Chapter 21
Adding Agency to Tinbergen's Four Questions

André Ariew and Karthik Panchanathan

Abstract This year marks the 60th year anniversary of the publication of Niko Tinbergen's "On aims and methods of ethology" which remains influential among today's biologists and social scientists for its introduction of four questions for a complete explanation for animal behaviors. In this paper we argue that a large part of the lasting appeal to Tinbergen's four questions was (and still is) the methodological commitment to treating organisms as objects as opposed to purposive agents. Tinbergen's approach reinvigorated the discipline of ethology, allowing it to shed its teleological and anthropomorphic associations and to better cohere with a philosophy of science that favors inductive procedures, causal and mechanistic analytic techniques, and an emphasis on Darwinian explanations. While Tinbergen's approach is still prized among today's biological social scientists, it ignores an important feature of many social organisms, that they are not merely objects, they are also purposive agents. We explore the implications that a shift from treating organisms as objects to treating them as agents has on both how we should interpret and answer Tinbergen's four questions. Updating Tinbergen's four questions with agency in mind not only makes them more applicable to the biological investigation of animal behavior, but also strengthens the value and applicability of biology-oriented research programs in the social sciences.

21.1 Tinbergen's Four Questions

One of Darwin's enduring legacies to the social sciences was to make legitimate the practice of biologizing human behavior. Humans are, after all, biological organisms and related to non-human animals by common ancestry. And so, social and

A. Ariew (✉)
Department of Philosophy, University of Missouri, Columbia, MO, USA
e-mail: ariewa@missouri.edu

K. Panchanathan
Department of Anthropology, University of Missouri, Columbia, MO, USA
e-mail: panchanathank@missouri.edu

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behavioral scientists can learn a lot from ethologists. In the 1960s, Nobel laureate Niko Tinbergen (1963) categorized the biological study of animal behavior into four distinct kinds of questions, each with domain-specific goals and methodologies, which could and should nevertheless be integrated. Tinbergen's four questions were:

- Causation: What causes the behavior?
- Survival value: What adaptive function does the behavior serve?
- Ontogeny: How is the behavior acquired?
- Evolution: How did the behavior become prevalent over evolutionary time?

Tinbergen formulated his taxonomy in reaction to what he understood at the time to be two kinds of dubious but common scientific practices: at one extreme, anthropomorphizing animal behavior and even ascribing purpose; and at the other, explaining animal behavior as mere reflexes to environmental cues. Tinbergen's goal was to usher ethology into the scientific fold by emphasizing the role of objective observation and controlled experiment, the hallmarks—he argued—of good biology. In Tinbergen's formulation, animal behaviors should be treated as organs, albeit complex organs. And just as biologists investigate adaptive organs through good scientific methods, so too should ethologists study animal behavior. Tinbergen did not claim to be offering a novel approach to the biological sciences. He believed he was highlighting and extending the ideas of twentieth century Darwinians, including Julian Huxley who introduced the distinction between causation, survival value, and evolution (Tinbergen added ontogeny), and, most of all, contemporary ethologist Konrad Lorenz who was at the forefront of articulating and adopting a Darwinian framework for scientific inquiry about animal behavior. According to Tinbergen, Lorenz's biggest contribution was to follow Darwin in treating behaviors as adaptive organs.

Sixty years later, evolutionary behavioral and social scientists still celebrate the contribution that Tinbergen's four questions made to the study of behavior, including human behavior. Nesse (2013) commemorates Tinbergen's identification of ethology's central questions as a "moment of discovery" for the biological sciences. Bateson and Laland (2013) honor Tinbergen's legacy in promoting the four distinct areas of research and their integration through evolutionary theory. Kapheim (2019) applies Tinbergen's framework to evaluate the current state of the study of eusocial insects, distinguishing those areas of investigation that have experienced rapid gains in knowledge and those in which we still know relatively little. In a recent special issue of *Philosophical Transactions B* (Legare & Nielsen, 2020), a team of evolutionary social scientists report on their attempts to employ an integrative account of human ritual by using Tinbergen's four questions of animal behavior. In the introductory article, Legare and Nielsen (2020) claim that collectively the work provides new avenues for theory and research into "this fundamental aspect of the human condition." What makes these scientists attracted to Tinbergen's framework is that it extends the Darwinian theoretical framework—especially its commitment to treating behaviors as adaptive organs—to the behavioral sciences. In this way, Tinbergen's four questions are an obvious example of generalized Darwinism, the theme of this

edited volume (for more discussion of what constitutes generalized Darwin, see the introduction to this volume).

Nevertheless, contemporary commentators agree that Tinbergen's original questions and methods require modification and reinterpretation, and that the sciences need to do a better job of integrating and synthesizing the four questions. Bateson and Laland (2013), for example, declare that Tinbergen's project of generating a comprehensive and integrated analysis over the four questions is far from complete in most areas (though they single out the science of bird song as a successful case).

We take a different approach and argue that Tinbergen's views are out of date with modern biological theorizing. To update Tinbergen's approach requires more than the kinds of mere tinkering that contemporary advocates propose, especially if it is to be usefully applied to the investigation of human behavior. Tinbergen's methodological prescription—to treat behaviors as organs, while useful for advancing ethology in the mid twentieth century, is overly simplistic and reductionist, especially in its reliance on clear demarcations between genetic programs and environmental conditions. While his ideas were an improvement over the simple dichotomy of innate vs. learned or nature vs. nurture thinking of his mid twentieth century interlocutors, he could not have known about the extended evolutionary synthesis (Oyama et al., 2001; Pigliucci & Miller, 2010; Jablonka & Lamb, 2014; Laland et al., 2015; see also Peterson, 2017) and its emphasis on ontogenetic processes and their effects, including developmental constraints on evolutionary change, plasticity, epigenetics, and niche construction.

