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Levels of Analysis and Explanatory Progress in Psychology: Integrating Frameworks From Biology and Cognitive Science for a More Comprehensive Science of the Mind

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Levels of analysis are crucial to the progress of science. They frame the epistemological boundaries of a discipline, chart its explanatory goals, help scientists to avoid needless conflict, and highlight knowledge gaps. Two frameworks in particular, *Tinbergen's four questions* from biology and *Marr's three levels* from cognitive science, hold immense potential for psychology. This article proposes ways to integrate the two frameworks and suggests that doing so helps resolve key confusions and unnecessary conflicts in psychology. Integrating these two frameworks clarifies what "mechanism" really means, sheds light on how to test evolutionary hypotheses in psychology, and specifies what is required for a comprehensive explanation of a behavior or cognitive system. Adopting and integrating these two theoretical frameworks has the capacity to spur progress in psychology and to clarify what is needed for a comprehensive science of the mind.

Keywords: levels of analysis, Tinbergen's four questions, Marr's levels of analysis, evolutionary psychology, mechanism

Why Do Foster Bird Mothers Feed Their Parasite Chicks?

Brood parasites are birds that deposit their eggs in other birds' nests, to be incubated and raised by unwitting foster parents (e.g., Payne, 1977). The parents take care of the parasite chicks, feeding them and raising them despite their lack of genetic relatedness. The parasite chicks can reach monstrous sizes—much bigger than their adopted siblings, whom they sometimes kill, and much bigger even than their foster parents. The foster mother works herself to the bone to feed a gargantuan interloper: a needy, hungry, siblicidal monstrosity—and a genetic stranger to boot. Why would a foster parent do this?

If you attempt to apply the principles of evolution to the behavior directly, the phenomenon is difficult to make sense of. Why would a mother bird waste her energy and allow her offspring to be deprived of resources so she can feed a genetic stranger? The phenomenon becomes explicable, however, when you home in on the information-processing level of analysis: Bird mothers' information-processing systems have evolved to attend to specific cues, including how loud the offspring beg and how conspicuously colored their gapes are (Davies et al., 1998; Gotmark & Ahlström, 1997; Kilner, 1997). Mothers use these specific cues to know how much food the offspring need. Brood parasites have evolved to "break the code" by mimicking these exact cues, producing even louder sounds than the host's offspring and displaying similarly colored conspicuous gapes (Davies et al., 1998; Hunt et al., 2023; Payne, 2005). In the case of hosts that have evolved sophisticated discriminatory abilities, such as the superb fairy wren, the brood parasite has *coevolved* a vocal signature that mimics the chicks of the host species (Langmore & Kilner, 2007; Langmore et al., 2003). In the case of hosts who detect parasite eggs and eject them, parasites have evolved to hijack parental systems by laying eggs that mimic those of their hosts (e.g., Brooke & Davies, 1988; Davies & Brooke, 1989; Feeney et al., 2014; Langmore & Spottiswoode, 2012; see also Dawkins & Krebs, 1979). Because they produce the very cues that the host mothers' information-processing systems have evolved to take as input, the parasite chicks successfully trick the mothers into treating them like genuine offspring.

Mother birds are also attuned to when eggs appear in their nest: If a brood parasite egg appears at the wrong time (e.g., before the mother has started laying her own eggs), then the mother knows it is not hers and rejects the intruder egg. Consequently, many brood parasites have evolved to break this code as well: They deposit their eggs at exactly the right time, right after the mother has begun laying her own, but before she has finished, such that she cannot be sure it is an intruder and cannot afford to risk killing it (e.g., Alcock, 2009; Langmore & Kilner, 2007; Moskát et al., 2006).

The mother's ostensibly maladaptive behavior seems mysterious at first, but the puzzle is resolved when you adopt an evolutionary perspective centered on the information-processing level of analysis. The puzzling behavior becomes understandable in light of the fact that the parasite chicks are *code-breaking*: Supplying the mother's algorithms with the exact cues they take as input, from the timing of

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the egg laying, to the pattern and color of the egg, to the loudness of the chick's begging, to the coloration of its mouth. This example illustrates how the specific combination of an evolutionary perspective with the information-processing level of analysis takes a behavior that initially seems incomprehensible and renders it explicable. This key point has broader implications for the importance of levels of analysis in the development and maturation of psychology as a science.

Levels of Analysis and Scientific Progress

Levels of analysis play an important role in scientific progress. They provide researchers with a map of the explanatory territory, help scientists to avoid needless conflict, highlight knowledge gaps, and have the potential to increase the speed at which science advances. In particular, two frameworks focused on different levels of analysis—*Tinbergen's four questions* from biology (Tinbergen, 1963) and *Marr's three levels* from neuroscience and cognitive science (D. C. Marr, 1982)—hold great potential for progress in psychology.

Tinbergen's Four Questions

Niko Tinbergen, corecipient of the only Nobel Prize ever awarded for the study of animal behavior, offered behavioral science a key insight: To fully understand or explain any biological phenomenon, including behavior, we must answer four separate questions: (a) Why did it evolve? (*function*), (b) How did it evolve over time? (*phylogeny*), (c) How does it develop in the animal's lifetime? (*ontogeny*), and (d) How does it work in the present moment; what mechanism underlies it? (*mechanism* or *immediate causation*; Tinbergen, 1963; see also Huxley, 1942). The first two questions are evolutionary and are sometimes grouped together as the "ultimate" level of analysis, whereas the second two pertain to the span of a single organism's life and are sometimes grouped together as the "proximate" level of analysis (see also Alcock, 2009; Bergman & Beehner, 2022; Mayr, 1961; Nesse, 2019a). The central insight is that to fully understand a behavior, we must tackle all four levels of analysis. Any answer that does not address all four levels is necessarily incomplete.

