Intelligence and uncertainty: Implications of hierarchical predictive processing for the neuroscience of cognitive ability

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ABSTRACT

Hierarchical predictive processing (PP) has recently emerged as a candidate theoretical paradigm for neuro-behavioral research. To date, PP has found support through its success in offering compelling explanations for a number of perceptual, cognitive, and psychiatric phenomena, as well as from accumulating neurophysiological evidence. However, its implications for understanding intelligence and its neural basis have received relatively little attention. The present review outlines the key tenets and evidence for PP, and assesses its implications for intelligence research. It is argued that PP suggests indeterminacy as a unifying principle from which to investigate the cognitive hierarchy and brain-ability correlations. The resulting framework not only accommodates prominent psychometric models of intelligence, but also incorporates key findings from neuroanatomical and functional activation research, and motivates new predictions via the mechanisms of prediction-error minimization. Because PP also suggests unique neural signatures of experience-dependent activity, it may also help clarify environmental contributions to intellectual development. It is concluded that PP represents a plausible, integrative framework that could enhance progress in the neuroscience of intelligence.

1. Introduction

Recent years have seen a surge of interest in the idea that environmental prediction represents a fundamental principle of brain organization and functioning (Bar, 2009; Bubic et al., 2010; Clark, 2013b, 2013a, 2015; Friston and Stephan, 2007; Todd et al., 2012). This idea relates to several intellectual traditions in cognitive science[1], and incorporates the neuro-computational principle of hierarchical predictive coding (Huang and Rao, 2011) as the key mechanism in an encompassing account of how the mammalian brain mediates perception, thought, and action. This "predictive mind" thesis holds that the whole of cortical information processing ultimately serves to (1) implement and dynamically adjust a hierarchy of predictions about the organism's expected sensory inputs and internal states, (2) estimate and tune the precision of those predictions, and (3) continuously minimize the resulting "errors" or violations of those predictions, which arise through environmental changes and the organism's actions upon its environment (Hohwy, 2013)[2]. In the course of generating and updating predictions, and minimizing the resulting deviations, the brain enables organisms to efficiently perceive the environment and undertake

adaptive action (Clark, 2015). In its most ambitious extension, the free energy formulation (Friston and Stephan, 2007), this general account has been expanded to encompass not only all of brain functioning but indeed all of behavior. In particular, it is argued that in the process of minimizing prediction errors, the brain implicitly minimizes the organism's likelihood of finding itself in phenotypically unexpected (and thus probabilistically maladaptive) states, thereby making environmental prediction the key way that organisms maintain homeostasis (Friston, 2010).

Simultaneously, advances have been made in the intelligence literature in terms of identifying and developing accounts of the most consistent neural correlates of overall cognitive ability (Deary et al., 2010; Haier, 2016). Most prominently, these include Parieto-Frontal Integration Theory (Jung and Haier, 2007) and the similar Multiple Demand system (Duncan, 2010), the Neural Efficiency Hypothesis (NEH; Haier et al., 1988), various findings linking white matter structure (Li et al., 2009; Penke et al., 2012; Schmithorst et al., 2005) and neural metabolite concentrations to IQ (Aydin et al., 2012; Jung et al., 1999, 2009; Nikolaidis et al., 2016), as well as the classic, modest relationship between overall brain size and intellectual ability (Gignac

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[1] The idea that experience and expectations are central to cognition is typically attributed most directly to Helmholtz' (von Helmholtz and Southall, 1924) ideas on unconscious perceptual inference (Clark, 2015; Friston, 2005; Hohwy, 2013).

[2] Here, predictive processing is meant to subsume an active engagement with—or sampling of—the environment. More generally, this is known as "active inference" (a corollary of the free energy principle, as outlined below).

and Bates, 2017; Pietschnig et al., 2015).

However, despite this progress, theoretical accounts of these phenomena leave many unanswered questions, and often only indirectly inform debates about the nature of intelligence. For example, while the importance of fronto-parietal networks has been increasingly established (Barbey et al., 2012; Basten et al., 2015; Colom et al., 2009; Gläscher et al., 2010; Woolgar et al., 2010), it is unclear whether they play the same role in all cognitive tasks (e.g., those involving more fluid vs. crystallized skills), as well as whether and how they interact with other neural networks in supporting momentary intelligence (e.g., Hearne et al., 2016). Most importantly, it remains to be established whether intelligence is identically organized at the neural level across all individuals.

Similarly, while NEH has helped to motivate and organize much of the functional activation literature, it appears that NE effects only hold within certain networks (Basten et al., 2013; Neubauer and Fink, 2009) and within just a limited range of task difficulties (Dunst et al., 2014; Neubauer and Fink, 2009). Given these caveats, it is unclear whether the NEH framework can accommodate the discrepancies, or whether an alternative model is needed instead. More broadly, despite meaningful progress in each of these sub-areas, the field as a whole still lacks an *overall* framework that integrates the anatomical and functional literatures, and which in turn could provide a priori, regional and directional predictions for any given experiment. In the absence of such a framework, physiological intelligence research runs the risk of accumulating ad hoc and conflicting conclusions, limiting its wider impact.

To that end, this article outlines the key features of predictive processing (PP) frameworks, and examines their adequacy and implications as a guiding paradigm for the neuroscience of intelligence. It is argued that PP not only accommodates the most critical aspects of the intelligence construct, but also implies a change of emphasis in understanding it, such that organisms' ability to effectively manage environmental uncertainty takes on a more central role (see the analogous account of anxiety in Hirsh et al., 2012). In turn, PP shows potential for integrating the neuroanatomical and functional correlates of intelligence, and offers specific, testable predictions based on the mechanisms of prediction-error minimization (PEM).

Given the long history of many of the ideas herein, the primary goal of this review is less to provide new ideas, and more to consider how PP might help integrate a number of longstanding ones. Accordingly, the present account clearly follows in the tradition begun by Shannon who related uncertainty and information directly (Shannon, 1948), and likewise owes much to previous informational perspectives on intelligence (e.g., Hunt, 1980, 2005), as well as other groundbreaking work (Deary, 2000; Gottfredson, 1997b; Haier, 2016; Jensen, 1998a; Marshalek et al., 1983; Stankov and Roberts, 1997). Overall, it merely extends these prior contributions, and attempts to lay out how PP, as a contemporary information-processing framework, can deal with various tensions in the intelligence literature and so may provide a plausible path forward.

The article is organized as follows: Section 2 briefly reviews the major conceptual features of PP frameworks and recent supportive findings, with key examples drawn primarily from the electrophysiological literature. The major implications of PP for intelligence are then outlined in Section 3, as are the crucial facts of intelligence that a PP framework must in turn accommodate. It is argued that PP is not only consistent with the major contemporary models of intelligence, but through its emphasis on uncertainty in task performance, it provides a unified framework for understanding intelligent behavior, cognitive task hierarchies, and their neural correlates. Section 4 reviews the major domains of neuroscientific intelligence research, outlining their key results and challenges. Section 5 then indicates for each domain how PP not only accommodates the major findings but also furnishes new predictions, and holds promise as an integrative account. The paper concludes with a discussion of broader implications and some outstanding issues facing PP as a guiding theory for intelligence

research.

2. The brain as a prediction engine

2.1. Key concepts

As recently detailed by Hohwy (2013) and Clark (2015), PP theories hold that the fundamental operating principle of the nervous system is to "minimize errors" in predicting its environmental inputs (Clark, 2013b, 2015; Hohwy, 2013). These errors comprise the neural signals transmitted from lower to higher levels within the hierarchically-organized nervous system, and correspond to deviations from neural models of the expected inputs that are generated at higher levels in the hierarchy (Rao and Ballard, 1999). These expectations represent prior predictions about the nature and features of environmental inputs, and manifest as backward (i.e., top-down) suppressing signals from higher to lower processing centers, thereby minimizing or dampening the error signals. Ultimately, these priors are implemented in the brain's structural connectivity and functional activity patterns, and hence develop in part over evolutionarily timescales, as well as over the organism's lifetime through its interactions with the external environment and its propio- and interoceptive experience (Friston and Stephan, 2007). Thus, these theories assert that, at a functional level, the brain supports cognition by implementing a hierarchy of predictions where higher levels predict ever more abstract aspects of the world (beginning with basic perceptual features and moving to integrated objects, emotions, semantic attributions, etc., Hohwy, 2013), while lower-level signals merely transmit deviations from these expectations upward in a continuous process of adjusting the overall model instantiated throughout[3].

In essence, an organism's activity, changes in its environment, or changes in its internal states (e.g., hunger and other states involving interoceptive signals) generate prediction errors. Error signals in turn motivate actions to suppress them (or changes in the internal model), and in the process create new expectations in the form of dynamically evolving priors across the neural hierarchy. Intuitively, one can imagine this playing out at the conscious level in instances such as turning one's head to investigate an unexpected noise, or shifting one's position based on an uncomfortable sensation. In each case, a change in either the state of the environment or the organism creates a violation of the predictive model currently in effect, thereby generating prediction errors and motivating both suppressive actions and new predictions.

Importantly, prediction in the current sense does not refer to conscious expectations that a person might explicitly verbalize, but rather to a neurocomputational process (Clark, 2015, p. 2), where the changing probabilities of various environmental and organismal states are continuously evaluated within the brain across spatial and temporal scales (e.g., the presence of an edge, a particular phoneme or word at the end of an utterance). Nonetheless, because the process is hierarchical, with top-down predictions determining the flow of error signals upward, it seems necessary that mechanistic "neural predictions" would ultimately converge at the top level with the unconscious and conscious expectations of the integrated organism (e.g., see Melloni et al., 2011).

Finally, as mentioned above, the free energy formulation extends this basic framework, ultimately unifying all of behavior under the idea that suppressing prediction errors fulfills a more general biological imperative to minimize the information-theoretic quantity of "free energy." As described by Friston and Stephan (2007), "free energy reflects

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[3] Implicit in these accounts, and consistent with their connection to unconscious perceptual inference and analysis by synthesis (Neisser, 1967), PP theories hold that perception is not merely a receptive process, but rather a highly generative one that arises through the dynamic interplay of generating neural predictions, suppressing the resulting prediction errors, and evaluating and tuning predictions across levels.

the probability of sensory input given the current state of the brain" and represents the difference between the model of the world encoded by the organism's nervous system and the world's true structure, given its phenotype, current context, and learned expectations (Friston and Stephan, 2007; Friston et al., 2012a, b). Because free energy tracks the expected likelihood of an organism finding itself in various sensory states (e.g., opening your bedroom door to find the hallway versus the Martian surface), the higher free energy engendered by a surprising state will accurately reflect the lower likelihood of being able to maintain homeostasis in that circumstance (Friston, 2010). In this way, the process of minimizing free energy (i.e., prediction errors) gains adaptive significance because the behaviors an organism engages in to minimize free energy will ultimately function to fulfill its various biological needs—that is, provided the organism expects the sorts of sensations that are consistent with being alive (Friston et al., 2012b). Because free energy is, mathematically, an upper bound on self-information (Friston, 2010), minimizing free energy is often referred to as "self-evidencing" (i.e., the agent's actions generate the evidence for its own model of itself and the world; Hohwy, 2016). Overall, because prediction errors arise dynamically through both external and internal environmental changes, this formulation entails that organisms are continuously motivated to suppress the resulting errors signals, thereby enabling them to sustain homeostasis.