More broadly, Tinbergen's methodological prescription to view behaviors as organs is predicated on a view that animals are mere ***objects***: biological machines made of separable parts, passive and inert, structurally fixed, and acted upon by internal and external forces. While this perspective might be useful for many research questions, it misses a key feature of biological organisms. Organisms that exhibit behaviors are also ***agents***, not merely objects, *still made of parts, of course, but self-organizing in their development and actively engaged in the modification of their environments* (Walsh, 2007, 2015).[1] This shift from an object-oriented approach to an agent-oriented approach has implications for how we interpret Tinbergen's four questions and how we should answer them. By updating Tinbergen's four questions with agency in mind we not only make it more applicable to the biological investigation of animal behavior, but we also strengthen the value and applicability of the Darwinian-inspired social science program because humans are paradigmatic agents. Critics of Tinbergen-inspired sociobiology and its descendent disciplines were right that treating sentient beings (among other animals) as objects makes for an impoverished research program. But critics are wrong to think that biology cannot incorporate agency. (Likely these critics were misled by outdated biological theories like Tinbergen's.) That is not to say there are no limits to an

[1] Okasha (2018) describes agents as having the following features: (i) organisms are the locus of goal-directed activities, (ii) organisms exhibit "behavioral flexibility", (iii) organisms possess adaptations that "appear designed for a purpose".

agent-oriented version of Tinbergen's framework, but at least the debate can continue along fresh lines. For an instance of a potential limit, consider that the behaviors of some agents (at least humans) contain within them consciousness and subjective experience. An explanation of social behavior that does not account for these phenomena is, for some kinds of investigations, incomplete. An update that incorporates subjective experience may require an additional kind of question—perhaps Tinbergen's Fifth question. We will return to this question in the concluding section of this chapter.

Our overall motivation is programatic. We aim to refocus the debate about the legitimacy of Darwinian approaches to the social and behavioral sciences beyond the usual questions of reductionism and determinism by showing how agency, along with its associated features of purposiveness, self-organization, and even consciousness, could be incorporated. This paper initiates the project of adding agency to Tinbergen's four questions with a focus on an exposition and criticism of Tinbergen's framework, including both Tinbergen's original formulation and on contemporary investigators—biologists and social scientists—who still espouse Tinbergen's object-oriented pre-suppositions. We then explore some of the ways in which an agency perspective adds to and changes how we think about Tinbergen's four questions.

21.2 Tinbergen's Mid-Century Ethology Program

Tinbergen's motivation for writing his 1963 paper was to evaluate the state of ethology, especially under the influence of his mentor, Konrad Lorenz. Ethology was improving by attending to both good general scientific methodologies and insights from mid twentieth century Darwinian biology. We should read Tinbergen's lessons in the context of his time. He devoted much of the essay criticizing animal behaviorists who veered from these practices. These included anthropomorphizers and teleologists who dragged down the legitimacy of the field by ascribing subjective experiences, intentions, or purposes as part of their explanation. According to Tinbergen, such entities were not legitimate objects of scientific study because they were not directly observable. At the other end of the spectrum, Tinbergen criticized reductionists of various stripes, including those steeped in conservative zoological traditions, who robbed the field of potential insights by over-emphasizing homology and anatomy while ignoring function, and behaviorists, who treated behaviors as simple reflexive reactions to external stimuli and failed to acknowledge the complexity of inner mechanisms and genetic programming. Tinbergen argued that Lorenz's ethology adhered to good scientific methodology by charting a middle path between these extremes.

Tinbergen's essay was and continues to be so influential because he managed to elevate ethology by articulating a philosophical view about what good scientific methodology entails along with a general account of what animal behavior is that made it suitable to scientific inquiry. To Tinbergen, ethology is a science that

identifies behavioral patterns through inductive generalizations, facilitates causal analysis in answering all its relevant questions, and adopts Darwin's theories of common descent and natural selection (we expound on these features below). To adopt these scientific principles, Tinbergen advocates an important auxiliary assumption about the ontology of behaviors: behaviors are organs no different than any other structural and physiological organ. In its fuller expression, animals possess species-specific adaptations which feature a complex ontogeny that involves an interaction of highly structured inner mechanisms (under genetic control) and external stimuli (in the sequence of environmental exposures during development). This is true regardless of whether these adaptations are behavioral, structural, or physiological in nature.

It is important to fully articulate these two aspects of Tinbergen's work—his philosophy of science and his account of animal behavior—because it provides the appropriate context to understand Tinbergen's four questions of animal behavior, why he chose them, and how he proposed ethologists generate scientific answers. This articulation is important for another reason—it shows how dated some of Tinbergen's views are. As Bateson and Laland (2013) note "almost every modern textbook on animal behaviour quotes his distinctions with approval" (p. 1). If today's biologists and social scientists wish to adopt the same kind of rigor that Tinbergen demanded in the mid-twentieth century, then they should be willing to revise Tinbergen's philosophy of science and account of what constitutes animal behavior to reflect recent advances. Bateson and Laland (2013) argue, in their commemorative, that Tinbergen's scheme remains useful to this day as a heuristic but given developments in the sciences over the last 50+ years, the questions require a "more nuanced interpretation than is traditional" (p. 1). Tinbergen's schema doesn't need nuanced refinement—it needs an overhaul. To further progress in our understanding of animal (and especially human) behavior, we need to admit that Tinbergen's account, looked at in the context of twenty-first century science is incomplete. It presupposes a view that individuals are mere objects, at the passive nexus of internal and external forces. Tinbergen did not consider organisms as agents that actively contribute to their conditions and generate behaviors according to their goals and needs. Agency is manifest in the entirety of the organic world and is most pronounced in the purposive behavior of humans. By adopting an agency view, we provide interpretations of Tinbergen's four questions that reflect not only a more complete biology but also a better biological underpinning for human social science. An agency view also reveals a limitation of Tinbergen's four questions—they cannot (by Tinbergen's own admission) apply to questions concerning subjective experience and consciousness, a goal for some social scientists and a requirement in the humanities.

Nesse (2013) argues that emphasizing the controversies that Tinbergen's questions generate when applied to today's science "can obscure Tinbergen's accomplishment which remains vastly under appreciated." We agree that Tinbergen elevated ethology to a science by adopting good scientific methodological principles and practices and by endorsing Lorenz's radical step of regarding animal behaviors as organs in order to accommodate causal analysis. In the next section we will

expound on this under-appreciated accomplishment. But, for Nesse, Tinbergen's other underappreciated accomplishment was to show that answers to all four questions are necessary for a complete biological explanation. We disagree. Without incorporating agency, we argue, Tinbergen's explanatory schema is incomplete. This is what we'll argue in the subsequent section of this paper.

21.3 Tinbergen's Philosophy of Science

We have claimed that Tinbergen elevated the investigation of ethology by infusing it with good scientific methodology. And, he did so by adopting Lorenz's heuristic of treating animal behaviors as adapted organs. To unpack this let's begin with Tinbergen's prescription for good scientific methodology followed in the next section with an exposition of how adopting Lorenz's heuristic informed Tinbergen's formulation of his four questions. Later, we will show how treating behaviors as organs is, for better and for worse, part of the "objectancy" approach to ethology (Walsh, 2015).