A second key point is that these levels are complementary, not conflicting: An answer at one level of analysis does not obviate the need for an answer at another level, and all of the levels are needed for a complete explanation of the phenomenon (Al-Shawaf, 2019; Nesse, 2019a; Tinbergen, 1963). The eventual goal is to achieve a comprehensive explanation of the behavior in question. In pursuit of this goal, the different levels of analysis are explanatory partners, not competitors.

Tinbergen's four questions serve as the background theoretical framework for all research in animal behavior and cognition. The framework has proven immensely useful in biology, and the proximate–ultimate distinction is widely considered a foundational organizing principle for the study of animal behavior and cognition (Alcock, 2001, 2009). The same organizing principle is also crucial to medicine (Grunspan et al., 2018; Nesse, 2019a; Nesse & Williams, 1994), anthropology (Hinde & Milligan, 2011; Shattuck & Muehlenbein, 2015), psychology (Al-Shawaf, 2019; Cosmides & Tooby, 1997; Lewis et al., 2017; Scott-Phillips et al., 2011), and psychiatry (Nesse, 1984, 2019b), although it has taken longer for its key implications to be widely appreciated in these fields. As biologist Ernst Mayr put it, "no biological problem is solved until both the proximate and the evolutionary causation has been elucidated" (Mayr, 1982).

Marr's Three Levels of Analysis

In the late 20th century, David Marr ignited progress in the cognitive and neural sciences with an important insight: for a complex system like the mind–brain, a complete reckoning requires three complementary levels of analysis (D. C. Marr, 1982). Marr called these the *computational theory*, the *algorithm*, and the *hardware implementation* levels.

In Marr's framework, the *computational theory* (Level 1) specifies what the function of a neurocognitive system is; what it does and why. This level focuses on what task or problem the system is supposed to handle. The *algorithm* (Level 2) specifies the information-processing procedures used by the system in order to solve this problem. This level of analysis emphasizes the representations the system operates on and the decision rules and algorithms it uses. Finally, the *hardware implementation* level (Level 3) specifies how this information-processing system is physically realized—how it is physiologically instantiated in the brain. Marr's insight was that all three levels of analysis are necessary for a comprehensive understanding of the mind–brain (Cosmides & Tooby, 1987; D. C. Marr, 1982; D. Marr & Nishihara, 1978). This framework has proven immensely useful in neuroscience and the cognitive sciences (Bechtel & Shagrir, 2015). Among other benefits, it has led researchers to pay more attention to the previously neglected computational theory level of analysis (Level 1) and has clearly illustrated that neurophysiological explanations of phenomena (Level 3) do not obviate the need for algorithmic or information-processing explanations (Level 2) of those same phenomena (e.g., Cosmides & Tooby, 1994a; Cooper & Peebles, 2015).

Integrating Tinbergen and Marr's Theoretical Frameworks

This article aims to show that uniting these two frameworks—Tinbergen's four questions and Marr's three levels of analysis—can propel psychology forward by clarifying what is needed for a comprehensive science of mind, helping to resolve stale and unproductive disputes, and highlighting what is missing from the discipline. How can we best integrate the two frameworks?

Marr's *computational theory* is roughly equivalent to Tinbergen's *function* because it specifies what a system is for or what problem it is meant to solve. Tinbergen's approach was more explicitly evolutionary than Marr's, but Tinbergen's function and Marr's computational theory both center on what problem the system is "trying" to solve, what task the system is meant to handle, and why the system does what it does.

As we shall soon see, Marr's second level, *algorithm*, is a key component of Tinbergen's *mechanism*. Marr's third level, *hardware implementation*, is the other key component of Tinbergen's mechanism. Tinbergen's mechanism, in other words, has two facets. They correspond to Marr's algorithm (the information-processing facet) and hardware implementation (the neurophysiological facet).

Tinbergen's other two questions, *ontogeny* and *phylogeny*, do not have exact counterparts in Marr's framework. The relationship

Figure 1
The Relationship Between Marr's Three Levels of Analysis and Tinbergen's Four Questions

	Ultimate	
Across Evolutionary Time	FUNCTION *Computational Theory* (Marr's Level 1. Specifies what problem or task the system is meant to solve.)	PHYLOGENY
	Proximate	
Across the Organism's Lifespan	MECHANISM *Algorithm* (Software; Marr's Level 2. Specifies the representations, algorithms and decision rules used by the system.) - **Step 1:** Inputs - **Step 2:** Decision rules and weighting algorithms - **Step 3**: Outputs *Neurophysiology* (Hardware; Marr's Level 3. Specifies how the system is physiologically instantiated.)	DEVELOPMENT

between Marr and Tinbergen's frameworks is shown in Figure 1[1] (see also Brase, 2014).

Clarifying how the two frameworks fit together is a useful conceptual step because it resolves some unnecessary conflicts in psychology, clears up common confusions about what the term "mechanism" really means, and specifies what is required for a comprehensive explanation of a behavior or cognitive system.