2.2. Physiological evidence for predictive processing

While a full review of the evidence for PP exceeds the present scope, several key examples are mentioned here. Recent electrophysiological findings are particularly compelling. Not only are these methods well-suited to reveal to the rapid dynamics putatively involved, but several studies now support the early hypothesis that various event-related potential (ERP) components should reflect distinct aspects of PEM (Friston, 2005). Among the most illustrative are studies that have examined the auditory and visual mismatch negativities (MMN) or variants of the P300 (P3). The MMN is elicited when infrequent, task-irrelevant, perceptually-deviant auditory or visual stimuli are presented within larger sequences of high-probability "standard" stimuli (Kimura, 2012; Näätänen et al., 2007), while the P3 reflects a more attention-driven process, elicited when novel or otherwise low-probability "target" stimuli violate broader contextual expectations (Polich, 2007), such as those that develop across trials. Because the MMN and P3 appear to be differentially sensitive to pre-conscious and conscious perceptual expectations (Sculthorpe et al., 2009), they provide especially compelling tests for the notion of a predictive neural hierarchy.

In regards to the MMN, particularly of interest are findings that, under certain conditions, the omission of an expected stimulus elicits an apparent MMN that is time-locked to the expected onset of the missing stimulus, and further, that more complex rule violations, such as violating the expected relations between paired stimuli, bring about an MMN as well (reviewed in Winkler and Czigler, 2012). On the basis of those and many similar findings, Winkler and Czigler (2012) concluded that the auditory and visual MMN may indeed reflect neural processes related to generative perceptual models (Winkler and Czigler, 2012, p. 140). Further support for this idea comes from studies modelling the neural generators of the MMN, which have shown that models comprised of both feedforward and feedback connections consistently better explain MMN effects than those containing feedforward connections alone (Garrido et al., 2008, 2007).

Other ERP studies have extended these findings, suggesting that the MMN reflects just one manifestation of a predictive neural hierarchy. For example, in a study that manipulated multiple levels of stimulus expectations, Wacongne and colleagues (2011) showed that while violating a low-level perceptual expectation elicits an MMN, and violating contextual expectations elicits the higher-order P3, the joint violation of both expectations elicits a larger response than that associated with either one alone. Moreover, the response to the joint

violation actually precedes that of either simpler component, thereby supporting not only a hierarchical model, but specifically a predictive rather than a feedforward one (Wacongne et al., 2011). Other research on the P3 advances this further, supporting different predictive roles for various components.

For example, using an "urn-ball" task, in which participants are asked to reason about hidden states based on limited information, Kopp and colleagues have found evidence that different aspects of the Late Positive Complex (commonly associated with the P3) may reflect distinct aspect of Bayesian inference in the brain (Kolossa et al., 2015; Kopp et al., 2016; Seer et al., 2016). Because the paradigm requires participants to select colored balls from a hidden urn and then guess the population from which the urn was drawn (i.e., the ratio of colored balls it contains), the task provides a means to operationally distinguish different aspects of predictive processing (Kopp, 2008). Using this approach, the authors observed that in this task the amplitude of the anterior P3a most closely tracks "updating of beliefs about hidden states" (beliefs about which type of urn is being sampled from), whereas, for example, the Slow Wave amplitude relates more to change in predictions about future events given the current observation ("postdictive surprise;" Kolossa et al., 2015). A second study by this group suggested that the fronto-central N2 and P3a components seem to distinctly track violations of more implicit versus explicit predictions about events, whereas the P3b seems to relate to both (Seer et al., 2016). Notably, the above role of the P3a in belief updating was also supported in a recent reinforcement learning study, which linked still another component (the Stimulus Preceding Negativity) to belief uncertainty in PP (Bennett et al., 2015).

Moving beyond the ERP literature, EEG studies on oscillatory processes have also found support for neural mechanisms of PP. Most significantly, several studies now support a role for pre-stimulus alpha oscillations (8–12 Hz) in mediating stimulus expectancy effects. For example, whereas it is well-established that pre-stimulus alpha activity is suppressed by the allocation of attention (Klimesch, 2012), it was recently shown that such modulations do not merely track the temporal onset of sensory targets, but more precisely, expectations around the onsets of their task-relevant dimensions (Bauer et al., 2014). Similarly, pre-stimulus alpha is stronger not only during experimental conditions where stimulus expectations are high, but also when perceptual quality is degraded, and furthermore, that larger pre-stimulus effects are associated with higher subsequent stimulus-related activity (Mayer et al., 2016). As those authors variously observed, such findings are consistent with a potential role for alpha in coding the precision of sensory expectations[4] (Bauer et al., 2014), as well as the idea that neural mechanisms of expectancy should be particularly implicated when sensory evidence is low (Mayer et al., 2016). Last, PP also predicts that feedforward and feedback activity should exhibit distinct oscillatory profiles (being associated with higher and lower frequencies, respectively; Bastos et al., 2012), as recently confirmed in a visual attention study that combined electrocorticography and Granger causality (Bastos et al., 2015).

Broader work in neuroscience and psychology provides additional support for PP, across other physiological modalities and research domains. Recent fMRI findings not only support hypotheses that predictable stimuli should elicit reduced neural activity in task-relevant cortices (Alink et al., 2010), but have also begun to explain how such

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[4] In this context, an internal model generates predictions of what would be sampled under a particular belief about how sensations are caused. Technically, these are referred to as "generative models." The ensuing prediction errors allow the generative model to be updated—in proportion to their reliability or precision. This means that the precision of sensory information (i.e., prediction errors) plays a crucial role in belief updating—and can be regarded as the confidence or attention afforded various sources of information (Feldman and Friston, 2010).

effects should interact with attention in enhancing perceptual gain for predicted stimuli (Kok et al., 2012). Neurodevelopmentally, basic research using cellular recordings has shown that both spontaneous and event-related activity increasingly comes to reflect the statistical structure of the environment across stages of brain development (supporting PP's notion the brain encodes a model of the world; Berkes et al., 2011). Further, work with human infants supports hierarchical predictive effects in babies as young as three months (Basirat et al., 2014). Indeed, as reviewed elsewhere (Clark, 2015; Hohwy, 2013), predictive coding accounts are now sufficiently widespread that the basic framework has been used to explain phenomena as diverse as perceptual illusions (Brown and Friston, 2012), ERP repetition suppression (Grotheer and Kovács, 2016), reinforcement learning and motivation (Den Ouden et al., 2012), the subjective sense of reality and the self (Seth et al., 2012), and even the clinical features of schizophrenia and autism (Lawson et al., 2014; Schmack et al., 2015; Van de Cruys et al., 2014).

3. Basic implications for intelligence research

Given that PP is emerging as a candidate paradigm for all neurobehavioral research (Friston, 2010), to the extent that its core premises prove correct, it will necessarily have implications for understanding intelligence and its neural basis. Of its various assertions, three main ideas have clear implications for intelligence research: First, PP holds that human brain functioning is inherently hierarchical, with higher levels strongly influencing the processing at lower levels. Notably, this clearly aligns with the widespread view of intelligence as a hierarchically-organized construct, and suggests specific implications for how it might manifest neurophysiologically (Sections 3.3, 3.4, 5). Second, because PP holds that predicting environmental (and interoceptive) events represents the fundamental organizing principle of human brain functioning, it further suggests the corollary that variation in intelligence and its neural mechanisms should be most strongly elicited under conditions that impede effective prediction. That is, under conditions of uncertainty. Third, due to the role of priors, PP also entails a view of cognition as partially dependent on expectations, as governed by current context and prior experience (Clark, 2013b). Thus, it requires an understanding of task performance, including performance on intelligence tests and during neuroimaging sessions, as at least in principle subject to those factors (Section 5.5), as increasingly supported (e.g., Duckworth et al., 2011; Kan et al., 2013), and long acknowledged by some (Matarazzo, 1972; Sternberg, 1999; Wechsler, 1950).

While each of those claims suggests ways in which PP might constrain and clarify accounts of intelligence, the most crucial facts of the intelligence literature should in turn set constraints on its viability as a guiding paradigm. That is, PP should be evaluated not only in terms of how well its premises might help to clarify outstanding questions about intelligence, but also in terms of how well it accommodates and explains the construct's basic facts. As suggested in Table 1, these might be heuristically termed psychometric, functional, and physiological domains of intelligence research.

Within the psychometric domain, the PP framework should at least accommodate the major psychometric findings, and also suggest ways in which neurophysiological data might be used to decide between opposing models of intelligence. It should further explain why various tasks and narrower constructs predict intelligence to one degree or another, and how these subsidiary abilities somehow all draw upon what appears to be a very general capacity. Within the (related) functional domain, PP should provide an explanation of what intelligence does (i.e., what it is *for*) that improves upon existing definitions—an issue that has proved famously intractable (Jensen, 1998a, Chapter 3). Finally, within the physiological domain, any neuroscientific account of intelligence should of course suggest a clear path toward explaining and synthesizing the major neural correlates, developing new predictions,

and connecting those results to the preceding domains.

3.1. Psychometric constraints on neural theories of intelligence

Among the psychometric findings that PP (or any neuroscientific account) should accommodate and help explain, three of the most critical of are: (1) the positive manifold phenomenon, or the observation that individuals who perform well on one cognitive task tend to perform well on others, such that cognitive tests nearly invariably positively inter-correlate, and factor analyses of diverse batteries produce a large first factor accounting for much or most of the variance between them (i.e., psychometric *g*; Jensen, 1998a; Spearman, 1904); (2) the finding that *g* is reliably modelled as the top of a cognitive hierarchy upon which various broad and specific abilities load on in turn (Deary, 2012; Jensen, 1998b; Major et al., 2012); and the related fact that various cognitive *tasks* thus also demonstrate a hierarchy or ranking of *g*-loadings (e.g., Burt, 1909), with sensory-perceptual tasks falling near the bottom, while those involving significant working memory or semantic demands rest near the top (Carroll, 1993); and (3) the finding that tasks which differ substantially in their content and the broad capacities they require can nevertheless predict *g* equally well (Spearman's "indifference of the indicator;" 1927).

Taken together, insofar as *g* provides a reasonable index of intelligence (Gottfredson, 1997b), these findings imply a view of the construct as an individual's overall or general cognitive capacity, which is tapped to varying degrees by all cognitive tasks, and which is broadly insensitive to the particular content of diverse but equally challenging ones. Whether or not those precise implications follow, the facts undergirding them nevertheless set criteria against which to evaluate PP's adequacy. Moreover, they motivate one of the central questions in the neuroscience of intelligence: How is it that intelligence somehow reflects a general and overarching capacity of the brain, which is nevertheless mediated by discrete neural circuits, nearly all of which have broadly identifiable and even modality-specific roles (Kovacs and Conway, 2016)?