Induction Ethologists practice inductive methods of data collection to support generalizations. To Tinbergen, the generalizations that mattered were the recognition that in the wild there exists an "enormous variety of animal behaviour repertoires" which were characteristic of individual species. Tinbergen's interlocutors missed the opportunity to ask questions like "why do these animals behave as they do" because they failed to even recognize their existence with their practice of singling out only a "handful of species which were kept in impoverished environments. . .and to proceed deductively by testing...theories experimentally."

Causal Analysis To Tinbergen, good scientists also adopt appropriate causal analytic techniques for answering each of the four questions. This is a pervasive theme in Tinbergen's essay. Adopting appropriate means of causal analysis allows biologists to dare to ask and even provide means to answer questions like "what causes this behavior?" and "what is this behavior good for?", while avoiding the looming specter of anthropomorphizing or teleology. Causal analysis takes on many forms in Tinbergen's analysis, including: mechanistic analysis of how a behavior contributes to a functional system, the careful investigation of cause-effect relations in trying to determine which of several effects promote survival value, a process of elimination to understand the differential effects of both the inner machinery and external environmental conditions in ontogeny, and the application of controlled selective pressures to determine the dynamics of evolution.

Darwinism Finally, Tinbergen's ethology is thoroughly Darwinian, a requirement of any twentieth century biology. Its scope and limits are co-extensive with Darwin's theories of common descent and natural selection. Natural selection provides the grounding for the "what for?" questions while Darwin's theory of common descent is at the heart of the elucidation of the course of evolution. Ethologists should judge

the degree of evolutionary divergence by the degree of dissimilarity between current behaviors and their common ancestors. A rigid adherence to Darwinism is obviously one of the reasons why Tinbergen's four questions remain so attractive to today's biologists and evolutionary social scientists alike. But this rigid adherence to the Darwinism of Tinbergen's day also carries over the limitations that can lead to bad biology and bad social science.

21.4 Tinbergen's View of Behaviors as Organs

Tinbergen formulated his four questions around a set of presumptions about animal behavior that allowed them to be the appropriate subject of good scientific theorizing. It is important to articulate the presumptions for the sake of understanding the motives and interpretations for each of his four questions. The most important is that animal behaviors are like organs. Earlier, we stated that Tinbergen's insight is that animals possess species-specific adaptations which feature a complex ontogeny that involves a complex interaction of highly structured inner mechanisms—under genetic control—and external stimuli, regardless of whether these adaptations are behavioral, structural, or physiological in nature. Let's now break this down into component parts to better appreciate how Tinbergen set the scope and limits of ethological investigation.

Tinbergen argued that behaviors are organs. This claim has two components. First, that behaviors are structural and physiological characteristics of animals as opposed to mental expressions. This is what makes ethology a science, as its investigation ranges over the physical features of objects, not the subjective experiences of agents. For Tinbergen, a good science ought to be based upon inductive methods where generalizations are supported from direct observations from both the field and from controlled experiments. Hence, ethologists should avoid ascriptions of subjective experiences and purposes ("teleology") to behaviors since both are, by their natures, not directly observable. Instead, ethologists should adopt the stance that animal behaviors are like organs which can be subject to inductive methods to uncover generalities, and causal analytic methods to generate explanations. Tinbergen emphasized the use of experiments to manipulate conditions and reveal important counterfactuals.

Second, like other organs, behaviors undergo ontogenetic development, a process that involves a complex interaction between an inner structure that is inherited from its parents and external features of the environment. Tinbergen stresses that there ought not be a methodological gap between ethology and neurophysiology as his interlocutors would have it. His interlocutors were simple behaviorists who thought behaviors as reflexes and hence over-emphasized the role of external stimuli. Tinbergen urged that behaviors are not reflexive expressions to external stimuli. Instead, they, like organs, undergo ontogenetic development.

Tinbergen also argued that behaviors, being organs, are species-specific adaptations. This claim also has two components. First, Tinbergen argued that behaviors

are characteristics of species. That gives specificity to the scope of ethology, emphasizing categories of behaviors as opposed to individual expressions. Ethology is interested in behaviors that are characteristic of species, not the idiosyncrasies of individuals. It is part of an explanation for what makes, say, geese different than ducks, as opposed to what makes certain geese different from other geese. As Tinbergen put it, "each animal is endowed with a strictly limited, albeit hugely complex, behaviour machinery which (if stripped of variations due to differences in environment during ontogeny, and of immediate effects of fluctuating environment) is surprisingly constant throughout a species or population." (1969, p. 414) This argument has consequence for the science of ethology because it "positively facilitated causal analysis": "this awareness of the repeatability of behaviour has stimulated causal analysis of an ever-increasing number of properties discovered to be species-specific rather than endlessly variable." Tinbergen's identification of the phenomenon of interest as categories of behaviors aligns with his views about good inductive science appropriate for naturalists in the field. The descriptive task of ethology (the "return to nature") is to catalog the variety of species-specific behaviors so that they can be subjected to causal analysis and experimental manipulations for the sake of answering each of the four questions.

Second, by emphasizing that animal behaviors are adaptations, Tinbergen appeals to both (i) the current flourishing of animals and (ii) a causal explanation for their origins. This distinction is important for Tinbergen and the reason why he expressed one of the four questions in terms of "survival value" rather than "adaptation" as a means of interpreting the question "what is a behavior for?" (i) Behaviors aid their possessors to survive and reproduce in their natural surroundings: "It is through Lorenz's interest in survival value that he appealed so strongly to naturalists, to people who saw the whole animal in action in its natural surroundings, and who could not help seeing that every animal has to cope in numerous ways with a hostile, or at least uno-operative environment." (*Ibid*, p. 417) (ii) By referring to behaviors as adaptations, ethologists have a ready explanation in Darwin's theory of natural selection for their origin story that explains their prevalence among species. Most importantly, appeals to natural selection allow for scientifically minded ethologists to answer "what for" questions about behaviors without appeal to metaphysically suspect teleological forces. It also grounds the use of common descent to answer questions concerning the course of evolution current features underwent as a divergence from common ancestry.