To see this, it helps to first unpack how these levels of analysis relate to the different branches of psychology.

Levels of Analysis and the Branches of Psychology: What Is Needed for a Complete Explanation of a Behavior or Cognitive System?

For more than a century, psychology has been largely focused on the mechanism level of analysis. Most branches of psychology restrict themselves to different aspects or facets of this level. For example, neuroscience, behavioral endocrinology, cognitive psychology, social psychology, personality psychology, and psychophysiology all tackle different facets of mechanism. This may initially sound surprising if you equate "mechanism" with "physiological mechanism," but mechanism is much broader than that: It refers to *how the system works*. Cognitive psychology explains how the system works in terms of information-processing structure, social psychology addresses its social inputs and outputs and how it operates in groups, behavioral endocrinology and neuroscience address its physiological underpinnings, and so on.

To be more precise, these branches focus *mostly* on mechanism. Exceptions to the rule include developmental psychology, behavioral genetics, and some areas of clinical psychology, which also attend to ontogeny; vision science, which also attends to function; and evolutionary psychology, which also attends to function and phylogeny. A precise characterization might be that the various branches of psychology are mostly focused on mechanism, occasionally incorporate development, and are almost always limited to the proximate level of analysis. They typically ignore the ultimate level of analysis.

At a minimum, to achieve a comprehensive science of the mind, we must expand our conception of *mechanism* to include both the information-processing level and the physiological level, and, recognizing that mechanism is only one of four of Tinbergen's questions, eventually reach a point where psychology tackles all four key questions and no longer ignores the ultimate level of analysis. Currently, our field is far from this goal.

Evolutionary Approaches to Psychology: From Function to Mechanism

It is often said that evolutionary psychology focuses on Tinbergen's *function*, asking why a certain phenomenon is the way it is, or why a psychological system or behavior exists in the first place. This distinguishes it from the rest of psychology, which focuses almost entirely on the proximate level of analysis.

This basic truth comes with the associated misconception that evolutionary psychology focuses *mostly or exclusively* on function (or on function and phylogeny; for an example of this error, see Bailey, 2020). This is incorrect: The main way one tests evolutionary psychological hypotheses about function is via the predictions they yield about mechanism. With some rare exceptions, ultimate hypotheses are typically tested via the proximate predictions they yield.[2] This point has important implications.

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[1] Note that this figure does not imply that Marr thought phylogeny and development were irrelevant. It simply means that Marr's classic levels of analysis are primarily focused on function and mechanism.

[2] An exception would be when a hypothesis about function (ultimate level) is tested via the predictions it yields about phylogeny (also ultimate level). For a few other exceptions—ultimate hypotheses that yield proximate predictions that are *not* specifically about mechanism—see, for example, Barclay (2006), Bjorklund and Pellegrini (2000), and Boyer and Bergstrom (2011). For some additional methods of testing, see Nesse (2011).

Hypotheses About Function Yield Predictions About Mechanism

Usually, the way one tests a hypothesis about the evolved function of a cognitive system or behavior is *by testing the proximate predictions that the hypothesis yields*. In other words, hypotheses about function lead to predictions about mechanism. For example, consider the hypothesis that disgust evolved to reduce our likelihood of infection. How can we know if that is the true function of disgust? We cannot peer into the past to see if that is why disgust evolved. Nor can we time travel, and disgust does not fossilize. But this does not matter, because researchers do not test hypotheses about function by peering into the past.

Instead, the way one tests a hypothesis about the evolved function of disgust is via the many proximate predictions it yields about how disgust ought to work in the present. For example, the disease-avoidance hypothesis about the function of disgust predicts that disgust should be a universal emotion (it is; Ekman, 1992; Sauter et al., 2010), that some stimuli should be universally disgusting (they are; Curtis et al., 2004), that these universally offensive substances should be pathogenic in nature (they are; Curtis et al., 2004), that we are more easily disgusted when we are sick or immunocompromized (we seem to be; Fessler et al., 2005), that triggering disgust or pathogen salience will make people behave in ways that reduce the likelihood of infection (it does; Mortensen et al., 2010), that disgust will be context sensitive and downregulated toward one's kin (it is; Case et al., 2006), that disgust will be characterized by a "better safe than sorry" error management bias (it is; Park et al., 2003), and that individuals who grow up in more pathogen-dense parts of the world will be more wary around other people (they are; Schaller & Murray, 2008). In other words, the way one tests this evolutionary hypothesis about the function of disgust is via the (many) proximate predictions it yields about mechanism, about how the system works, and about what triggers the emotion and what upregulates and downregulates it. Hypotheses about function are tested via the predictions they yield about mechanism because hypotheses about what a system is for (what its function is) specify how the system must work in order to achieve that function. This is why hypotheses about function generate predictions about mechanism, and indeed why functional hypotheses are tested via the mechanistic predictions they yield.