Whereas the view that *g* implies a unitary, latent, and overarching intellectual capacity is well-supported and widely held (Deary, 2012; Jensen, 1998a), whether this or an alternative model best reflects the true structure of intelligence remains an important area of debate (Bartholomew et al., 2013; Gignac, 2014; Kovacs and Conway, 2016; van der Maas et al., 2006, 2014). Neurophysiologically, unitary accounts seem to imply that a single core network underlies, or at least constrains, individual differences (e.g., the P-FIT model). Yet, to the extent that the brain is modular, with individuals varying in their relative strengths and weaknesses (e.g., verbal vs. spatial abilities), these latter considerations seem to favor alternative accounts. In those latter frameworks, *g* is fundamentally non-unitary, and arises from the contributions of multiple underlying processes in various configurations (the sampling and mutualism models: Bartholomew et al., 2009; Thomson, 1920; van der Maas et al., 2006), which may even differ across individuals (Bartholomew et al., 2013, p. 230).

Returning then to PP, given its status as an explicitly hierarchical theory, it seems immediately plausible that it not only accommodates a hierarchical model, but likely favors one. Specifically, since PP argues that higher-order neural predictions exert a strong top-down influence on the activity at lower levels (Wiese and Metzinger, 2017), it suggests that the efficacy of higher processes might well set a ceiling on the system's functioning as a whole (Sections 3.4 and 5.3). Not only could such an "upper-bound" or "bottleneck" account help explain why intelligence appears to reflect largely domain-general variation, but it further accords with the view that working memory capacity (Colom et al., 2015, 2004) and other executive processes (Kovacs and Conway, 2016) might constrain intelligence in such a fashion. Thus, although individuals may differ substantially in the relative "tilt" of their cognitive profiles (i.e., patterns of *within-subject* strengths and weaknesses; Coyle et al., 2014), higher-order processes may nonetheless impose

Table 1
Relation of the Predictive Processing Framework to Major Concepts in Intelligence Research.

Domain	Current Framework	Open Questions and Evidence Needed
Psychometric		
Positive Manifold Phenomenon	Top-down processes constrain lower-order variation	Causal evidence that PEM and priors mediate IDs
Structure of Intelligence	Hierarchical	Evidence that higher-order PEM disproportionately constrains *g*
Cognitive Task Hierarchy	Task level reflects net indeterminacy resulting from stimulus-response discrepancies	Operational criteria for quantifying subjective indeterminacy
Indifference of the Indicator	Highly *g*-loaded tasks entail comparable amounts but distinct types of indeterminacy	Across cognitive domains, tasks with comparable *g*-loadings should involve similar net demands on PEM
Functional		
Definition of Intelligence	The cognitive capacity to respond appropriately despite indeterminacy	Counterexamples? Role of conative variables?
Role of Complexity and Difficulty	Reflect the type and amount of task-related indeterminacy	Do discrete aspects of PEM distinguish complexity and difficulty?
Role of Learning	Intellectual development involves the development of priors contingent on experience	Development of priors may underlie multiplier effects hypothesized in Gene x Environment interactions
Physiological		
ERP-IQ Correlations	Amplitude-ability correlations reflect the discrete computational indeterminacy entailed by particular tasks	The same component amplitudes will variably relate to ability, contingent on precise task demands
Parieto-Frontal Integration Theory	f-p networks form the top of the cortical hierarchy, and are necessary for IDs in *g*, but insufficient for broader intelligence	As indeterminacy increases, f-p activity should increasingly, but asymptotically, predict cognitive IDs
Neural Efficiency Hypothesis	Indeterminacy is partly determined by experience, which in turn should moderate activity-ability relationships	Neural priors should mediate NE effects among individuals who possess experiential advantages

limits that drive the *between-subjects* effects relevant to the positive manifold (see Detterman, 2002; and Jensen, 1998a, p. 93). Finally, insofar as PP implies at least a hybrid model of intelligence with some hierarchical features, this lends it important practical value for testing those theories. Thus, PP not only accords well with the hierarchical view, but it may also help bridge the gap between those psychometric accounts and their physical realization.

3.2. The cognitive hierarchy and conceptual tensions in intelligence research

Taking the key psychometric findings in turn, PP should not only accommodate the emergence of *g*, but should further account for its relation to lower-order abilities, in what has been termed the cognitive hierarchy. As reviewed by Deary (1994, 2000), this phenomenon was first established by Spearman (1904) and his contemporary Burt (1909) who both observed smaller correlations between sensory discrimination and estimated intelligence relative to increasingly demanding types of mental tasks. Since then, task complexity has become a broadly accepted, process-neutral explanation for this pattern of effects (Detterman, 1987b; Gottfredson, 1997b; Neubauer and Fink, 2003; Nisbett et al., 2012a); where the former has been defined in terms of the number of different of processes (and their interrelations) required for doing a task (Guttman, 1954; Marshalek et al., 1983; Stankov and Crawford, 1993; Stankov and Raykov, 1995). As complexity increases, a task more strongly predicts intelligence. Overall, this provides a compelling answer to the question of what intelligence is for (i.e., navigating a complex world; Gottfredson, 1997b), and finds strong support from task process analyses which reliably find that the tasks which best predict *g* tend to be those that involve the most components (Carpenter et al., 1990; Sternberg, 1977).

Despite its success however, the complexity account shows its limits near the bottom of the cognitive hierarchy, in the realm of psychophysical tasks. In particular, while it helps explain findings like the smaller correlation between IQ and simple than choice reaction time (RT) (Deary et al., 2001; Sheppard and Vernon, 2008), it says little as to why these and other apparently simple tasks (e.g., pitch or color discrimination; Acton and Schroeder, 2001) should relate to intelligence at all. That is, while complexity is a good explanation for the pattern of correlations between tasks in the hierarchy, it fails to give the basis for any individual task-ability relationship (Detterman, 2002, p. 232; Kovacs and Conway, 2016, p. 155). This failure to specify the processes governing complexity itself limits its application to the more reductive

domains of intelligence research, and undermines its potential as a complete explanation.

These concerns also highlight a more general dilemma that arises in attempts to characterize the nature of intelligence. On the one hand, there has been a strong tradition of trying to reduce intelligence to one or more, more specific processes, such as mental speed (Jensen, 2006; Schubert et al., 2017) or various executive constructs (Colom et al., 2015; Duncan et al., 2008; Kovacs and Conway, 2016). Because they are reductive, these approaches have the benefit of providing relatively clear guides as to what their substrates might be. However, by the same token, they run the risk of defining intelligence too narrowly and excluding important aspects (e.g., verbal skills), and thus misdirecting the neural search. On the other hand, an alternative tradition has emphasized broader, process-neutral explanations, like domain-general relational skills (Chuderski, 2014; Spearman, 1927), or the capacity to deal with complexity, novelty, or ambiguity in adapting to the environment (Binet and Simon, 1905; Burt, 1909; Kanazawa, 2004; Sternberg, 1999; Sternberg and Gastel, 1989). Because these latter definitions seem to apply to a wider range of situations, they may better accommodate the full cognitive hierarchy and the indifference of the indicator, and hence the true diversity of scenarios in which intelligence manifests. Yet, they of course face the opposite problem of under-specifying their potential mechanisms.

Overall, while some of these approaches better navigate this dilemma than others, the very fact that it exists reveals a central challenge: Because intelligence is so broad, any attempt to reduce it to specific, narrower processes may inevitably fall short. Further, while some degree of reduction may ultimately prove successful, there seems likely to be an inverse relation between its explanatory success and its reductive ambition. In other words, the fact that intelligence seems to resist satisfactory reduction should perhaps be instructive—it may be that in order retain the full breadth of the construct, while still seeking a *complete* account of its mechanisms, a different approach will be needed at each level of analysis. Psychologically, it is likely the very breadth of intelligence that accounts for its potency and relevance (Gottfredson, 2004); however, this same breadth complicates efforts to isolate its mechanisms. Thus, rather than favoring reductive potential at the cost of psychological scope (or vice versa) in defining intelligence, a hybrid approach may be needed instead. As outlined below, PP offers one such approach, by combining a broad, process-neutral explanation with a specific set of neural mechanisms.
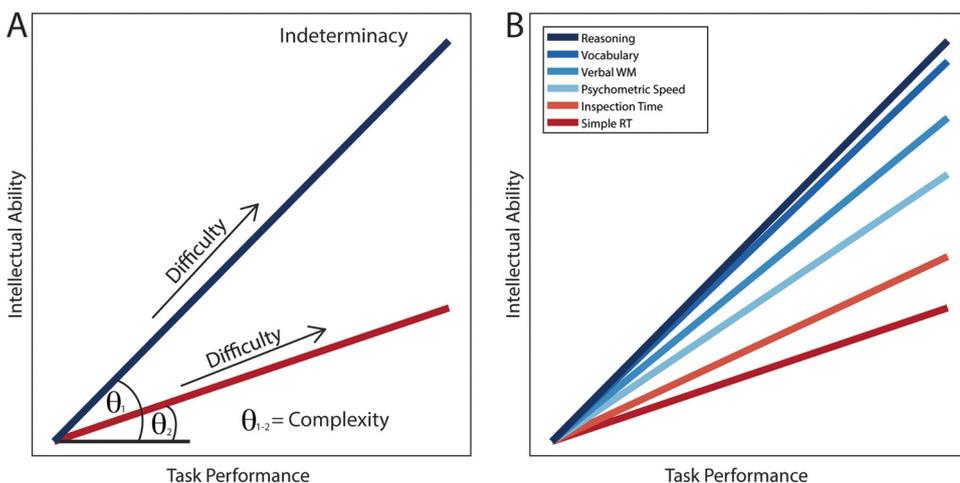
Fig. 1. Task-Ability Effects in relation to Complexity, Difficulty, and Indeterminacy.

A. The complexity of a task sets the slope of its correlation with intelligence (depicted by the angle θ), while higher difficulty is indicated by a more rightward position on the regression line (Marshalek et al., 1983; Stankov and Raykov, 1995). Movement in either dimension of this space is a function of indeterminacy (top right), as a potentially absolute information-theoretic quantity.

B. Schematic depiction of the absolute empirical correlations between performance on various cognitive tasks and *g*. As each task entails greater net indeterminacy, its *g*-loading increases. Higher-ability individuals tend to occupy the top-right portion of the space. The slope of each line was taken from representative publications. RT = reaction time; WM = Working Memory. RT and Inspection Time values were taken from Sheppard and Vernon (2008). Values for Psychometric Speed, Verbal WM, Vocabulary, and Reasoning reflect *g*-loadings reported by Benson et al., (2010) for the WAIS-IV Symbol Search, Letter-Number Sequencing, Vocabulary and Figure Weights subtests. Note that Vocabulary and Reasoning exhibit comparable *g*-loadings despite highly diverse content.