21.5 Tinbergen's Four Questions

Tinbergen's explanations for each of ethology's four questions presuppose his methodological commitments to what constitutes science and his 'adapted organs' account of animal behavior. Let's briefly go through each type of question, with an emphasis on how Tinbergen used his pre-suppositions to articulate how ethologists should provide scientific answers to each question.

1. The **causation** question is about "what causes the behavior?" To provide an appropriate scientific answer, one must avoid subjective, anthropomorphic, and teleological language. To say that "the animal attacks because it feels angry" is to ascribe a behavior that "can be observed by no one except the subject." Since we cannot observe an animal's feelings, the true source of the ascription must be derived from the human experimenter. Ethologists are often guilty of such teleological language. To refer to "innate reflexing mechanisms" is to characterize a mechanism in terms of achievement, making causal analysis difficult. Tinbergen prescribes treating a behavior like an organ that causally contributes and is causally integrated in sometimes very complex ways to a larger mechanistic context which provides its inputs and utilizes its causal outputs. Tinbergen envisions a future in which ethologists bridge the "no man's land" between ethology and neurophysiology through a hierarchy of causation, in which complex behaviors are broken down into component parts with the in-principle ability to continue the analysis down to molecular biology.
2. The **survival value** question allows us to distinguish from the various causal effects a behavior might have the one that explains "how the behavior works" by reference to its adaptive function. For example, a "releaser" is not merely "anything that provides stimuli" but "an organ characterized by a function." Darwinian natural selection is at the basis of questions of survival value because, like organs, species-specific behaviors owe their prevalence to their adaptive function. Tinbergen notes that in post-Darwinian biology, questions about survival value got a bad reputation from the tendency of practitioners to make "uncritical guesses" from the "armchair", what Gould and Lewontin (1979) would later call "just-so stories". But, there are causal methods for testing function and survival value. Any hypothesis can undergo observational and experimental studies for the sake of revealing important counterfactuals. "Nest showing" among male sticklebacks can be shown to serve a causal function through the aid of dummies to control behavior and determine whether the behavior contributes to and is even indispensable for successful reproduction (p. 420). Tinbergen devotes a significant portion of this section on the distinction between past and current function. Past function explains how the behavior became prevalent, but the current function explains how an organism manages to survive in its current environmental state. Tinbergen argues from a methodological perspective that survival value for current environmental state should be established first since such hypotheses can be subject to observational and experimental studies. All together the hope is to provide a full story of cause-and-effect relationships to undergird the scientific explanation for what a behavior is for.

Bateson and Laland (2013) argue that Tinbergen's question should be understood today in terms of "current utility" rather than "adaptive significance" because it helps to emphasize the difference between a trait's etiological and current function. Nesse, instead, prefers "adaptive significance" over "current utility" because the latter invokes teleology of the noses are for supporting eyeglasses sort (2013, p. 682). Each side thinks that the dispute is more than

terminological. We agree, but we side with Tinbergen who was: (i) articulate about the need to distinguish between etiological and current function (as Bateson and Laland urge), and (ii) was explicit about providing non-teleological answers. Tinbergen recognized the difference between the question "how did the species-specific evolve?" from the question "how do contemporary animals utilize their species-specific behaviors to flourish in their current environmental circumstances?" And, by promoting Darwinian evolutionary theory, ethologists can replace any teleological connotations with references to causal explanations about origins and current utility.

3. The **ontogeny** question investigates the "change of behavior machinery during development." Every aspect of Tinbergen's explanation for behavior development is infused with causal mechanistic analysis and a commitment to viewing behaviors as adapted organs. Explanations for how behavior develops involve first a distinction between the internal machinery and the external factors from the environment that make a difference, and second a method of "elimination" which involves varying environmental conditions to see if it makes a difference to the developing machinery. Labeling a feature as "innate" under this process is understood as a "negative" label, for it indicates that some number of external factors have been eliminated as candidates for making a difference in the development of the machine. For example, "if we raise male Sticklebacks in isolation from fellow members of its own species, subject them as adults to test with dummies, and find that they attack red dummies just as selectively as do normal males, we are entitled to say that exposure to red males cannot be responsible for the development of this selectiveness of response." (1969, p. 424) However, it does not follow that "innate" features do not require any "interaction with the environment". The appropriate conclusion is a description of the environmental aspects that were "shown **not** to be influential". It may be that certain environmental factors are required in other parts of the developmental process, or, possibly, it is required for proper functioning. For example, while juvenile Sticklebacks could be raised in darkness, they would not be fully functional. Innate in this context is the opposite of "environmentally-induced". Likewise, the interaction of internal machinery to environmental factors that are not eliminated from experimental manipulations are thought to serve to contribute to the internal machinery's developmental "programming". According to Tinbergen, there are two means by which organismal machinery is programmed in the individual: first, by evolutionary "trial-and-error-interaction with the environment which results in the specializations of the genetic instructions", and second, by "the ontogenetic interaction between the individual and its environment." Because programming could have its source in evolution, Tinbergen stresses that questions about causation of ontogeny are dependent upon the question of survival value, both rooted in Darwinian explanation.
4. **Evolution**. According to Tinbergen we should recognize that some behaviors are species specific and, like structures, can be studied comparatively between species, invoking Darwin's theories of common descent and natural selection. This is reasonable on the background assumptions that "individuals and

populations differ as much in their hereditary behaviour 'blueprints' as in their hereditary structural blueprints"; and, "the genetic variation on which natural selection can act" is found in the hereditary blueprints.

The objective, then, for evolutionary explanation is to both elucidate the course of evolution and unravel its dynamics. The methods of the former are the same employed by the evolutionary taxonomist investigating physiological or structural characteristic. Beginning with a monophyletic group, the investigator judges the degree of evolutionary divergence by the degree of dissimilarity between innate traits ("of those characters that must be considered highly environmental-resistant ontogenetically"). Evolutionary dynamics are explained by both the methods of "geneticists" who identify the effects of mutations and cross-breeding on the evolution of the feature in question, and by the natural selectionist, who investigate either the survival value of the species-specific character or conduct controlled selection pressure experiments over a series of generations.