This is the main—and most important—way researchers test hypotheses about evolved function in the psychological sciences. To phrase it in more cognitive terms, a hypothesis about the evolved function of an information-processing system leads to predictions about how the system must be structured to achieve that function: What inputs it must take, what inputs it is expected to ignore, how it organizes inputs in a hierarchical manner, what algorithms and representational formats it employs, and what outputs the cognitive system yields. This is precisely what the conceptual tool of evolutionary task analysis is used for: You start with an analysis of the problem that must be solved, and this yields predictions about how a psychological system capable of solving the problem must be structured (Al-Shawaf, 2016; Al-Shawaf et al., 2016; Cosmides & Tooby, 1987; D. C. Marr, 1982; Tooby & Cosmides, 1990). In other words, the *function* level of analysis yields predictions about *how the mechanism is expected to work.*

In Biology and in Psychology, "Form Follows Function"

This is why scientists use the phrase "form follows function" (e.g., Cosmides & Tooby, 1994b; Pisanski et al., 2022): It means that a system's evolved function (the ecological problem a system evolved to solve) determines the form (the shape or structure) that the system takes (e.g., Sznycer et al., 2021). For example, consider the hypothesis that bats must have evolved a solution to the problems posed by loud sound waves, which risk damaging their sensitive ears. This is a hypothesis about function, and it leads to a prediction about mechanism: The bats will shut their hearing off every time they send out a loud sound wave, and turn it back on again every time the sound wave returns (which is exactly what they do; Dawkins, 1996).

In the case of anatomy, the word "form" in the phrase "form follows function" refers to the literal form or structure of the body part in question. For example, the function of the lungs (respiration) determines the shape they take as well as the fact that they include alveoli and cilia that help them accomplish their tasks. In the case of psychology, where the subject matter is cognitive systems rather than anatomical parts, "form" refers to the structure of the information-processing system. Here, the phrase "form follows function" means that the hypothesized function of a psychological system yields predictions about the information-processing facet of mechanism—predictions about how the cognitive system is expected to work (what inputs it is expected to take, how it will organize and process those inputs) in order to achieve its supposed function. There is a direct line from hypotheses about function to predictions about mechanism.

It is via these predictions about mechanism that we test hypotheses about evolved function. For example, consider the hypothesis that humans are equipped with psychological systems to avoid incest (Lieberman et al., 2007). This function-level hypothesis leads to the proximate prediction that cognitive systems for kin detection and incest avoidance will process two key informational inputs: childhood coresidence and watching your mother breastfeed another child (maternal perinatal association)—because both of these cues would ancestrally have meant this person may be your sibling. In this example, a functional hypothesis is leading to mechanistic predictions about which cues the cognitive system will take as input. The hypothesis leads to another mechanism-level prediction as well, which is that the incest-avoidance system will treat these cues hierarchically: If maternal perinatal association is present, the system will ignore childhood coresidence. However, if maternal perinatal association is absent, the system will take childhood coresidence as input (Lieberman et al., 2007). This is a very precise prediction about mechanism that was made a priori on the basis of a hypothesis about function: Older kids will be exposed to the breastfeeding cue, and so for them, the cue of childhood coresidence does not provide any extra predictive utility. By contrast, younger kids will not be exposed to the breastfeeding cue, so they will need to take the childhood coresidence cue as input. What we have here is another example in which a hypothesis about evolved function (incest avoidance) leads to specific predictions about mechanism at the information-processing level (which cues the system will process as inputs, and how it will rank those cues hierarchically).

It is widely underappreciated that this is the most common way to test hypotheses about evolved function in psychology. This is a key point because it belies the notion that evolutionary approaches to psychology study function without attending to mechanism, or that evolutionary approaches involve spinning stories about function without testing them (see also Alcock, 2018; Al-Shawaf, 2020b; Al-Shawaf et al., 2018; Lewis et al., 2017). It is difficult to hold these misconceptions when the logic of testing evolutionary hypotheses is made clear: Hypotheses about function are generally tested via the predictions they yield about mechanism.

In Many Cases, You Simply *Cannot* Study Function Without Studying Mechanism

In many cases, it is downright impossible to test hypotheses about function without studying mechanism. For example, the characteristics of a rabies infection—increased aggression and biting, frothing at the mouth—have often been interpreted as evidence of parasitic manipulation because these precise symptoms are well-suited to helping the rabies virus spread itself to other organisms. However, a closer look at the proximate mechanisms involved suggests that these symptoms may be caused by the host's immune response, not by the parasite itself (Hemachudha et al., 2002), and that behaviors such as increased aggression are governed by regions of the brain that are *not* inhabited by the rabies virus (Pinel, 1993). Furthermore, a substantial fraction of rabies victims become "dumb" (paralytic) not "furious" (aggressive or encephalitic)—and yet both types experience the salivation, even though only the encephalitic type experiences increased aggression (Thomas et al., 2005). This suggests that increased aggression in rabies may be unlikely to be the result of parasitic manipulation as once thought, and instead may be a byproduct of pathology. Examples like this underscore the point that researchers usually test ultimate hypotheses via the proximate predictions they yield, and draw attention to the corollary that the details of the proximate mechanisms can help researchers disentangle conflicting hypotheses about function from one another.

Here is a different way of putting it: If it is true that a cognitive system has evolved to solve a problem in the social or ecological environment, then there must be a correspondence between the structure of the psychological system (its *form*) and the problem it supposedly evolved to solve (its *function*)—there must be a reasonably good engineering fit between problem and solution (e.g., Sznycer, 2019). At its core, each hypothesis about an evolved psychological function specifies what information-processing form the cognitive system is expected to take in order for it to work—in order for the system to solve the problem that supposedly shaped its evolution.