3.3. Indeterminacy as a unifying task dimension

The potential of PP to navigate the issues above relates to its second major implication for intelligence research. Simply put, if prediction is the overriding goal of the brain, then individual differences (IDs) in brain functioning should be most strongly elicited when prediction is impeded—under conditions of uncertainty. A re-examination of canonical tasks used to assess and study intelligence seems to support exactly this view, in that, every task which elicits IDs appears to ultimately do so by inducing *indeterminacy* around the correct response (Fox and Mitchum, 2012). That is, for any task, regardless of content, as the discrepancy between the information provided to the examinee and that needed to produce the correct response increases (1) performance on the task correlates with intelligence increasingly well, and (2) better performance indicates higher intelligence. As will be shown, this not only provides an encompassing framework for understanding the cognitive hierarchy, but also an organizing principle for physiological intelligence research.

To take some examples, the role of indeterminacy is readily seen on standard IQ tests, where the most *g*-loaded tasks are those that require the greatest extrapolation from the stimulus prompts. In the case of a highly *g*-loaded vocabulary task (Benson et al., 2010), the examinee is presented with minimal instructions and fairly impoverished stimuli (the printed text of a word and its pronunciation) and is asked to provide a definition. If no further guidance is given, they can rely only on their understanding of what's being called for in the situation (is it best to give a synonym?; Fox et al., 2014), and some combination of their prior exposure to those words, the facility with which they've acquired the relevant associations, and their ability to infer meanings based on the prompts alone. Assuming they are motivated, they presumably bring whatever skills and prior knowledge they can to bear on providing a correct response, and as the target words become more uncommon, they experience the task as more difficult and are less likely to respond correctly.

Similarly, in the case of auditory working memory span, where examinees are required to repeat longer and longer strings of numbers in various orders, the increasing string length and more complex manipulations combine to render the correct response increasingly indeterminate relative to the information presented. Here again, it is the extent to which the correct response is specified by the stimulus prompt alone that determines both the item's indeterminacy and its value for discriminating between levels of intelligence. Finally, near the lower end of the cognitive hierarchy, consider how the least *g*-loaded measures on IQ tests typically assess processing speed, and consist of timed

tasks involving rapid visual search, matching, or discrimination. In every instance, the correct response to each item is highly specified by the stimulus prompts themselves, and as a result, if the tasks were not timed, they would elicit no meaningful IDs (Carroll, 1993, p. 459). Thus, indeterminacy is quite low in these tasks, and correspondingly they are the poorest predictors of IQ within the larger battery (Benson et al., 2010; Wechsler, 2008). Ultimately, it appears that this same case can be made for any task that elicits cognitive differences, where the extent to which it predicts IQ appears to be a function of the total indeterminacy it induces.

At this point, two concerns might arise. To anticipate the first, it should be emphasized that this in no way suggests that various tasks do not rely on separable functions with dissociable neural substrates (to the contrary, see: Barbey et al., 2012; and Gläscher et al., 2010), or that those functions are unimportant to intelligence (Colom et al., 2004; Major et al., 2012; McGrew, 2009). Rather, it merely highlights that, as long shown (Spearman, 1927), tasks that leverage any given process to one degree or another necessarily characterize only a subset of the possible situations that will elicit variation in intelligence. Thus, to the extent that intelligence fundamentally represents an *overarching* and *general* capacity, definitions that emphasize particular lower-order constructs run the risk of being somewhat arbitrary (and at worst, misleading) from the perspective of truly characterizing it.

Second, it might also be noted that the discussion thus far somewhat elides the distinction between task complexity and difficulty (Jensen, 1970; cited in Marshalek et al., 1983; Stankov and Raykov, 1995). As above, complexity explains the between-task differences relevant to *g*-loadings and (hypothetically) demands on different types of mental processes, while difficulty refers to the within-task probability of passing a single item, and demands on similar processes. When considered in the context of regression analysis, complexity corresponds to the slope of the line describing the relation between a task and overall intelligence, while difficulty (or its inverse, ability) roughly reflects the position of an item (or person) along the line itself (see Fig. 1).

However, while that distinction helps to organize thinking within that psychological space, it provides little guidance as to the processes ultimately involved (Detterman, 2002, p. 232). This is of course where indeterminacy can come in to better ground that thinking in the actual currency of the brain: For any task, it is the amount and type of uncertainty it induces that determines its difficulty and complexity. Moreover, the type of uncertainty invoked by a task provides strong clues as to the neural processes that should be most relevant to its relation with intelligence (Sections 5.1 and 5.3; and see Friston et al., 2017; and Kahneman and Tversky, 1982 on levels and types of

uncertainty). Thus, while complexity says little about why seemingly simple tasks might relate to intelligence at all, indeterminacy brings chronometric measures and the like under the umbrella of the cognitive hierarchy. In turn, by combining these three concepts, neuroscience can gain leverage from which to deconstruct the between-task and between-person dimensions that govern the physiology of intelligence.

Finally, a third objection might also arise here, as to whether the idea that all cognitive tasks hinge on uncertainty is merely trivially true. To the contrary, although references to neural "information processing" are ubiquitous in the literature, arguably few high-level neuroscientific studies actually pursue the implications. For example, whereas there is agreement that the brain performs some sort of computations, PP reveals the hidden vagueness of this claim, by further holding these computations to be fundamentally *statistical*. Likewise, whereas most chronometric studies implicitly presume the standard, feedforward model of visual processing (e.g., how rapidly can one "take in" information from the environment), PP holds the opposite view, that feed*back* activity should dominate perception. These points of course relate to PP's broader, controversial claim that the brain encodes a model of world and is designed to minimize deviations from that model. Finally, unlike the standard, generic appeal to unspecified information processing, the present account follows from a comparatively detailed theory of how the brain is functionally-organized to carry out those tasks. Thus, it permits taking the ambitious step of conceiving of intelligence as an absolute, information-theoretic quantity, and possibly ultimately measuring it on a true ratio scale (Haier, 2014).

Explicitly then, a view of intelligence based on PP, and in turn on uncertainty, aims to span the gap between process-focused and process-neutral accounts by balancing the strengths and limitations of each. Consistent with the latter, it is broadly agnostic about the role of lower-order cognitive processes in overall intelligence, and instead accepts it as an inherently overarching capacity (Wechsler, 1971). Nevertheless, it still seeks to clarify its underlying mechanisms, primarily through appeals to individual task-ability relationships. That is, by systematically deconstructing the cognitive hierarchy. Thus, in contrast to cognitive models, the present framework preferentially emphasizes the two adjacent levels of analysis of (1) the integrated organism within its immediate adaptive context, and (2) its underlying neurophysiology as conceived in information-theoretic terms.

At the organismal level, PP emphasizes the fundamental functional dynamic shared by all cognitive tasks—the fact that each ultimately compels a response that is in some fashion under-determined from the organism's perspective, relative to the information present in the immediate environment. As such, this view aligns closely with Donahoe and Palmer's (2004) "biobehavioral" formulation of problem solving, where a problem is said to occur "whenever an important consequence is contingent, at least in part, on conditions that are not currently in effect" (Donahoe and Palmer, 2004, p. 270)[5]. Solving such a problem thus "requires emitting a response in a context that does not directly evoke" it (Donahoe and Palmer, 2004, p. 272). By extending this definition only slightly to include instances in which brief stimulus durations, incentives to respond quickly, or minute perceptual differences render correct responding indeterminate, it becomes possible to conceptualize all cognitive tasks within this general framework[6]. Interestingly, as a reviewer points out, this also gives intelligence an intuitive meaning from a formal (information-theoretic) perspective: If intelligence is the ability to minimize expected free energy (i.e., expected self-information; Friston, 2010; Friston et al., 2017) then intelligence just *is* the ability to resolve uncertainty. This follows from the

fact that expected self-information is entropy and entropy is the formal measure of uncertainty (Cover and Thomas, 2006). It will be seen later on that, in hierarchical models, the ensuing measure of intelligence or self-evidencing rests upon distributed beliefs over the cortical hierarchy, with both experimental and anatomical implications (Sections 5.2 and 5.3).

In turn, at the neurophysiological level, PP's emphasis on indeterminacy also provides a means for tracing the effects of task parameters directly into the brain. Specifically, because it highlights indeterminacy as the relevant dimension driving behavioral and presumably neural variation, it sheds light on the most crucial features of any task in relation to intelligence. This in turn helps to bridge psychological or subjective indeterminacy as experienced by the individual with indeterminacy in a more stringent, information-theoretic sense, as a potentially physiologically-meaningful quantity (Street, 2016). Because psychophysical and other simple tasks manipulate more narrow perceptual indeterminacy, they constrain the range of possible responses, and likely the relevant neural networks. Greater resilience to those effects relates to higher intelligence, but only weakly so. Conversely, as tasks become more complex, they involve higher-order indeterminacy and presumably impinge upon more distributed circuits. In the process, they elicit more neural variation that is relevant to intelligence. Overall then, because PP and indeterminacy accommodate the full range of tasks that are relevant to research on intelligence, they may support a more systematic and comprehensive approach to isolating its neural mechanisms.

3.4. Bridging psychometric and neural hierarchies

Returning to the cognitive hierarchy, within the PP framework, the overall pattern of task-ability relations can be readily attributed to the role of indeterminacy in determining task-specific recruitment. Since unimodal sensory discrimination entails only modest indeterminacy, it should only impede prediction within a circumscribed network. Although variability in these low-level predictions may measurably contribute to behavioral variation (as in RT-IQ correlations), insofar as those levels are concerned with predicting relatively discrete sensory features, they should contribute only weakly to the aggregate success of the overall system. This should be especially true given the inordinate stabilizing influence of top-down predictions. In contrast, because more complex tasks and ecological situations of high adaptive significance (e.g., securing food in conditions of scarcity; Kanazawa, 2010; competing for mates; Miller, 2011) entail significantly higher-order and multiplexed indeterminacy, successfully navigating them should involve prediction of much higher-order models, thereby leveraging the capacity of the brain as a whole to cope with the relevant uncertainty.

Thus, PP implies that variability in PEM may be differentially important at different hierarchical levels, such that IDs in low-level neural prediction, although measurable, may have relatively constrained effects within the hierarchy and hence limited adaptive significance. Conversely, failures of more abstract prediction should not only undermine the stabilization of lower levels, but will also relate more directly to global predictions about situational states and outcomes, and thus are likelier to prompt maladaptive actions. As greater portions of the hierarchy are recruited to predict the more global events that guide decisions and actions, predictive failures throughout the system may accrue, with higher-level failures being more consequential, and relating more to overall intelligence. Thus, by combining the broad concept of response indeterminacy with the specific hierarchical mechanism of PEM, the present view offers possible explanations for why any given task correlates with intelligence at all, to what degree, and what the shared neural processes might be. To the extent that the type and level of indeterminacy entailed by any task can be successfully quantified, those involving higher levels should better predict intelligence, and more closely approach the construct itself.

