. (2017) provided evidence of the recognition of the seeing-knowing link in wild chimpanzees, and Krupenye et al. (2017) showed that the gaze of chimpanzees and other apes indicated they may even compute the false beliefs of one individual with respect to the whereabouts of another; (iii) *Tactical deception* (Hall and Brosnan, 2017); rhesus monkeys stole whichever of two options a human was most likely not to hear or not to see (Santos et al., 2006); (iv) *Social learning and culture* (Galef and Whiten, 2017); naïve chimpanzees would discriminate by observation, and typically acquire, whichever of two alternative tool-use techniques they witnessed, generating traditions (Whiten et al. 2005); (v) *Co-operation* (Gilby, 2012); chimpanzees pulled a peg to release a conspecific helper when needed for a collaborative task, and moreover selected the best collaborators (Melis et al. 2006); (vi) *Vocal communication* (Zuberbuhler 2012); chimpanzees were more likely to alarm bark to an experimentally-introduced snake when companions were ignorant of it (Crockford et al. 2012); and (vii) *Gestural communication* (Liebal et al. 2013; orangutans moderated their gestures intentionally according to the comprehension of target individuals (Cartmill and Byrne, 2007). It is the whole suite of such capacities for managing life in complex societies we thought it apt to tag specifically as ‘Machiavellian Intelligence’. For further recent overviews of what we have learned about such social cognition in primates and other animals, together complementing this present issue, see those edited by Seyfarth and Cheney (2015b), Meunier et al. (2017) and Di Paolo et al. (2018).

Hypothesis 2: Social complexity selects for greater general intelligence

Humphrey's paper was entitled 'The social function of intellect', aligning it with the discussion above and with the third hypothesis we shall meet below. However, it was framed as a solution to why many *non-social* tests had indicated heightened intelligence in primates. Accordingly, some researchers have sought to test whether social complexity begets greater general ('domain-general') cognitive performance, rather than cognition specifically serving social functions. This can be seen as a form of 'social intelligence hypothesis' (Ashton et al. 2018) yet is not concerned with the aspects of Machiavellian Intelligence indicated above.

The approach can be illustrated by a recent intra-specific comparison between Australian magpies living in different sized groups, presented with four different kinds of learning tests, such as for spatial memory or reversal learning (Ashton et al. 2018). The average performance in larger groups was found to be superior on all four tests, the scores on which were inter-correlated, leading the authors to conclude that an effect of social complexity on a 'general intelligence factor' was implicated. Cognitive performance further predicted reproductive (fledging) success, providing evidence that cognition may indeed by favoured by natural selection in more complex (larger) societies, with potential longer-term evolutionary consequences.

Few such studies testing whether variation in sociability predicts differences in general cognition have been completed (see reviews in Bond et al. 2003; Ashton et al. 2018). The necessary measures are difficult to engineer and implement, the more so in long lived animals such as most primates. An alternative approach was pioneered by Dunbar (1995), testing for relationships between the typical group size of a species as a proxy for their social complexity, and brain size ('encephalization') instead of cognition. In this approach brain size, or a variety of related measures such as relative size of the neocortex, may be regarded either as proxies for cognitive power, or as interesting variables in their own right (hence the underlying theory was dubbed a 'social brain hypothesis' (Dunbar 1998). Unless such encephalization can be partitioned between social and other functions, it should provisionally be seen as an index of general intelligence, and indeed there is empirical evidence for such a relationship across primates (Deaner et al. 2006).

A variety of studies have reported the predicted positive relationships between group size and encephalization, not only in primates (Dunbar and Shultz, 2007) but in other taxa such as ungulates and carnivores (Perez-Barberia et al. 2007). Some more recent studies report convergent results both for primates (Street et al. 2017) and cetaceans (Fox et al. 2017). However, other recent studies, exploring more extensive databases and different methodologies, have suggested that the support for Humphrey's ideas offered by these approaches may be more dependent on particular methodologies or databases utilized than it had previously seemed (de Casien et al. 2017; Powell et al. 2017). This line of work has accordingly become complex (some might say, tangled) and controversial of late. In any case, gross size of the brain or particular components of it are crude measures of both cognitive and neural functioning (Healy and Rowe, 2007), just as social group size is a crude measure of the kind of social complexity outlined in *Machiavellian Intelligence,* as illustrated by examples listed under 'Hypothesis 1' above (Whiten, 2018b).

It is to be hoped that future work will assess social complexity more directly (for diverse examples, see Burish et al., 2004; Bouchet et al., 2013). Whiten (2000) explored the dissection of primate social complexity into a number of measurable elements including polyadic complexity and the number of factors required for behavioural predictions, a framework adopted in recent United Nations Environment Programme attempts to take account of our discipline's discoveries about animal culture and social complexity in conservation strategies (Culture Expert Group report, 2017) – a perhaps surprising but exciting and very welcome impact of our work.