Three additional points are worth mentioning. First, natural selection can often implement a function in many different ways; i.e., there are sometimes several different mechanism instantiations that can serve the same function (see, e.g., Penn & Frommen, 2010). Consequently, there is not always a clear one-to-one mapping between function and mechanism; a given function can be served by different mechanisms. This complicates the picture—but if anything, it leads to more cautious and conservative conclusions: Psychologists may generate mechanistic predictions that turn out to be wrong even though their broader functional hypothesis is correct. Psychologists using this approach risk drawing false negative conclusions much more often than false positives. Second, natural selection is a satisficing or "meliorizing" process, not an optimizing one, so the expected fit between form and function may be quite good, but need not be perfect (e.g., Dawkins, 1999; Maynard Smith, 1983; see also Simon, 1956). Third, in generating and testing mechanistic predictions, psychologists do (and should) make full use of the different aspects of mechanism discussed earlier: social inputs, physiological underpinnings, individual differences, and so on. In doing so, predictions about mechanism should include not only expectations of when an effect should be observed, but also predictions about when it should be downregulated or turned off (e.g., boundary conditions linked to contextual factors and individual differences; see Al-Shawaf et al., 2019; Lewis et al., 2017).

In essence, researchers seeking to test ultimate hypotheses about evolved function do so by specifying the proximate predictions their hypothesis yields about mechanism, and testing those predictions directly. Although there are many psychologists who study mechanism without giving much thought to evolved function, it is very nearly impossible to do the reverse.

Mechanism Is More Than Just Physiology

Oddly, the word "mechanism" in the human sciences is often narrowly taken to mean "the physiological details of how the system works." But the full picture is broader than this: *Mechanism* in psychology includes how the system works in the brain, how it works cognitively, how this is affected by the presence or absence of others, how personality traits and individual differences may affect the operation of the system, how genes, hormones, and culture affect how the system works; and so on. Broadly speaking, these many facets of mechanism can be approached from two overarching levels: the physiological level and the information-processing level. Together, these two levels constitute mechanism.

This idea is well-established in cognitive science, where it is widely held that neurocognitive systems can be described at both the neural level (the hardware) and the information-processing level (the software; D. C. Marr, 1982). Neither the hardware alone nor the software alone provides a full accounting of the system. Each is understood to be one facet, and neither one can be ignored.

These facets can be described using the terminology of Marr's three levels of analysis: the information-processing facet of mechanism corresponds to Marr's *algorithm*, and the neurophysiological facet corresponds to Marr's *hardware implementation*. A complete understanding of any given phenomenon must address both the algorithm and the neurophysiology. In psychology, there has been a reflexive, automatic tendency to equate the word "mechanism" with physiology and neuroscience. This may impede progress in our discipline because it leaves out a key part of the mechanism level of analysis.

The above analysis suggests two reasons why it is wrong to think that evolutionary approaches study function but ignore mechanism: First, it is nearly impossible to study function without studying mechanism, since functional hypotheses are most often tested via the predictions they yield about mechanism (see the section titled "Hypotheses About Function Yield Predictions About Mechanism". Second, there is a tendency in psychology to narrowly equate "mechanism" with physiology—and although evolutionary approaches to the mind spend a great deal of time at the mechanism level, they typically focus more on the information-processing facet of mechanism than the physiological facet (Al-Shawaf et al., 2016; Cosmides & Tooby, 1987; Lewis et al., 2017; Tooby & Cosmides, 2005).

This raises the obvious question: Why do evolutionary perspectives put so much emphasis on the information-processing facet of mechanism?

The Centrality of Information Processing From an Evolutionary Perspective

Evolutionary approaches to psychology emphasize information processing for three key reasons. First, if you go directly from the principles of evolution to behavior, skipping the information-processing level of analysis, this can lead to mistakes in explanation and prediction (Al-Shawaf et al., 2018; Cosmides & Tooby, 1997; Cosmides & Tooby, 1987). The example that opened this article, code-breaking in brood parasites, illustrates this point. Viewed purely behaviorally, the phenomenon doesn't make much sense. It is only when a spotlight is shone on the information-processing rules that generate the behavior that the phenomenon becomes interpretable.

Ignoring the Information-Processing Level of Analysis Can Lead to Mistakes in Prediction and Explanation

The odd behavior of fireflies highlights the same key principle. Males of the firefly genus *Photinus* routinely fly right toward females of the genus *Photuris*, where they are devoured by the females that beckoned them (Lloyd, 1965, 1975). Why do *Photinus* males fly right toward their predators? The answer is that each species has its own specific flashing–lighting code that it uses to communicate with conspecifics. *Photuris* females successfully mimic the *Photinus* code, luring the males in with the promise of copulation and then devouring the hapless seekers (El-Hani et al., 2010; Lloyd, 1965, 1975). As with the brood parasites, the male fireflies' behavior initially appears mysterious and inexplicable, but it makes sense as soon as you focus on the information-processing level of analysis: *Photuris* females are code-breaking, supplying the exact cues needed to trick the information-processing algorithms of *Photinus* males. From an evolutionary perspective, the information-processing level of analysis is key. It renders otherwise mysterious and puzzling behavior explicable and comprehensible.[3]

The case of incest aversion illustrates the same idea in humans (Lieberman et al., 2007). If incest aversion is the norm, why are there rare cases of biological siblings who end up sexually attracted to each other (e.g., Childs, 1998)? The evidence suggests that in many such cases, the siblings were separated at birth and reared apart in different homes. This means that their algorithms never got the key inputs of maternal perinatal association and coresidence during childhood, so they failed to tag each other as siblings. Depriving the cognitive system of these key inputs leads to a lack of incest aversion and generates the possibility of sexual or romantic interest later in life.