21.6 Tinbergen's View of Organisms as Objects

It is important to put Tinbergen's program in historical context. Tinbergen's idea to regard behaviors as organs was a necessary step in the development of ethology as a scientific and, more importantly, a post-Darwinian discipline. Organs are objects with material constitutions, not subjective qualities as past animal behaviorists regarded behaviors. Hence, the ontological commitment to objects elevated ethology to a materialistic science, invoking the method of generalization of characters by inductive inferences over direct observations. It facilitated causal analysis by regarding the subject of study as part of the causal nexus of internal and external forces (as are ordinary objects or complex mechanistic ones), and allowed ethology to be subject to genetic analysis of ontogeny and evolutionary analysis of phylogeny. Darwinian evolution (especially post-Modern Synthesis with its emphasis on genetics) operates within the same ontological commitments. Denis Walsh labels this set of commitments "objectancy", for it treats individuals as material objects with intrinsic causal dispositions, or "propensities to behave in certain ways when they encounter certain external conditions." (2018, p. 3).

The objectancy approach harkens back to a Newtonian paradigm, that refers to the natural properties of objects and the external conditions that cause them to change. The natural state of an object is not to do much at all—in motion and at rest they remain in their initial states until subject to external forces. In fact, many of the relevant properties that explain an object's change exist independently of the object (p. 9). Consequently, there is a clear demarcation between objects, which largely remain unchanged, and the forces that cause them change or transformation (either internally or externally), which exist independent of the object. Tinbergen adopts the same distinction between organisms and the forces that determine development and evolution. He treats organisms as objects that remain unchanged unless

they are subject to "influences" (Tinbergen's word) that exist independent of them. These influences might exist internally to them, as part of the "machinery" (again, Tinbergen's word, 1969, p. 424) that unfolds according to the complex interactions involving the species-specific genetically program, or the particular environmental conditions that the unfolding machinery encounters.

Further, Tinbergen's ethology relies on clear distinctions between organisms and the external conditions that determine their change. Organisms are demarcated by internal processes that generate variations of a genetical type which are then subjected to external forces, the environment, that selects among the variants. Both the internal processes and the external forces largely exist independent of the organism. The internal processes are dictated by a genetic program that is passed down to the organisms (from the outside) and was originally formed by external evolutionary processes. As Tinbergen said, the analysis of development is largely a matter of a process of elimination: vary environmental conditions and see if it makes any difference at all to the outcomes; if not, then, label the behavior as "innate". The internal-genetic explanation of development serves Darwinian evolutionary theory well because it explains differences between species—wolves, whales, and wallabies—in terms of genetic differences between them. Genetic differences are the stuff of evolution. The internal processes that genes control produce mutations and recombinations that are then tested for acceptability in the external environment (Lewontin, 1985, p. 42).

An advantage of the object-oriented approach to investigating organisms and their behaviors (as organs—another class of object) is that it provides us with a sense of regularity and order out of the chaos of individual variation. Newtonian physics is, again, the inspiration. Drop feathers from a height and they land in a scatter. But the scatter has a discernible pattern, beginning with a central cluster where most feathers land and radiating out where the fewer feathers lie. The Newtonian explanation distinguishes between regular and accidental causes. The regular causes are expressed as natural laws that determine the propensities of the object acting in the conditions of its state space. The center of the scattering is where each feather would land had it been subject to the main forces of gravitation, without interference from minor forces of wind and friction. The latter can be largely ignored, because the main objective is to see through the blooming, buzzing confusion of individual variation to find an underlying order. Tinbergen adopts the same approach for ethology. The unit of analysis is behavior that an individual expresses that is typical of its species. That allows Tinbergen to investigate "puzzling behaviour patterns" (1969, p. 412) in a systematic way, taking advantage of Darwin's theory of common descent. Behavioral patterns are treated as species-specific organs with features that are intricately adapted to their environment. By focusing on species-specific behaviors, ethologists can see past the buzzing, blooming confusion of individual variation and regard common regularities, the functions that adapted the feature to its environmental conditions.

Another way the objectancy stance provides order to the universe and its myriad of objects is by imposing a hierarchy of ascending functional systems where each system can be broken down into smaller sub-systems. The relation between the

containing systems and the systems within them are a matter of causal connection—each sub-system produces an effect which together with its conspecifics produces the causal properties of a whole. Thinking about the universe in this way is advantageous to investigators of the natural world because of our natural cognitive ability to analyze and break down complex ideas into their simple parts recognizing how each part contributes to the whole. The critical assumption is that there are clear demarcations between objects from each other and from the containing system to which they contribute. On Tinbergen's view, animals are machines with internal parts and each part is seen as producing effects that contribute to a containing system. Individuals are a nexus of a variety of internal and external forces. Complexity has an easy measure by this machine style of analysis—to be more complex means that the system has more interlocking parts, sometimes with more feedback mechanisms. The point is, on Tinbergen's treatment, complexity is still a matter of cause/effect of the various components that make up the functional unit; there is no need to invoke teleological language to explain observed complexity. The view of individuals and their characters as objects facilitates the use of this venerable style of mechanistic analysis (hierarchies of systems within systems) that has served physics and chemistry well since at least the seventeenth century and is prominent in Tinbergen's questions.

In sum, Tinbergen's ethology, including his approach of providing answers to the four questions—causation, survival value, ontogeny, and evolution—is based upon treating organisms as objects with vestiges of a Newtonian paradigm: behaviors of interest are species-typical (i.e. typical of a type; variations within the type are accidental), organisms exist at the nexus of independent forces that determine both their internal development and external selection, explanations largely refer to what happens to organisms (rather than what organisms do), and how organisms and constituent parts contribute to the hierarchy of mechanistic systems.

21.7 Organisms as Agents

The problem is that the objectancy approach to organisms and their features is an incomplete foundation from which to ground an investigation of life and behavior. The objectancy approach had the desired effect of facilitating causal analysis, but it gets a lot about ontogeny, causation, survival value, and evolution wrong. And it neglects important questions about behaviors generated by advances in developmental and evolutionary biology, as well as questions generated by thinking about the limits of the biologizing research program for human behaviors. Most importantly, objectancy ignores the role organisms and historical processes play in answering each of the four questions. Put another way, the objectancy approach, as Walsh (2018) puts it, ignores "agency". Agents are not mere objects. Objects remain the same until they are subject to forces. Agents have an additional feature from that of objects, they initiate their own changes. Tinbergen was so determined to avoid any association between ethology and teleology that he neglected to provide a

means to explain patterns of purposive behaviors that are well-confirmed by good observational data. This entire object-oriented version of Darwinian biology, with its main goal of "facilitating causal analysis" is inadequate to the task of explaining animal behavior (both human and non-human) because it ignores what the agent's contribution is to causation, survival value, ontogeny, and evolution. As Lewontin put it: "classical Darwinism places the organism at the nexus of internal and external forces, each with its own laws, independent of each other and of the organisms that is their creation...The organism is merely the medium by which the external forces of the environment confront the internal forces that produce variation." (1985, p. 88 cited in Walsh 2018, p. 11).