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[5] And see Fox and Mitchum (2012, p. 980) and citations therein regarding the relevance of indeterminacy to complex problem solving.

[6] Note that this also incorporates prior thinking about the role of novelty in intelligence (Snow and Lohman, 1984; Sternberg, 1999, 2012; Sternberg and Gastel, 1989) as a special case of indeterminacy.

4. The neuroscience of intelligence: major findings and challenges

While the preceding sections outline the ways in which PP's basic concepts align with the major psychometric aspects of intelligence, its primary contribution to that literature will instead relate to its usefulness for advancing neuroscientific research. In particular, despite significant progress, and especially in neuroanatomical research, significant challenges remain. For example, although numerous studies point to the importance of fronto-parietal (f–p) networks, their precise role at various levels of the cognitive hierarchy remains unclear, as does their relation to other networks (e.g., the default-mode; Hearne et al., 2016) in the momentary control of adaptive behavior. In functional activation research, the Neural Efficiency Hypothesis (NEH) is easily the most central theory, yet it is unclear how well it generalizes to either the full cognitive hierarchy or all neural networks, and hence whether it remains viable as a comprehensive account. Finally, in the realm of ERP research, despite meaningful progress by individual studies (e.g., Schubert et al., 2017), work in the area is comparatively under-developed and isolated from the preceding domains. This latter issue is emblematic of a major challenge facing the field as a whole, in that, despite the progress within each sub-area, none on their own shows promise for providing an overall synthesis. Yet, in the absence of a more integrative framework, physiological intelligence research runs the risk of proceeding on an ad hoc basis, limiting its contribution to broader problems in the field. With that in mind, the following sections review the major findings in each of these sub-areas, with the goal of outlining the challenges they face and the potentially integrative solutions that PP may offer.

4.1. Parieto-frontal integration theory: overview and status

In their now-seminal article, Jung and Haier reviewed the then-extant imaging literature and documented that across numerous different modalities and task types the overall pattern of findings implicated a set of primarily frontal and parietal regions as being most reliably related to intelligence and complex task performance (Jung and Haier, 2007). In the time since, many studies have provided additional, though at times qualified, support for P-FIT's core premises that cognitive ability is preferentially related to f–p structures and functioning. These include studies of gray matter volume (Colom et al., 2009; Haier et al., 2009; Ryman et al., 2016), cortical thickness (Karama et al., 2011; Narr et al., 2007; Román et al., 2014), lesion burden (Barbey et al., 2012, 2014; Gläscher et al., 2010; Woolgar et al., 2010), resting-state and task-related functional connectivity (Song et al., 2008; Vakhtin et al., 2014), and fMRI activation (e.g., Basten et al., 2013; Ebisch et al., 2012; Shamosh et al., 2008; Woolgar et al., 2011a, b). Whereas the majority of this research has been correlational, lesion studies are particularly significant, in that they appear to support a necessary relationship between the integrity of f–p systems and psychometric *g* (Barbey et al., 2012; Gläscher et al., 2010).

Functionally, the significance of f–p networks in particular has generally been considered to reflect their collective role in supporting overall "information integration and control" within the brain (Naghavi and Nyberg, 2007). This capacity relates in part to the location of the lateral parietal cortices at the convergence of sensory association areas (thereby enabling subregions to serve as "epicentres" of various integrative cognitive functions; Mesulam, 1998), and may reflect a more general principle of cortical organization, whereby the greater a region's spatial distance from primary sensory and motor cortices, the more integrative, abstract, and heteromodal it becomes (Margulies et al., 2016). For their part, the lateral, medial, and rostral prefrontal cortices have each been implicated in various aspects of cognitive control (Botvinick, 2008; Burgess et al., 2007; Miller and Cohen, 2001; Stuss, 2011; Ullsperger et al., 2014), such that through their participation in broader networks (Dosenbach et al., 2008), they enable various goal states to influence the selection, maintenance, and use of

perceptual information in highly flexible, situationally-dependent ways.

This domain generality of f–p networks is further supported by several authors' observations of the striking overlap between the core P-FIT structures and the task-positive network (Basten et al., 2013; Duncan, 2013), which consists of a group of regions that are commonly activated by any task requiring goal-directed attention (Fox et al., 2005). Finally, research on the highly similar Multiple Demand (MD) system of regions (Crittenden et al., 2016; Duncan, 2010) not only supports the role of f–p regions in complex task performance and attentional control, but suggests their further subdivision into two discrete networks, respectively involved in more momentary behavioral adaptation versus longer-term task set maintenance (Crittenden et al., 2016; Dosenbach et al., 2008; Duncan, 2013).

Interestingly, despite the clear trend for neuroimaging studies to implicate f–p regions in cognitive IDs, precise anatomical replications tend to be lacking, suggesting a more complex picture. Of particular note is a recent meta-analysis that examined the convergence of findings across both structural (gray matter volume) and functional imaging studies (positive and negative fMRI activation) conducted in the last two decades (Basten et al., 2015). In that study, although the respective sub-analyses confirmed the relative importance of f–p regions to intelligence differences, a conjunction analysis of the two modalities demonstrated no precise convergence. The authors explain that while the original P-FIT model characterizes anatomical overlap between studies at the relatively low spatial resolution of Brodmann areas, the higher voxel-level resolution of the studies themselves (and the resulting meta-analysis) entirely allow the possibility of no precise overlap between different voxel groups that nevertheless occupy the same general regions (Basten et al., 2015). Indeed, even when the P-FIT model was first proposed meaningful inconsistencies between studies were evident (Colom et al., 2007), and in the time since precise replications have remained elusive (c.f. Colom et al., 2009; Haier et al., 2009).

4.2. Emerging questions in the neuroanatomy of intelligence

Based on the above, some of the inconsistencies among P-FIT studies could be explained by the generally broad scale of the theory, and relatively mundane differences between studies in terms of their imaging methods, etc. Notably however, while similar factors will impede replications within any area of neuroimaging, there are several more substantive issues that are somewhat unique to P-FIT and intelligence itself. First, not only is there evidence that the core P-FIT structures might constitute not one but two networks (Crittenden et al., 2016), but other evidence suggests that those same networks are among the most anatomically-variable of any in the brain (Mueller et al., 2013). Second, given its status as an apparently hierarchical construct, intelligence poses the special requirement that studies clearly distinguish between the instruments and types of tasks used to assess it, versus the latent construct itself (typically operationalized by *g*; Jensen, 1998a, Chapter 10). As discussed by Colom and colleagues (Colom et al., 2013; Colom and Thompson, 2011; Haier et al., 2009; Martínez et al., 2015; Román et al., 2014), to the extent that studies differ in their means of operationalizing intelligence, and in turn fail to distinguish between neural variation related to *g* versus various sub-constructs or particular tests, zero-order correlations of imaging data with performance on specific tasks or batteries will also obscure these distinctions, with discrepancies between studies reflecting unknown contributions of each.

These issues were recently examined by Román et al., (2014), who evaluated anatomical correlates at each level of the cognitive hierarchy (beginning with *g*, and moving down to broad factors like crystallized intelligence, and then to specific tests). The results demonstrated "a reversed hierarchy" such that IDs in *g* were associated with the *fewest* neural correlates (confined to frontal structures for surface area and gray matter volume in that study), with a progressively broader distribution of regions being involved as one moves down the hierarchy to

broad factors and then to the tests themselves (Román et al., 2014). While these results support the view that discrepancies between studies reflect failures to distinguish between constructs at different levels and the tests used to measure them, a second and potentially bigger challenge is the finding of a reversed hierarchy itself—a pattern which has also been observed in lesion research (Barbey et al., 2012; Gläscher et al., 2010). Thus, this group of findings suggests either that despite capturing variance common to all cognitive measures, g actually relates to only a small set of brain regions, and/or that it relates to broader substrates, but which vary across people. This latter possibility is consistent with the findings of a subsequent study by the same group, which aimed to characterize the consistency of brain structure-ability relationships across different image analysis pipelines, and across separate, but carefully matched samples (Martínez et al., 2015). There, the key finding was that although the sub-samples were essentially identical in terms of their anatomical distributions of mean cortical thickness and variability, they showed no significant overlap (and even opposite effects) in some of their brain-ability relationships (Martínez et al., 2015).

Overall, these studies suggest that the more general an ability construct is, the fewer structural correlates it is likely to have, and also, that such structure-ability relations tend not to replicate (at least in healthy samples). While each finding is certainly striking in its own right, together, they suggest the deeper and more intriguing possibility that cognitive ability might be structured somewhat differently in different individuals (see: Haier et al., 2009; Johnson et al., 2008; Martínez et al., 2015). That is, insofar as intelligence is fundamentally hierarchical and could allow multiple routes to the same outcome (i.e., an IQ score), imaging approaches that strongly emphasize inter-subject consistency may be looking for convergence that does not ultimately exist. If this is the case, it would suggest that a version of sampling theory may be correct (Bartholomew et al., 2009; Section 3.1), such that different configurations of networks, or different roles for various sub-regions, might differentially comprise any one person's abilities.

In summary, the extant neuroimaging literature supports an important but somewhat under-specified role for f–p networks in intelligence. Insofar as the P-FIT model proposes a fairly large set of higher-order regions, defined at comparatively broad resolution, it is perhaps unsurprising that the literature as a whole would affirm its core claims, while precise replications might be difficult to achieve. On that basis, key questions for research in this area concern the precise position of f–p networks in the cognitive hierarchy, and the consistency of that role across individuals.

4.3. The neural efficiency hypothesis and activity-ability relations

Within the intelligence literature, NEH represents the functional counterpart to the P-FIT's anatomical framework. In brief, the NEH represents a model of the relationship between brain activity and intelligence, wherein higher-ability individuals exhibit less neural activation compared to their lower-ability counterparts when performing identical tasks. In the last major review of this literature, Neubauer and Fink (2009) found support for this general pattern of findings across studies examining a number of different neurophysiological measures and task types, with many showing evidence for both more spatially-distributed as well as higher activation levels among lower-performing subjects.

Importantly, while those authors concluded that essentially 50–80% percent of the studies provided some support for NEH, they also highlighted several qualifying effects. These included interactions with participant sex and task type, cortical region, and task difficulty and expertise (Neubauer and Fink, 2009). In short, there was evidence that (1) male participants showed NE for spatial tasks while females participants tended to show NE for verbal tasks (consistent with the evidence for sex-specific advantages in aspects of those domains; Halpern, 2004; Miller and Halpern, 2014), (2) that NE was more reliably

observed in frontal than parietal regions (e.g., Neubauer et al., 2004), (3) that expertise can mitigate intelligence-related NE (Grabner et al., 2003; but see: Neubauer et al., 2005), and finally (4) that while NE was generally observed for moderately difficult tasks, as difficulty further increases, higher ability individuals actually show *greater* neural activation than lower ability participants (thereby reversing the effect). This last finding was thought to indicate a greater capacity of high ability participants to volitionally exert additional resources under difficult conditions (Neubauer and Fink, 2009).