The opposite case of Taiwanese minor marriages is also instructive (Lieberman & Symons, 1998). In this phenomenon, a young boy and girl are betrothed to one another as children, and they grow up together in the boy's home with his parents. When they reach reproductive maturity, they are expected to act as husband and wife: love each other, be sexually intimate, and have children. In reality, the marriage often fails: They fail to develop sexual attraction to one another, they have affairs and fall in love with other people, and they have high rates of divorce (Lieberman, 2009; Lieberman & Lobel, 2012). Why? The information processing level of analysis once again helps to explain what is going on: Because the children grow up together, they process the input of childhood coresidence from an early age, so they mistakenly tag each other as siblings, develop a lack of sexual attraction to each other, and may even feel disgusted at the idea of consummating the marriage. If you try to apply the principles of evolution directly to behavior, it is difficult to make sense of sibling incest or sexual aversion in Taiwanese minor marriages. Attending to the information-processing level of analysis resolves both confusions, and it does so more readily than any other level of analysis (see also Al-Shawaf et al., 2018; Cosmides & Tooby, 1987; Tooby & Cosmides, 1989).

Conflicting Cues and Complex If-Then Rules

A second reason why the algorithmic level of analysis is so important is that organisms sometimes encounter multiple conflicting cues that need to be integrated. For example, if I encounter an in-group member who is high in social status but evinces signs of contagious illness, what should I do? To predict the result, we need to know how the mind's information-processing algorithms integrate conflicting cues of pathogens (which incline me to stay away) and coalitional value (which warn me against shunning this high-status person).

To take a nonhuman example, mouse parents who are fighting an infection will stop parenting their offspring when their pups are in mild danger, but will ignore their own illness and protect their offspring when the danger to their pups is more serious (Aubert et al., 1997; Schrock et al., 2020; Weil et al., 2006). To understand if-then contingencies like this, and especially to predict them in advance, we must understand the information-processing rules the mouse is using. In this case, the rule is something like "when sick, ignore offspring if the threat they face is mild, but if a cue of serious danger is detected, ignore sickness and attend to offspring. If not sick, attend to offspring." It is easier to understand—and to predict in advance—the mice's exquisitely context-sensitive behavior if you attend to the algorithmic level of analysis. Without this level of analysis, much context-sensitive adaptive behavior appears confusing or maladaptive. And from an evolutionary perspective, context-sensitive behavior is crucial and ubiquitous (Al-Shawaf et al., 2019).

The Cognitive Programs That Drive Behavior Operate on an Organism's Internal Representations, Not Directly on the External World

There is a third reason why evolutionary approaches to psychology highlight the importance of the algorithmic level: Sometimes, the most relevant factor in understanding an organism's behavior is not variable X in the external environment; instead, it is the organism's internal representation of variable X. For example, in a clever set of studies, Robertson and colleagues showed that the best predictor of shame is not whether somebody actually did something wrong, it is whether *they think that others think they did something wrong*, even if in reality the actor is innocent and they know they are innocent (Robertson et al., 2018). In triggering shame, it is not what a person did that matters most, it is what the person thinks other people think they did. The organism's internal representation of the external state of affairs is what's key—and this requires attending to the information-processing level of analysis.

Similarly, imagine a person who is very attractive, but has a poor self-image. They may fail to approach potential mates. Why? Because it is not really their "objective" mate value that drives their mate-seeking behavior, it is their internal representation of their own mate value. Which will better enable you to predict the courtship behavior of a

[3] While the behavioral ecologists who discovered these phenomena do not tend to focus on internal cognitive processing, the information-processing level of analysis nonetheless makes immediate sense of the data and makes it clear what is going on.

narcissist of average attractiveness: His true level of attractiveness or his inflated self-perception? It is the latter. In other words, an organism's representation of its own mate value can deviate, for systematic or random reasons, from its "objective" mate value. When the two conflict, the organism's internal representation will be more useful than the organism's "objective" mate value with respect to predicting and explaining the organism's behavior (see also Schmitt et al., 2017).

The argument is not restricted to shame or mate value, of course. An organism's behavior is driven by cognitive programs, and these programs operate on the organism's internal representations of the external world; they do not operate directly on the external world itself. The consequence is that from an evolutionary perspective, information processing—Marr's algorithm—is inescapably crucial when it comes to explaining and predicting behavior.[4]

John Tooby and Leda Cosmides made a similar point eloquently long ago:

> The fact that the brain processes information is not an accidental side effect of some metabolic process. The brain was designed by natural selection *to be* a computer. Therefore, if you want to describe its operation in a way that captures its evolved function, you need to think of it as composed of programs that process information. (Tooby & Cosmides, 2005, pp. 16–17)

In sum, there are three key reasons the information-processing facet of mechanism (Marr's *algorithm*) is so crucial from an evolutionary perspective. First, skipping the information-processing level can lead one astray in prediction and explanation. Second, for multi-cue integration problems and complex if-then rules, the information-processing level is essentially unavoidable. And third, for many problem sets that an organism confronts, it will not be the external variable that is most relevant in driving behavior; it will be the organism's internal representation of that external variable. For these reasons, an evolutionary perspective suggests that the information-processing facet of mechanism is indispensable for explaining and predicting behavior, and that careful attention to Marr's three levels is invaluable for evolutionary psychologists (see also Al-Shawaf et al., 2018; Lewis et al., 2022).