21.8 Adding Agency to Tinbergen's Four Questions

We have argued that Tinbergen's objectancy perspective is incomplete. In this section, we will explore some of the ways in which an agency perspective adds to and changes how we think about Tinbergen's four questions. This is not meant to be an exhaustive discussion, but instead a speculative introduction meant to motivate further exploration.

1. The **causation** question is about "what causes the behavior?" Recall that Tinbergen's goal was to put ethology on firm scientific grounds and to reject mystical appeals to anthropomorphism and teleology on the one hand and the overly reductionist approach of behaviorism on the other. Around the same time that Tinbergen was reformulating animal ethology, psychology was undergoing the cognitive revolution and abandoning its behaviorist past. In contemporary cognitive science, invoking concepts like intentions, goals, and desires are perfectly reasonable and perfectly scientific. Explanations at this level can comfortably co-exist with explanations at other levels, including the neurophysiological. In fact, a complete psychological account should involve explanations at level of computation, algorithm, and implementation (Marr, 1982). In Tinbergen's approach, the goal was to get as close to the level of implementation as possible; higher levels were considered less scientific. However, it's precisely these higher levels that feel more natural when talking about agency. At the level of computation, we can ask about the kinds of goals that agents have, or about the kinds of goals that components of their cognitive system have. Returning to our previous discussion of causation, from an agency perspective, it's perfectly scientific to say that "the animal attacks because it feels angry". This is not to deny any kind of lower-level, neurological understanding, but instead add to it.
2. The **survival value** question seeks to explain "how the behavior works" by reference to its adaptive function. In the object-oriented approach, the environment is supposed to present a population of organisms with some set of adaptive problems. The process of random mutation generates candidate solutions, in the form of variation in the population, and natural selection favors better solutions.

Over time, the form of behaviors will be fashioned to adaptively function in the environment. While this textbook account no doubt captures many cases of adaptation, it is by no means the only way in which adaptation occurs. Take, for example, the process of "genetic assimilation" (Waddington, 1953; West-Eberhard, 2003).

Let's imagine a mainland population of birds adapted to a generalist foraging strategy with a generalist's morphology to match. Suppose that a small group or even just a pregnant female are blown off course and end up on a faraway island. The ecology of this island does not match the mainland ecology to which the bird was adapted. In fact, let's imagine that the only edible foodstuff on the island is an orchid like plant with a long flowering body that provides nectar. At first, the birds will frantically search the island for edible items and find little success. Eventually, the birds will learn about that these flowers and how to extract nectar from them. Assuming there is no social learning in this species, each generation of birds must learn to feed on the nectar of these flowers. This process of learning within each generation sets up a recurrent phenotype-environment match. But the match is entirely driven by the goal-directed actions of the birds (i.e. seeking nutritious foods from the environment). Now, imagine there is genetic variation in this population, as there must be. Any mutation that changes beak morphology to better extract nectar from these long flowers will be favored by natural selection. Likewise, any changes to gut morphology to extract calories more efficiently from nectar will be favored. And, natural selection will also favor learning systems that are prepared to associate those particular flowers with food. Over time, the bird population will become behaviorally and morphologically adapted to being a specialist feeder on this flower. However, the process by which this happened involved the purposive and goal-directed behavior of birds, generation after generation. These birds were not passive objects that were transformed by the processes of mutation and natural selection. Instead, these birds created the conditions that led mutation and natural selection to reconfigure their behavior and morphology.

3. The **ontogeny** question investigates the "change of behavior machinery during development." Tinbergen's view of ontogeny has all the hallmarks of a commitment to viewing organisms as objects. It begins with the genetic program sourced from the outside—the parental organisms. The process of development is largely a matter of mapping how this species-typical genetical program combines with the set of environmental conditions to which it is exposed. On this view, the organism is passive; development happens to it. As Lewontin (2001) argues, this approach ignores the myriad of ways in which organisms play an active role in determining how the "environment" influences their development.

   - Organisms **determine** which elements of the external world are put together to make up their environments. A Phoebe and a thrush can both co-exist in a plot of land, but it doesn't mean they share the same environment. A Phoebe uses grass for nesting, has no use for the stones that the thrush uses as an anvil.

- Organisms actively **construct** a world around themselves. Earthworms make burrows in land that are filled with the aqueous substance similar to that of an ocean from which their ancestors thrived for 50 million years (Gilbert & Ebel, 2015, p. 466).
- Organisms **alter** and transform matter and energy, passing along one form to others which then can be used as a resource (2001, p. 55). Mycorrhizae is a symbiotic relationship between plants and fungi which have effects on individual life cycles, gene expression and inter-species systems of energy transfer. The fungus benefits from direct access to essential carbohydrates that the root tissue provides. In exchange, orchids acquire carbon that the fungi provide, without which the seeds could not germinate (Gilbert & Ebel, 2015, p. 86). The wood wide web refers to the energy network formed by the mycelia of fungi that colonize a roots of various plant species. The result of this complex and reciprocal transformation of energy is a distribution system and even a communication network. This is a remarkable example, because out of features of two different kinds of agents, plants and fungi, is a third order agency constructed out of the symbiotic relationship. There is a fledging research program around the idea that organisms are really "holobionts", composed of an ecosystem involving a variety of systems sharing and outsourcing some essential functions.
- Organisms **modulate** the statistical properties of external conditions. Plants photosynthesize when energy is available during the day but not the night. Desert plants may have an opportunity to germinate and grow only on one out of five years. Modulation is an individual's way of flourishing despite the fluctuations in availability of essential resources. Rituals like feasts and potlatches, artifacts like grain sheds, freezers, and even the creation of currency are important human manifestations for the need to modulate environmental fluctuations.
- Organisms **transduce** one kind of physical signal to another one. Organisms do not simply receive information from the signals they encounter from the world but they convert the signal into a different kind so it can be perceived by the organism's functioning system. Mammals convert rise in air temperature by the hypothalamus to an endocrine signal which causes changes in a number of chemical, neural, and anatomical activities. Ironically, Lorenz's and Tinbergen's work provided breakthroughs in understanding some of these kinds of signal transductions, but Tinbergen did not recognize the theoretical ramifications against the objectancy approach: organisms are not passively responding to external conditions, but actively commingling with their environment, adjusting in ways that enhance their flourishing.