Hypothesis 3: Social complexity selects for more sophisticated levels of social cognition

On the basis of all we have learned about animal social cognition in the past decades, this truly 'Machiavellian intelligence' hypothesis has come to be seen by a majority of researchers as at least highly plausible, and even as a working assumption (Seyfarth and Cheney, 2015a). But has this hypothesis really been tested? What is required to do so? If the Australian magpie study outlined above were extended to find that social complexity, as indexed by group size, predicted yet more heightened performance on

tests of *social* cognition, in turn predicting reproductive success, then this domain-specific hypothesis would be addressed. Perhaps the closest studies in primates are those comparing closely related species. For example MacLean et al. (2013) compared six related species of lemur, showing that typical group size predicted a social cognition measure (taking account of attentional focus in simulated competition over food) but not a non-social cognition measure (a test of inhibitory control). These results and those of a similar comparison of four species of macaques (Joly et al. 2017) thus support the social intellect hypothesis (although not the social brain hypothesis, insofar as no relationship with absolute or relative brain size was found in the lemur study).

Does the scarcity of such studies imply a council of despair for Hypothesis 3? I suggest not, because if we recast the hypothesis as 'Does much cognition in socially-complex animals serve social functions?', this has arguably been amply confirmed by the last three decades of research. Indeed, such behavioral and cognitive domains as were listed under Hypothesis 1, like social knowledge, social computation, mindreading, deception, social learning, cooperation and vocal and gestural communication, are arguably *defined* by the social functions they have been documented as serving. This conception of 'function', as in 'the social function of intellect', refers to relatively short-term consequences that are inferred to be the raison-d'être of the entity of interest. So just as 'the function of the heart is to pump blood' we have 'the function of social knowledge is to support social manoeuvering' and 'the function of social learning is to acquire cultural information' and so on. The assumption then is that this is a consequence of past selection, although it remains a further empirical question whether variance in the performance of such functions can be shown to affect fitness (reproductive success), along the lines of the Australian magpie study. With these thoughts in mind, I briefly and selectively discuss two illustrations of specifically social cognition: mindreading and cultural learning.

Mindreading. Contemporaneously with *Machiavellian Intelligence*, Whiten and Byrne (1998b) reported the results of surveys of primatologists' reports of 'tactical deception'. We tentatively proposed that many of these reports suggested that to succeed in the kinds of deception they evidenced, individuals were taking into account certain psychological states of their protagonists, such as their intentions or what they could or

198 could not see, a theme developed further in the second edition of our book (Whiten and
199 Byrne, 1997). In later years, an ingenious series of experiments reported results
200 consistent with the earlier observations, summarised in a comprehensive review by Call
201 and Tomasello (2008) as suggesting, in chimpanzees at least, that they 'understand
202 others in terms of a perception-goal psychology" (p. 187); these authors added "as
203 opposed to a full-fledged, human-like belief-desire psychology" but that is now
204 challenged by the findings of Krupenye et al. (2017) on false belief recognition noted
205 above.
206 Such findings in relation to primate recognition of what others can or cannot see, or
207 hear, have become available so far only for relatively complex social species (Call and
208 Santos 2012), so we lack variance in social complexity with which to directly tackle
209 Hypothesis 3. Evidence for related abilities in quite different, avian species (Clayton et
210 al., 2007; Bugnyar et al., 2016), whilst exciting, often relies on different methodologies
211 that so far thwart direct comparisons, although the corvid species involved are also large
212 brained amongst birds. Some studies do at least provide developmental perspectives on
213 relevant cause and effect. Sallet et al. (2011) found that macaques reared in relatively
214 larger groups displayed neural changes that included more extended grey matter
215 connectedness in regions strongly associated with social functions, including the
216 superior temporal sulcus and prefrontal cortex, regions associated with mindreading
217 functions in humans. Noonan et al. (2014) further showed covariation of these regions
218 in relation to both social network size and social status. They concluded that "this
219 cortical circuit may be linked to the social cognitive processes that are taxed by life in
220 more complex social networks and that must also be used if an animal is to achieve a
221 high social status" (p. e1001940).
222
223 **A cultural intelligence hypothesis.** Noting that the lack of social complexity in great
224 ape genera such as orangutans does not appear to fit the relationships between social
225 group size and encephalization reported in primates more generally, Whiten and van
226 Schaik (2007; van Schaik et al. 2011) suggested that more recent findings of cultural
227 complexity in the great apes (recently extended to all three genera: Whiten, 2017) may
228 offer an alternative explanation of their special intelligence and encephalization. This
229 'cultural intelligence hypothesis' has both ontogenetic and evolutionary elements.

Ontogenetically the proposition is that cultural inheritance of accumulated skills such as foraging techniques can make an individual smarter than otherwise; and in turn, this selects for advances in cultural cognition and brain structures that will support such processes, as well as, perhaps, technical intelligence such as understanding tool use, to capitalise on all that can be acquired culturally. This hypothesis can be regarded as an offshoot of earlier social intellect hypotheses, or as a competitor to them (Whiten and van de Waal, 2017;). It is early days in the testing of this hypothesis (Pasquaretta et al., 2014). A recent example is the finding that in 'level playing field' tests in zoos, the slightly more encephalized Sumatran orangutans outperformed their Bornean cousins on a battery of cognitive tests, as predicted by the greater cultural richness of the Sumatrans in the wild (Forss et al. 2016).

In Conclusion

In many ways, all the discoveries that fit under the heading of Hypothesis 1 far outstrip the progress made in relation to Hypotheses 2 and 3 and their evolving derivatives like the Cultural Intelligence Hypothesis. These are inherently more challenging to put to the test than was anticipated in the excitement of the 1970s and 80s. The encouraging result is that we now know an enormous amount about the social cognition of primates and other socially complex taxa, providing substantial foundations to tackle the further questions the efforts of the last three decades have generated.

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