Levels of Analysis Help Dissolve False Conflicts Between Evolutionary and Non-evolutionary Hypotheses

As noted earlier, the way one tests hypotheses about evolved function is via the proximate predictions the hypotheses yield. This point has important consequences for how we should think about the conflict—or lack thereof—between evolutionary and non-evolutionary hypotheses.

Recall that in Tinbergen's four questions, mechanism and development can be grouped together as the *proximate* level of analysis, whereas phylogeny and function together constitute the *ultimate* level of analysis.

With this in mind, imagine an evolutionary hypothesis and a sociocultural hypothesis about the same phenomenon. The evolutionary hypothesis will typically begin with function *(ultimate level)*, and this hypothesis about function will yield predictions about mechanism *(proximate level)*. By contrast, the sociocultural hypothesis will typically begin and end at the proximate level: A proximate sociocultural hypothesis yields proximate sociocultural predictions. The ultimate level of analysis does not come into it at all. This simple point has three key implications.

First, it highlights the fact that only the evolutionary hypothesis makes any claims about the function level of analysis. The ultimate function specified in the evolutionary hypothesis has no counterpart in the sociocultural hypothesis. As a consequence, there can't be any conflict between the two hypotheses at this particular level of analysis (Al-Shawaf, 2020a).

Second, and by contrast, the evolutionary and sociocultural hypotheses both yield proximate predictions about mechanism—so it is possible for them to conflict at this level of analysis. This conflict will exist if the evolutionary hypothesis happens to yield predictions about mechanism that disagree with the sociocultural hypothesis's predictions about mechanism (Lewis et al., 2017). An example might be in facial attractiveness research: Sociocultural perspectives predict greater cross-cultural variation in what faces people find attractive, whereas evolutionary perspectives predict greater cross-cultural uniformity (some studies suggest that actual correlations between cultures are approximately +.90; Langlois et al., 2000).

Third, this makes it clear that while sociocultural and evolutionary hypotheses *can* conflict at the mechanism level of analysis, they do not have to. It is possible for these supposedly dueling approaches to yield the exact same predictions about mechanism. For example, both evolutionary and sociocultural hypotheses predict that viewing media images of unrealistically attractive models will serve as a key input into systems generating dissatisfaction with self-image and symptoms of body dysmorphia (Buss, 2019; Clay et al., 2005; Hefner et al., 2014). In such cases, evolutionary and sociocultural approaches can agree with one another. It is a major conceptual mistake to regard evolutionary and sociocultural hypotheses as being automatically or necessarily in conflict—if there is a conflict, it is a contingent fact, not a necessary one. Possible conflicts must be assessed on a case-by-case (hypothesis-by-hypothesis) basis rather than assumed.

To summarize, evolutionary and non-evolutionary hypotheses do not conflict when it comes to ultimate function, as most non-evolutionary hypotheses do not address this level of analysis at all, yielding no conflict.[5] By contrast, both hypotheses yield predictions about how the system works. Consequently, at the proximate level, evolutionary and non-evolutionary hypotheses can conflict—but they are not bound to by necessity. They will sometimes conflict and sometimes agree.

This picture is strikingly different from the default assumption in the field, which is that evolutionary hypotheses are necessarily and automatically in conflict with sociocultural ones. The "necessary conflict" view is a conceptual mistake caused by conflating different levels of analysis (e.g., Al-Shawaf et al., 2018, 2019), and it impedes progress and understanding in psychology.

Thinking clearly about levels of analysis has the benefit of clarifying when evolutionary and non-evolutionary hypotheses conflict and when

[4] In simple cases, it will sometimes be possible to explain and predict behavior despite skipping the information-processing (algorithmic) level of analysis. But in many cases, a researcher's chances of success will be diminished, and in some cases, they will reach the wrong conclusion (see also Cosmides & Tooby, 1987). Ultimately, if our goal is to understand behavior—especially if we seek to predict it a priori, not just explain it ex post facto—we must take seriously the step that precedes and produces it. From an evolutionary perspective, the information-processing facet of mechanism is indispensable.

[5] Certain branches of psychology such as vision science also address function, but vision science's functional approach is often implicitly or explicitly evolutionary.