4. The question of **evolution** entails the unraveling of the evolutionary dynamics that led to the current behavioral form. In the objectancy perspective, and as with the question of survival value, this amounts to treating the population of organisms like a bunch of billiard balls subject to various evolutionary forces. In the agency approach, organisms become active participants in the processes that

shape their evolutionary histories. As discussed in the section on ontogeny, organisms act upon the environment just as the environment acts upon them, making apportioning causal responsibility much more interactive and holistic. As Walsh (2015, p. 157) puts it, "Just as the actives of the system as a whole are the causal consequences of the activities of the component parts, so too the activities of the component parts are controlled and regulated by the system as a whole." When the aggregate actions of a population of organisms result in measurable changes to the environment, the adaptive landscape has been altered. In this way, organisms shape the environments in ways that result in novel selection pressures acting on subsequent generations, a process called "niche construction" (Odling-Smee et al., 2003). A canonical example of this process is provided by beavers constructing dams across river systems, thereby creating lakes, and changing the flow of water through the environment. These changes not only affect the subsequent evolution of beavers, but also of other organisms in the environment.

21.9 Objects Languish, Agents Flourish

Recall that Tinbergen formulated his object-oriented approach to organisms and behaviors in part to combat mystical teleological thinking inherent in the ethology literature at the time. However, as Okasha (2018) points out, there are good reasons to treat organisms as agents, regardless of their cognitive abilities: (i) organisms are the locus of goal-directed activities, (ii) organisms exhibit "behavioral flexibility", (iii) organisms possess adaptations that "appear designed for a purpose". Lewontin's (2001) description of the various things that organisms actively do in their environment provides many instances of what Okasha is talking about. Examples of goal directed and flexible behaviors including determining which elements of the external world are put together to make up "their" environment, and actively constructing a world around them. Okasha adds examples of courtship behavior, way-finding or homing, and food storage and retrieval, which are commonplace in nature.

To be sure, nothing in Okasha's three reasons for adopting agency necessitates an overhaul in Tinbergen's approach to answering the four questions. In fact, Okasha means to demonstrate that all three rationales are defensible from conservative biological practices. However, as Walsh (2015) points, treating organisms as purposive, self-regulating, goal-directed entities turns traditional Darwinian thinking on its head: "there is no need to think of selection as a discrete cause that introduces adaptive bias into population change." (p. 157) That is to say, a consequence of taking the agency view seriously is that Darwinian evolution is no longer the theoretical structure at the center of explaining adaptive change, the developmental system is.

To see how deeply this upsets Tinbergen's objectancy approach to answering his questions recall how Tinbergen treats the question of survival value and evolution of adaptive behaviors. On the evolutionary approach, behaviors are adaptive because they confer fitness-enhancing benefits. To answer evolutionary questions about a

feature's origins, we invoke Darwinian theory: adaptations are genetically inherited variants that in the past conferred fitness-enhancing benefits. Over time the direction of evolutionary population change favored these variants. To answer questions about current survival value, Tinbergen stressed that the current selective regime need not be the same as what a population experienced in the past. That's why Tinbergen introduced survival value as a distinct question from evolutionary history. But the underlying mechanism is the same—adaptation explained by Darwinian selection. But, by putting agency at the center of the investigation, you detach adaptation from its genetical, fitness-enhancing interpretation, and replace it with a broader notion of "flourishing". Flourishing in this sense is not a throw-back to Tinbergen's spiritual interlocutors. Rather, the concept of an agent's flourishing is grounded in modern-day views about ontogeny (as we have described, above). As Walsh (2015) puts it: "In development organisms orchestrate, integrate, accommodate and negotiate the various causal influences from genes, genomes, epigenetic factors, cells, tissues and environments in the production of a stable, highly adaptive responsive entity. That, in turn, requires acknowledging the significance of organismal purposiveness for evolution."

21.10 Bridging Evolution and the Social Sciences with Agency

One advantage of this theoretical freeing of flourishing from its evolutionary (fitness-enhancing) interpretation is it makes the program of biologizing behavior more palatable for traditional social sciences. In addition to criticizing Tinbergen's approach to the four questions as an insufficient biology, we also criticized it an insufficient social science. To see why, let's start with a critical look at those precincts of the social sciences that have adopted evolutionary approaches and in implicit or explicit ways engage in human ethology within Tinbergen's framework.

The first iteration of evolutionary social science was in the form of sociobiology (Wilson 1975). This paradigm was rightly criticized for reductionism gone too far in its attempt to explain every instance of human behavior in terms of fitness maximization (Gould & Lewontin, 1979). This was a level of reductionism that might have made even Tinbergen cringe. In this approach, only one question matters: How does the behavior increase survival value? In this framework, there is no scope for mechanisms as there is apparently a direct causal connection between adaptive problem and fitness-enhancing behavior. Likewise, development and evolution drop away. In a way, the sociobiology approach adopts an agency perspective, but a strange kind of agency in which organisms, including humans, seek to maximize their inclusive fitness, ultimately and faithfully serving their genetic masters.

In the wake of human sociobiology arose "three styles" of doing evolutionary social science (Smith, 2000): human behavioral ecology, evolutionary psychology, and cultural evolution. While these disciplines represent much more sophisticated

approaches to the study of human behavioral and social science, they are still firmly rooted in what Walsh calls the objectancy perspective. In their own ways, each of these disciplines ignore the role for agency in human affairs.