In synthesizing the NE literature overall, Neubauer and Fink outlined a general account of activity-ability relationships that seems to reconcile the original hypothesis with the various moderating factors above, through an appeal to the roles of frontally-mediated cognitive control and subjective task difficulty. In essence, they argued that tasks which require less cognitive control for a given individual will elicit comparatively reduced prefrontal activation, and be perceived as subjectively easier, despite equivalent behavioral performance (Neubauer and Fink, 2009). Thus, this potentially organizes the various findings pertaining to sex effects, task complexity, and expertise under a single umbrella, where in each case, NE should be observed in those participants who perceive the task as less difficult, and hence require less cognitive control to perform equally well.

In recent years, several studies have further refined this formulation. For example, Dunst and colleagues (2014) demonstrated that although lower-ability individuals exhibited greater insula fMRI activation than high-ability counterparts when completing the same set of reasoning problems, when each group completed items *matched to their own abilities*, no differences in activation or performance were observed (Dunst et al., 2014). Similarly, in a study of training and difficulty effects on EEG event-related desynchronization (ERD), Nussbaumer et al. (2015) observed an NE effect on frontal ERD, in the context of matched performance between high and lower-ability groups on a moderately-difficult task. However, when the two groups were trained on a much more demanding, adaptive task, and hence were pushed to their individual capacities, no NE effects were observed at either pre or post-testing. This is particularly interesting given that the higher-ability group performed better at baseline, while both groups improved to a similar level after training (Nussbaumer et al., 2015). Thus, taking all the findings together, NE effects do not seem to emerge when high-ability participants perform better on equivalent tasks (i.e., the pre-test findings of Nussbaumer et al., 2015), or when high and low-ability individuals are both maximally challenged (as shown by Dunst et al., 2014, and the post-test findings of Nussbaumer et al., 2015). Rather, NE effects most often arise when higher-ability individuals perform tasks that are less subjectively challenging. Thus, recent results support the notion that NE does not solely reflect ability, but more directly one's need for cognitive control, vis-à-vis subjective task difficulty.

Finally, the anatomical scope of NEH has also been further qualified, most significantly in the study by Basten and colleagues (2013), who found opposite patterns of effects in the task-positive and task-negative networks (TPN/TNN). In brief, they observed that despite equivalent performance between higher and lower-ability groups, higher ability was consistently associated with increased TPN and decreased TNN activation. That is, in contrast to the classic NEH, more intelligent subjects showed *more* TPN activation than lower-ability counterparts. Yet, consistent with NEH, higher-ability participants also down-regulated the TNN less (see Basten et al., 2013 for details and discussion).

In sum, while many studies support aspects of NEH, its scope has been increasingly refined. Anatomically, the NE phenomenon only holds for particular networks, and where it arises, it seems to more closely reflect subjective difficulty than intelligence per se. When taken with the previous refinements (e.g., applying to moderately-challenging but not very easy or difficult tasks), the overall picture is one of mounting caveats to NEH, and an apparently low likelihood of finding a single function that describes activity-ability relations across all tasks and neural networks. In light of that, while NEH remains viable in many

scenarios, and especially for thinking about difficulty effects, there is room for additional frameworks that could expand upon it and address these limitations.

4.4. ERP-intelligence research

Because NEH seems not to apply to elementary cognitive tasks (ECTs; Inspection Time, the Hick paradigm, etc.), most ERP-intelligence research has fallen outside of its purview, and has typically proceeded based on more study-specific predictions. Overall, that literature is broadly divided into studies that have related intelligence to the MMN and P300 as elicited by oddball tasks, and those that have examined more traditional ECTs, or other tasks of more direct theoretical interest. Among the former, larger group of studies, most have found a positive correlation between cognitive ability and component amplitudes (Amin et al., 2015; Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; Fjell et al., 2007; Jaušovec and Jaušovec, 2000; De Pascalis and Varriale, 2012; De Pascalis et al., 2008; Shajahan et al., 1997; Troche et al., 2009; Wronka et al., 2013), and an inverse relationship between ability and component latencies (Amin et al., 2015; Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; Fjell et al., 2007; Jaušovec and Jaušovec, 2000; O'Donnell et al., 1992; De Pascalis and Varriale, 2012; De Pascalis et al., 2008; Shajahan et al., 1997; Troche et al., 2009; Zurrón and Díaz, 1998). However, several of these and other studies have also observed various negative and mixed findings (e.g., Egan et al., 1994; Nieman et al., 2002; Polich and Martin, 1992).

In the ECT literature, a handful of studies have examined ERP correlates of Inspection Time, with early studies finding mixed results for relations between intelligence and aspects of the N1-P2 complex (Burns et al., 1996; Morris and Alcorn, 1995; Zhang et al., 1989). The most recent studies favor a similar pattern to that of the oddball literature, with evidence for negative latency and positive amplitude effects on those same components in relation to ability (Burns et al., 2000; Hill et al., 2011). Overall, while this same general pattern of positive amplitude and negative latency effects has been observed across quite diverse tasks (c.f., Euler et al., 2017; Houlihan and Stelmack, 2012; Jolij et al., 2007; Sculthorpe et al., 2009), particular paradigms can induce opposite effects (e.g., Brumback et al., 2004; Peltz et al., 2011).

Notwithstanding the overall trends above, progress in ERP-intelligence research has generally been slow, due to a number of factors. The first is perhaps an accident of history, wherein the advent of neuroimaging displaced EEG as a primary approach in physiological intelligence research (e.g., compare the number of results returned annually between Pubmed searches for "EEG, ERP, intelligence" versus "fMRI, intelligence" from 1988 to 2017). A second and related issue is the fact that many of the more topical studies on ERP correlates of intelligence were conducted almost two decades ago. As such, they were subject to methodological conventions of the era like limited electrode montages and relatively small samples, which naturally limit their ability to inform strong conclusions about the roles of particular neural circuits. Third, even despite progress in broader electrophysiology, EEG studies of intelligence have sometimes failed to keep pace. This has manifested not only in being slow to adopt more powerful methodologies (e.g., high-density montages, time-frequency analysis), but also in occasional failures to integrate conceptual developments.

For example, as recently highlighted by Wronka and colleagues (2013), a failure to distinguish between the P3a and P3b sub-components may help explain why some studies have observed opposite effects for P3 amplitude-IQ correlations. As they emphasize (Wronka et al., 2013), whereas perceptual tasks generally elicit positive correlations, tasks that require memory or other cognitive processes are apt to elicit negative relationships instead (e.g., Peltz et al., 2011). However, while the task-dependence of P3 amplitudes (Kok, 2001; Polich, 2012), and many other components (Luck, 2014), is well-

established in broader electrophysiology, just a small number of ERP-IQ studies have addressed this in their research (e.g., Houlihan et al., 1998; Wronka et al., 2013). Thus, while many studies have made important individual contributions, the field as a whole lacks an organizing framework from which to derive a priori predictions. Insofar as many ERP-intelligence relations may be inherently task-dependent, such a framework is needed to foster greater progress. As outlined below (Section 5.1), not only do PP and uncertainty provide a natural principle for thinking about ERP-IQ correlations, but they also permit testing highly-detailed, circuit-level hypotheses.

5. Prediction and uncertainty as an organizing framework

To summarize Section 4, each major sub-domain in the neuroscience of intelligence faces important questions in the period ahead. The precise role of f–p networks requires better specification, as does the expected direction of activity-ability effects throughout the brain and across the cognitive hierarchy. Moreover, beyond their individual challenges, the various sub-areas should all seek to converge on a comprehensive account of how the brain supports intelligence. Whether or not PP can achieve this naturally remains to be seen, but as a unifying framework, it shows promise nonetheless.

For example, because PP is hierarchically structured, its mechanisms should naturally scale across the cognitive hierarchy. This means that, in principle, it can avoid the problems encountered by NEH in dealing with tasks of varying complexity, and should equally accommodate the chronometric and ERP literatures, as well as the more complex paradigms relevant to NEH and P-FIT (and which better approximate intelligence itself). Likewise, whereas NE has often been construed as a property of the entire brain, PP promotes a more local approach for determining how neural processes should relate to intelligence, and under what conditions, and why. Yet, at the same time, PP retains global principles (indeterminacy and PEM) that plausibly unite the relevant hierarchies. Finally, because PP entails particular functional mechanisms, it is also open to falsification. For any task, it should be possible to specify the discrete physiological markers thought to index the relevant processes, and their proposed role in the task's correlation with intelligence.

Returning to the notion that the cognitive hierarchy may be key to understanding activity-ability relations (Section 3.3), an immediate complication arises when one considers the apparent gap between chronometric studies and those that examine higher cognitive processes. Whereas the former involve rapid, ostensibly low-level processes, and hence typically focus on ERPs, more complex tasks better lend themselves to analyses of temporally-extended activity, such as ERD/ERS and BOLD signal changes. Thus, research on the neural correlates of intelligence mirrors the distinction within the field between "speed" and "level" tasks, as defined by whether the rate versus accuracy of performance better captures cognitive IDs (for an introduction, see Carroll, 1993, Chapter 11). However, unlike the extant neural theories which remain comparatively isolated within their own sub-domains, PP should equally apply to both discrete and more extended and distributed processes. On that basis, it shows promise for spanning the speed/level distinction.

5.1. A role for uncertainty in ERP-IQ effects

Beginning near the bottom of the hierarchy, it can be seen how PP might help organize ERP-IQ research, and potentially resolve long-standing issues in mental chronometry. In the first instance, although ERP latencies generally inversely relate to intelligence, ERP amplitudes have shown inconsistent effects (Section 4.4). While this may reflect methodological issues, it also raises the more substantive question of whether these effects might vary across tasks. A recent study on the Hick paradigm raised this exact possibility, where it was shown that although the task elicited four different components (the N1, P2, N2

and Slow Wave), three of which predicted Decision Time, only P2 amplitudes predicted IQ (Euler et al., 2017). Yet, if intelligence is mediated by fixed neural substrates, why would a given component (e.g., the N1; Hill et al., 2011) predict IQ in one task but not in another?

Uncertainty provides a compelling framework for exploring these issues, in that it directs thinking away from fixed neural substrates and more towards the momentary demands of particular tasks. In the case of the Hick paradigm, which manipulates uncertainty about the location of an upcoming target, it makes sense that the P2 might be a reliable locus of IQ-related variance, given its enhancement in response to unexpected vs. expected cues (Freunberger et al., 2007; Golob et al., 2002). Conversely, although Inspection Time also elicits the N1 and P2 (Burns et al., 2000), recent evidence suggests that only the N1 predicts IQ in Inspection Time, perhaps reflecting its demands on early visual attention (Hill et al., 2011). Similarly, while oddball paradigms elicit these same components (Polich, 2007), it is likely their emphasis on cross-trial contingencies that explains why they more often produce P3-IQ correlations.