Table 1
Summary of Some Key Points

Key points	Explanation	Examples (discussed in the body of the text)
Tinbergen's 4 questions and Marr's 3 levels can be profitably integrated	Tinbergen's *function* corresponds to Marr's *computational theory*. Marr's algorithm (software) and neurophysiology (hardware implementation) together constitute Tinbergen's *mechanism*.	See Figure 1
Integrating Tinbergen and Marr resolves unnecessary conflicts in psychology	Many stale disputes in psychology are false conflicts born of a failure to distinguish between different levels of analysis.	Evolution versus learning Evolved versus sociocultural Cognitive versus neural
Clarifies what *mechanism* really means	Mechanism is not just physiology. It is "how the system works," which involves social and cultural inputs, hormones, neurophysiology, information processing, individual differences, and more. Cognitive systems must be understood at both the neural level and the information-processing level at a minimum. These (hardware and software) can be understood as the two broad facets of *mechanism*.	
Specifies what is needed for a comprehensive explanation of a behavior or cognitive system	To fully explain a behavior or cognitive system, we must address all four of Tinbergen's questions. Additionally, within Tinbergen's *mechanism*, we must tackle both algorithm and neurophysiology at a minimum.	
Evolutionary hypotheses are typically tested via their proximate predictions	Ultimate hypotheses (about *function*) are typically tested via the proximate predictions they yield (often about *mechanism*).	Disgust Incest aversion Rabies
The cognitive or information-processing level of mechanism (*algorithm*) is key for understanding evolved *function*	Hypotheses about function often yield predictions about information-processing more readily than they yield predictions about neurophysiology. Cognition or information-processing is key to understanding evolved function.	Code-breaking in brood parasites Code-breaking in fireflies Incest avoidance in humans Complex if-then rules Multi-cue integration problems The true trigger of shame (organisms' cognitive programs operate on internal representations of external variables, not directly on external variables themselves)
Levels of analysis are crucial to the progress of a science	They frame the epistemological boundaries and explanatory goals of the field. They highlight which pieces of the explanatory puzzle are still missing. They help dissolve false conflicts. They are necessary for a comprehensive science of mind and behavior.	

they do not. This conceptual clarity helps dissolve some of the most impactful and stagnant false dichotomies in psychology: evolved versus sociocultural, innate versus learned, and biological versus cultural (Al-Shawaf, 2019, 2020a; Lewis et al., 2017). Attending carefully to levels of analysis highlights the central mistake, helps dissolve the false conflicts, and shows what is still needed for progress in our field. It is difficult to overestimate how important this kind of conceptual clarity is for a science like psychology that is still finding its footing and that frequently falters due to false conflicts.[6]

Metascience, Philosophy of Science, and Progress in Science

In the midst of the replication crisis (Nosek et al., 2022; Open Science Collaboration, 2015) and theory crisis (Muthukrishna & Henrich, 2019) in psychology, there has been a welcome trend of trying to improve the field by focusing on methodological and philosophical issues surrounding best practices in science. This has led to greater emphasis on replication (Simons, 2014), heightened interest in questions of successful theory and model building (Borsboom et al., 2021; Fried, 2020), growing emphasis on data from underrepresented cultures (Henrich et al., 2010), enhanced research transparency (Klein et al., 2018), and scientists publicly acknowledging when they have lost confidence in one of their findings (Rohrer et al., 2021). These are welcome and salutary changes for psychology—they are a sign of the maturation of our discipline and the intellectual humility of some of its practitioners,

[6] For other examples of false conflicts and dichotomies in psychology, see also Fleeson, 2004 and Lewis et al., 2020.

and they herald further progress in the advancement of the science of the mind.

A key piece of this revolution in the social and cognitive sciences—one that remains underappreciated—is that we need to pay much more attention to levels of analysis (see also Hofstadter, 1979; Hunt et al., 2023; D. C. Marr, 1982; Pietraszewski & Wertz, 2022). We gain conceptual clarity and make empirical progress by asking what the relevant levels of analysis in our field are, what distinguishes them from one another, what relation they bear to each other, and what the proper integration of apparently incommensurable frameworks looks like. Levels of analysis are crucial because they frame a science and define the epistemological boundaries and explanatory goals of the field.

Summary and Conclusion

The marriage of Tinbergen's four questions with Marr's three levels of analysis provides a preliminary roadmap for a comprehensive science of the mind, one that begins to dissolve unhelpful conflicts rooted in the conflation of distinct levels of analysis. For example, Tinbergen's levels dissolve the false conflict between evolution and learning by highlighting that function lies at the ultimate level of analysis, whereas learning lies at the proximate level (Al-Shawaf et al., 2019, 2021). Evolved adaptations may involve some learning, no learning, or a lot of learning (Alcock, 2009; Al-Shawaf, 2019; Symons, 1979), and the existence of evolved learning mechanisms highlights the fact that evolution and learning are explanatory partners, not explanatory competitors. Similarly, Marr's levels highlight the fact that to understand a neurocognitive system, you need to understand what it is supposed to do and why (the computational level), how the software accomplishes this (the algorithmic level), and how the software is neurophysiologically instantiated in the brain (the hardware implementation level). Answers to these different questions are complementary, not conflicting, and it is only when we have addressed all of them that we can hope to approach a full explanation of the behavior or cognitive system in question. Thinking about the relationship between these two influential frameworks shines light on the different facets of "mechanism," clarifies how researchers test hypotheses about evolved function, and shows that the two frameworks can be usefully integrated for the benefit of psychology.

This integration is a first step. Future work would benefit from developing these ideas further, as well as connecting this integration with other levels-of-analysis frameworks in psychology (e.g., Pietraszewski & Wertz, 2022).

Ultimately, paying greater attention to levels of analysis makes it easier to think clearly about the phenomena we're interested in, helps resolve false conflicts, and shows us which pieces of the explanatory puzzle are still missing (see Table 1 for a summary of key points).

Levels of analysis provide a map of the terrain a science needs to chart in order to fully explain its phenomena of interest. They are not an optional add-on or a diplomatic bridge-building afterthought. They are indispensable in the path toward a comprehensive science of mind and behavior.

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