1. Human behavioral ecology (Borgerhoff Mulder, 1991; Cronk, 1991; Smith & Winterhalder, 1992) drew inspiration from economics and posited the ability for humans to behave in ways that were optimized for their environment in terms of fitness maximization. This approach typically invokes the "phenotypic gambit" (Grafen, 1984) and "black boxes" the mechanisms underlying behavior, including its acquisition and evolution. As with sociobiology, there's a kind of agency here if we're willing to assume that organisms are trying to maximize fitness. In this case, agency doesn't reside within organisms; instead, the agents seem to be the underlying genetic programs which seek to maximize their own fitness by having their host organisms optimize behavior in ways that correlate with fitness maximization. However, most practitioners of human behavioral ecology do not make this assumption. Instead, the phenotypic gambit is taken as an epistemological approach, not an ontological commitment. As such, the approach has little to say about the issue of agency.
2. In evolutionary psychology (Barkow et al., 1992; Buss, 2014; Gaulin & McBurney, 2003; Pinker, 2003), there's no agency left. Instead, all causal force is attributed to natural selection which shapes the cognitive and behavioral mechanisms to behave in adaptive ways. In this view, development is similar to Tinbergen's sense of development, a species-typical genotype is exposed to a set of environmental conditions which results in an unfolding process of development.
3. Cultural evolution (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981) draws inspiration from the "blank slate" view of human nature. In this view, natural selection shaped the capacity for cultural transmission, thereby creating the conditions for a second evolutionary process that affects human evolution: culture. If in evolutionary psychology it was natural selection that adapts humans to their environment, in the cultural evolution approach, it's culture. There are various forces of cultural evolution which, over time, adapt a population of humans to their environmental conditions. This approach tends to treat individual humans are passive parts of this process, blank slates upon which culture can inscribe norms, values, and behaviors.

While these various schools of evolutionary social science have been successful at guiding the study of human behavior, they seem to leave little room for agency, at least agency within individual organisms. This matters because humans are the most complex types of agents out there. If an agency approach to ethology results in better biology, then it seems to be a requirement for any attempt at an evolutionary social science. Furthermore, interest in agency has been an important part of the social sciences, especially in the last fifty years. If the goal of the evolutionary social sciences is further penetration into the social sciences and humanities, then it seems to be of paramount importance to offer an evolutionary approach to human ethology with agency at its heart.

Obviously, exploring the ways in which evolution and agency can work together in fashioning a new kind of social science is a daunting task. Here, we focus on one example to see how an agency approach may help to narrow the gap between evolution and the social sciences. We'll consider ritual as this has long been a topic of interest in the social sciences, and a recent issue of *Philosophical Transactions* (Legare & Nielsen, 2020) has focused on how Tinbergen's four question approach can contribute to the study of ritual.

Rituals are a series of actions, which are regularly repeated over the years and generations by a community of individuals, and which embody the beliefs of that group of people and foster a sense of community. The study of ritual has a long and deep history in many social science disciplines, especially sociology and anthropology. For example, Durkheim and later functionalist anthropologists of the mid twentieth century focused on the socially integrative functions of rituals. For anthropologists like Clifford Geertz and Victor Turner, rituals were important in terms of their symbolic meaning to practitioners.

In the recent special issue on ritual, the authors apply Tinbergen's four questions to the study of ritual. The claim is that this approach will revolutionize the study of ritual. However, as with the evolutionary social science disciplines discussed above, the authors in this special issue adopt an objectancy perspective. The humans engaged in these ritual activities are relatively passive participants. A well-known example of this approach involves the work of Richard Sosis. As Sosis and Bressler (2003) point out, many collective rituals involve costly displays on the part of the practitioners. Drawing on costly signaling theory, they argue that one of the main functions of these costly rituals is to selectively filter out those individuals who are not committed to the long-term goals of the community. Many communities are sources of cooperation. The problem with cooperation is the presence of free riders, those who partake in the gains of cooperation without contributing to it. The authors argue that costly ritual displays act as a filtering device. Those who are willing to pay the costs of cooperation are also willing to bear the costs of the ritual. Those who seek to free ride on the hard work of others are less willing to incur the costs of rituals. We believe that there is much to this argument. However, this approach treats individuals as coming in one of two fixed types: cooperators and free riders. Some process of cultural evolution, external to the cultural practitioners, has created the institution of costly rituals as a way of filtering among individuals, admitting cooperators into the community and rejecting free riders.

But this is not the only function of ritual. Malinowski, an early figure in anthropology, argued that rituals give humans a comforting sense of control, especially during times of uncertainty. In this view, humans have beliefs about how the world works and engage in ritual behavior in order bring about useful interventions. The work of Evans-Pritchard (1937) is instructive. Evans-Pritchard argued that the Azande had two kinds of explanations for unfortunate events, one materialistic and one intentional. For example, suppose that a child suddenly falls out of a tree and dies as a result. The Azande would certainly agree that the death resulted from the fall. However, they would ask another question: "Why was it this boy that fell from the tree and not some other boy?" This second question involves a different kind of

answer, one often involving the practice of witchcraft. Someone in the village must have wished ill for that boy and, as a result, the boy falls from the tree. While we may not agree with this causal logic, it has real world consequences for the Azande, including rituals to uncover who the witch was. Explaining this kind of ritual is very different than the kind of explanation Sosis and Bressler offer from costly rituals. An important aspect of rituals is to make sense of the world and gain some sense of control over it. This is not the kind of thing that an object would do. This is the kind of thing an agent does.

This approach to studying behavior is to take the program of biologizing behavior in a different direction than what Tinbergen envisioned. Rather than regarding behaviors as parts of objects for the sake of applying a mechanistic methodology, regard them as expressions of their goal-directed, behaviorally flexible, purposive activities. This is closer to what human social sciences endeavor to do.

21.11 Tinbergen's Fifth Question

While an agency-focused approach to Tinbergen's four questions would do a lot to make evolutionary approaches more palatable to some social scientists, it may not be enough for others. One aspect of agents, as opposed to objects, is their ability to actively participate in their own transformational processes and in modifying their environments. We can think about this as one kind of agency. But there's another kind of agency, especially for humans: consciousness. Conscious agents not only act upon the world, they have a subjective experience of themselves and their world. They realize what they are doing to the world and what the world does to them. Mary the color scientist not only sees the wavelengths of light corresponding to the color red, but upon seeing an apple for the first time she has the subjective experience of red (Jackson, 1982). Nagel's (1974) question "What is it like to be a bat?" seems to offer a difficult challenge for the Tinbergen approach to studying behavior. While we can map the mechanisms, ontogeny, function, and evolution of echolocation, we will never be able to experience what that form of navigation is like. The degree to which this kind of consciousness or subjective experience makes a difference in explaining and predicting how organisms, especially humans, behave may make a difference. But it's not clear how to deal with this kind of phenomenon within Tinbergen's framework. Perhaps this requires another kind of question: Tinbergen's Fifth.[2]

[2]For an excellent discussion on the problem of agency and the problem of subjectivity in the social sciences, see Blute, 2010.

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