Overall, to the extent that ERP amplitude-IQ effects may reflect task-specific processes, and hence the contributions of (relatively) discrete neural networks (Section 3.3), it seems to also follow that the size of those relations might *scale* according to their depth into the neural hierarchy. On the basis of anatomical hierarchies alone, later components might relate more strongly to intelligence by virtue of the fact that they: (1) index more variance in CNS functioning overall, (2) index more complex and abstract information processing, and/or (3) reflect processes that are more susceptible to beneficial and adverse developmental influences on intelligence by means of (1) and (2); and see Section 5.5. Going further, however, PP also suggests the deeper claim that the domain-general aspects of intelligence should speak to higher levels in hierarchical generative models. Thus, a fourth consideration is that since beliefs or expectations deeper in the hierarchy will be expressed later in evoked responses, later evoked potentials may be better neural correlates of intelligence for this reason as well. Here, P300 (i.e., latent or endogenous) responses are an especially compelling focus of research, in that, interestingly, they are thought to reflect the novelty, and concomitant changes in uncertainty provided by a re-evaluation of context. Indeed, some studies that have examined both MMN and P3 amplitudes appear to support larger effects for the later P3 (see Bazana and Stelmack, 2002; Sculthorpe et al., 2009), while at the extreme low end of intelligence, dynamic causal modelling (DCM) of evoked responses suggests that people in a minimally conscious state lose these later response components, due to impaired top-down influences from the prefrontal cortex (Boly et al., 2011; and see further discussion of DCM below)[7].

Notably, even beyond these hypotheses, PP supports still other, more specific predictions. Returning to chronometry per se, it remains an open question whether ECT-IQ correlations reflect variability primarily due to "low-level," perceptual mechanisms, or whether motivation or other higher-order processes might instead drive these effects (see Deary, 2000, Chapter 7). In a fairly novel contribution, PP now suggests a means for differentiating the unique neural signatures that might decide the issue. Specifically, it may be that the relevant N1 and P2 effects reflect IDs in feedforward prediction errors, and hence what have classically been construed as bottom-up processes. Under that scenario, one might expect IQ-related variance to mostly relate to the amplitudes of those early ERPs. On the other hand, if the behavioral correlations reflect the tendency of higher-ability individuals to preferentially exert top-down attentional modulation on early perceptual networks, one might instead predict that broader oscillatory processes

would also contribute to the task-ability relationship. This latter prediction also follows from PP, for the reason that top-down oscillations might act to increase the gain on perceptual signals that are expected to yield high-precision prediction errors (Clark, 2015, p. 77; and see: Haegens et al., 2011; van Dijk et al., 2008). Indeed, along these very lines, Bauer and colleagues (2014) recently showed a close linkage between pre- and post-stimulus oscillatory dynamics, stimulus probability, and reaction times. Strikingly, whereas alpha modulation increased with the probability of *impending* stimulus events (thereby tracking the precision of sensory expectations), gamma power (40–150 Hz) showed opposite effects, being reactive to stimuli, and highest during the least predicable intervals. This, and the fact that gamma power inversely related to stimulus probability, aligns strongly with the notion that lower and higher frequencies may distinguish predictions vs. errors (Bastos et al., 2012; Bauer et al., 2014).

Finally, because PP can also be operationalized through the mathematical framework of DCM (David et al., 2006), it is in principle possible to test competing, a priori models of chronometric effects even down to the roles of particular cell types in cortical networks (Daunizeau et al., 2011; Kiebel et al., 2009). Indeed, a recent MEG study linked variation in RT to particular synaptic effects in posterior parietal cortex (FitzGerald et al., 2015). Note that this is still to say nothing of the potentially Bayesian computations (Section 2.2) that might be investigated for their role in intelligence. In summary, not only does uncertainty provide a potential organizing framework for ERP-IQ research, but together with PP and DCM, it affords a potentially transformative level of experimental specificity.

5.2. From active inference to complex reasoning

Given its evidence base in the ERP and modelling literatures, PP integrates well with mental chronometry and event-related electrophysiology. However, unlike chronometric tasks, which are explicitly designed to isolate mental processes, many if not all highly *g*-loaded tasks inherently involve multiple components (Stankov and Crawford, 1993; Stankov and Raykov, 1995), and thus are much less amenable to an event-related approach. Reasoning tasks in particular represent some of the best measures of general intelligence (Haier, 2016, p. 124), and have long been understood to involve multiple components which unfold over a series of steps (Carpenter et al., 1990; Hunt, 1980; Sternberg, 1977). Thus, to be applicable to research on more *g*-loaded tasks, PP must also have a means of dealing with componential and step-wise cognition. This requires appealing to the free energy account of overt behavior, in what has been termed "active inference" (Friston et al., 2010).

Recalling Section 2.1, PP holds that PEM can be accomplished in one of two ways: by changing the internal model generating predictions, or by changing the state of the organism such that the ongoing predictions better align with the current environment (Adams et al., 2013; Clark, 2015, p. 121). It is this latter case that active inference addresses. To understand this, consider the example in which a sudden crash in the kitchen causes you to get up and investigate. In this instance, the unexpected noise (perhaps quickly recognized as a pitcher of lemonade you had left on the counter), has generated prediction errors, which can only be fully resolved by heading toward the kitchen. At a first level, the very recognition of the sound as a glass object hitting the kitchen floor (and the associated gush of ice and liquid) has already entailed the tentative resolution of two sources of prediction error—those pertaining to the likely identity and location of the objects that gave rise to the sound. Note however, that whereas it was possible to resolve the initial errors by changing the operative internal model (i.e., perceiving the crash itself), that same process has generated a now-conscious prediction of spilled lemonade in the kitchen. Unlike the auditory case, however, this latter prediction and the errors it engenders can only be resolved through recourse to action.

Specifically, insofar as you maintain a goal to avoid insects and

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broken glass in your kitchen, the spilled lemonade hypothesis will elicit internal prediction errors (possibly emotional and interoceptive in origin; Seth, 2013) that call for acting in the world. Note however, that even in the course of standing from a chair and turning toward the kitchen, the various motor sequences entailed would each generate a cascade of lower-level visual and somatosensory prediction errors that require minimization. Although this would seem to cause a tension within PP (by initially increasing rather than decreasing prediction error), free energy holds that selective actions ultimately decrease net prediction error, by themselves giving rise to expected patterns of inputs (Friston, 2010). That is, in the course of controlling their own, particular actions, an organism's very movements engender expected patterns of prediction errors relative to the brain's generative model (e.g., the expected visual and proprioceptive consequences of saccades; Friston et al., 2012a, b; Friston et al., 2010). In turn, these expectations motivate selective, contextually-appropriate actions that minimize prediction errors over the long term, by bringing about the information needed to guide behavior. Indeed, recent formulations of active inference under Markov decision processes have now highlighted the information-seeking, epistemic affordance implicit in minimizing the free energy expected following an action. In brief, this lends (active) inference and planning a dual aspect sometimes summarized in terms of epistemic and pragmatic value; namely, information-seeking and goal-seeking parts (Friston et al., 2015).

To summarize then, in the course of our ongoing interactions with the world, active inference holds that each movement and sensory event generates a cascade of prediction errors and evolving predictions, that is continuously updated through further environmental exchanges. Changes in the internal and external environment generate unexpected prediction errors that are resolved either through appropriate actions, or via perceptual updating. Each action generates new errors, thereby continuing the cycle. Interestingly, not only does this set up a view of ongoing behavior as a series of perception-action cycles, but insofar as internal models instantiate "beliefs" about potential states, these prior predictions and the movements they evoke can be further construed as hypotheses and experiments (see the aptly titled article by Friston et al., 2012a). As those authors observe, visual search provides an exemplary case where proactive saccades operate by selectively orienting the eyes to locations that are expected to yield highly salient information (Friston et al., 2012a). Not only does each saccade generate an expected proprioceptive error, but the visual error it brings about is crucial for adjudicating between higher-order models (Donnarumma et al., 2017; Friston et al., 2012a). These models are themselves in competition to minimize net-prediction error (Clark, 2015, p. 65; Pezzulo, 2014). Finally, note that as in the case of walking to the kitchen to clean up the lemonade, not only is each saccade or movement of the limbs motivated by the expected low-level errors it will produce, but the overall course of action must itself be motivated, such that the currently perceived states may or may not sufficiently resolve higher-order, *goal-driven* prediction error.

At this point, it can be seen how the active inference account of behavior parallels much of what is known about how people approach complex problems, and specifically the inherently componential and step-wise nature of reasoning and other highly *g*-loaded tasks. In perhaps the most comprehensive process analysis on the Ravens matrices (Raven and Court, 1998) to date, a key finding was "the demonstrably incremental nature of the processing" such that visual fixation data, verbal protocols, and error patterns from human test-takers all converged on the idea that people invariably approach such tasks by breaking them into smaller problems that they then further deconstruct (Carpenter et al., 1990). When visual fixation data was examined in relation to participants' contemporaneous statements while attempting the items, it suggested that the rules governing each problem were induced one at a time. Fixations corresponded to participants' successively seeking evidence for and recognizing shared features among the problem elements, and ultimately their inter-relations (Carpenter et al.,

1990). Note how this is an explicitly hypothesis-testing approach, which like active inference, appears to involve successive cycles in which expectations are generated and then followed by selectively sampling the perceptual space.

Relating this back to PP then, there are three essential features that extend the base account of active inference as it pertains to overt step-wise behavior to also incorporate more complex, goal-directed, internal cognition. First, regarding the transition from overt behavior to internal cognition, this is possible because PP is at bottom a *generative* account of the brain's role in perception: It allows that the same neural architecture that creates conscious experience of the immediate environment can also be used to build representations of imagined and future states (Clark, Ch. 3). As recently argued by Pezzulo and colleagues (2012, 2014; 2016), as this capacity developed during evolution, it would have also enabled organisms to mentally "rehearse" and predict the consequences of potential future actions (Pezzulo and Cisek, 2016). Early-on in phylogenesis, this would have allowed organisms to implicitly represent the various behavioral opportunities (i.e., affordances) that could be brought about through competing potential behaviors. However, it also set the stage for a basic form of reasoning (Pezzulo, 2012; Pezzulo and Cisek, 2016).

Second, because PP is hierarchically structured, it allows for increasingly higher-order models to learn and implement (in the form of predictions) the more complex and temporally-protracted associations that define various contingencies of adaptive significance. Within active inference this process occurs at various timescales and settings, as a function of hierarchical level. For example, whereas a vestibular prediction error could immediately be minimized by moving one's head, an emerging autonomic signal might activate higher-order predictions that bias ongoing action toward foraging behavior. In the latter case, the discrete actions themselves are not specified in advance but are dynamically selected over the course of successive, lower-order perception-action cycles. Because higher-level models can represent multimodal and remote contingencies (e.g., past injuries that were sustained when foraging outside of one's territory), such models institute goals as *priors* that structure and contextualize (but do not necessarily specify) the sub-routines that manifest in ongoing behavior (Pezzulo, 2012; Pezzulo et al., 2015)[8].

Finally, the most recent treatments of active inference have now explicitly articulated its account of information-seeking behavior, though appeals to Markov decision processes (which model decision-making under uncertainty; Friston et al., 2015, 2017). In short, when confronted with a problem that consists in many parts, an individual continuously and iteratively faces a choice among various options. At any stage, they may immediately respond (i.e., take direct action towards the ultimate goal), or temporarily divert, to gather additional information that will resolve the remaining uncertainty obscuring the correct path (the exploration-exploitation dilemma). It has now been shown that active inference construes these evolving decisions as naturally flowing from the need to minimize *expected* free energy, such that the agent implicitly evaluates the set of subsequent counterfactual actions they might take (and their expected consequences), and enacts the behavioral stream with the lowest expected free energy (Friston et al., 2017).

Thus, in the case of solving a typical matrices problem, this might entail momentarily focusing on either the columns or rows to discover the relevant rule, where the choice might be dictated by the path that appears to give the best chance of resolving the immediate uncertainty. Importantly, this perspective entails that agents will be motivated not only to minimize surprises regarding future environmental *states*, but also regarding the contingencies and rules that give rise to those states.

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[8] Note also that this general account of hierarchical cognitive control is not unique to active inference, but has an independent basis in recent research on the prefrontal cortex (Badre, 2008; Botvinick, 2008; Voytek et al., 2015).

This in turn then supports an entire account of curiosity and structure learning (deriving the rules that underwrite contingent relations) around the imperative to minimize expected free energy (Friston et al., 2017). Not only do intelligent agents need to generally avoid momentary surprises, but to do so successfully over the long run, they must also learn (and seek information about) the lawful relations that govern all of their interactions in the world. This then ties free-energy minimization back to intelligence and self-evidencing, as the process of resolving uncertainty across multiple hierarchical levels. Note also that under this framework, even conscious reasoning itself can be construed as a learned behavior that comes to be selected by certain task contexts—whenever an overarching goal requires recourse to thought, the imperative to minimize expected free-energy should induce individuals to engage the previously-acquired mental sub-routines (encoding the problem, inferring relations, etc; Sternberg, 1977) that are appropriate for resolving the relevant uncertainty (and see: Pezzulo et al., 2015, p. 26).

In summary then, active inference extends the basic PP framework in three crucial ways to also address information-seeking behavior, such as encountered in reasoning experiments and problem-solving scenarios of adaptive significance (and for an example with a simulated agent, see: Friston et al., 2017). Moreover, as outlined just below (Section 5.3), it also accommodates the features that differentiate high- and lower-ability test-takers, and supports novel hypotheses about the neuroanatomy of intelligence.

5.3. Fronto-parietal networks under uncertainty: framework and predictions

Recalling Sections 4.1 and 4.2, the current evidence supports an important role for f–p networks in intelligence, such that they appear to comprise a domain-general substrate for higher-order information integration and control in the brain (Duncan, 2010, 2013). Insofar as lesions studies support their necessary role in psychometric *g* (Barbey et al., 2012; Gläscher et al., 2010), the literature overall accords with Naghavi and Nyberg's original contention that f–p networks may form a "backbone" atop the neural hierarchy "by which otherwise fragmented…information [is] integrated and managed (Naghavi and Nyberg, 2007, p. 162)." The strengths of this picture notwithstanding, the findings that precise replications tend to be limited (Basten et al., 2015; Martínez et al., 2015), and that particular tasks elicit broader correlates than latent factors (Barbey et al., 2012; Gläscher et al., 2010; Román et al., 2014), leave several open questions about the precise role of f–p networks across different individuals and task types.

In particular, while some inconsistencies in the literature likely reflect methodological issues, it is also possible that the very generality of intelligence entails some idiosyncrasy in the networks involved. That is, although f–p networks may be essential to complex information integration and control, it is not clear whether they are equally explanatory at all levels of the cognitive hierarchy and in all individuals. To the contrary, while it is possible to isolate the circuits involved in very circumscribed behaviors (e.g., eyeblink conditioning, Christian and Thompson, 2003), the reversed hierarchy suggests a continuum, where as a construct becomes increasingly abstract, and bears on cognition *in general* (and IDs therein), its neural substrates may be increasingly elusive. As such, there appears to be two main possibilities regarding the precise role of f–p networks in intelligence, each with unique implications for the construct itself.

On the one hand, to the extent they are necessary, f–p variability may in fact mediate IDs on all cognitive tasks. If they also prove to be comparably important in all individuals, this would be compelling evidence that intelligence is indeed meaningfully unitary in a physiological and ultimate sense. However on the other hand, IDs in lower-order tasks may predict intelligence by virtue of more domain-specific neural variation. If this were true, or if overall intelligence (or even just complex tasks) permit meaningful variability in the strategies or networks involved (e.g., Kirchhoff and Buckner, 2006), this suggests that

the neural basis of intelligence may be somewhat more diverse.

Here again, uncertainty may provide a framework for situating these various possibilities. Foremost, a hierarchical view of f–p networks clearly aligns with the core claims of PP, such that one would expect them to play a disproportionate role in higher-order tasks (Section 3.4). Note however, that at least thus far, the literature appears to support the primacy of f–p networks in *g*, as a slightly narrower construct, than in intelligence per se (Haier, 2016, pp. 10–11; Reynolds et al., 2013). Thus, as anticipated by Detterman's systems theory of *g* (even in the absence of an identified network), if the latter relies on interactions between separate but interdependent processes, to the degree that some of those are more central than others, their efficiency will set limits on the system as a whole (Detterman, 1987a, 2002; Detterman et al., 2016). Note also that this accords with considerable other data (Carpenter et al., 1990; Colom et al., 2004; Duncan et al., 2008, 1996) that support various f–p functions as being most important to distinguishing different levels of ability (working memory, goal management, etc.). Following from this and PP then, f–p networks may play exactly this role, as the top of the cortical hierarchy through which all subsidiary networks are coordinated.

However, insofar as intelligence is in fact broader than *g*, and individuals differ in their cognitive profiles, the underlying substrates will likely differ as well. Thus, whereas f–p networks may be necessary for and hence also *reliably* implicated in cognitive IDs, it does not follow that they are also exhaustive. Rather, to the extent that both healthy samples and lesion data support a reversed hierarchy, this suggests the potential for at least some diversity in the neural networks that support any one person's intelligence. As such, given that what is ultimately common to cognitive tasks is not a strict form of uncertainty but rather subjective indeterminacy, different individuals may leverage their more unique neural resources in course of responding adaptively. Thus, at the broadest level, the present framework suggests that intelligence may reflect one's ability to coordinate *any* given neural network in coping with indeterminacy, albeit with the f–p system disproportionately constraining that capacity.

On that basis, several other predictions follow. First, if intelligence is broader than *g*, one would expect f–p functioning to most directly predict the latter. This means that among individuals matched for overall IQ, but with opposite profiles (e.g., stronger verbal vs. spatial skills) one might expect variation in more domain-specific networks to more fully predict their intelligence, with f–p variation being more closely linked to *g*. Second, and as also predicted by Detterman (2002), this "central-processing" account may also help explain cognitive differentiation, or the finding that cognitive skills become less-interrelated at higher ability levels (Jensen, 1998a; Tucker-Drob, 2009). Here, the present framework would predict that the relevance of f–p networks to overall ability should be a function of ability level itself, with domain-general f–p processes having a positive, but asymptotic relationship with overall intelligence (see Fig. 2). In other words, at average and lower levels, f–p networks should constrain intellectual functioning, but beyond a given threshold, higher-ability individuals may leverage other networks in developing more differentiated skills.

Finally, by pairing these general considerations with the more detailed active inference framework, still more specific hypotheses may follow. These include: a rostral gradient of higher-order priors (Badre, 2008; Pezzulo and Cisek, 2016), distinct neural signatures of priors versus errors (Bastos et al., 2012, 2015), and a particular role for f–p networks in representing predicted demands on cognitive control (Jiang et al., 2018). Moreover, for the most abstract and complex tasks, successfully resolving the relevant uncertainty will entail minimizing errors over multiple levels of hierarchical generative models—beginning from basic perceptual state estimation up through minimizing expected surprise around the sequences of actions that will not only resolve proximal uncertainty, but will ultimately disclose the rules (and hence strategies) that govern the task as a whole (see Friston et al., 2017; and Section 5.2). Because all of this uncertainty is held to be modelled and
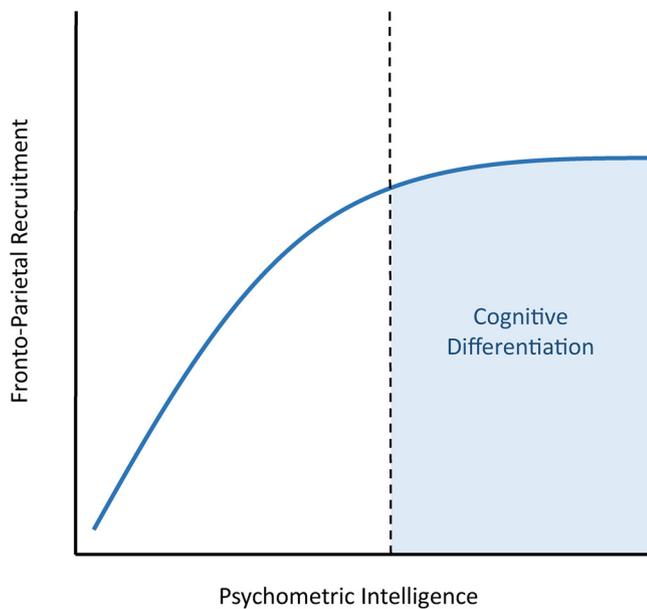
Fig. 2. Predicted Relation between f–p Network Functioning and Intelligence Across Ability Levels.

Hypothesized asymptotic relationship between f–p functioning and psychometric intelligence in relation to cognitive differentiation, as adapted from Detterman's (2002) system theory. As measured IQ increases, cognitive abilities become more differentiated and f–p functioning predicts overall ability level less strongly.

minimized within a distributed hierarchy, active inference should motivate inquiries into each of these functions as they pertain to the role of f–p networks in cognitive IDs.

5.4. Synthesis: spanning the speed-level distinction?

Putting the above together, it can now be seen how PP might facilitate increased integration within the neuroscience of intelligence. In short, if the job of the brain is to predict, then anything that impedes prediction should elicit variability in the neural mechanisms involved in that process. In turn, from an organism's perspective, in its efforts to maintain and act on the basis of an inherently probabilistic model of the world, indeterminacy becomes the most meaningful common dimension of cognitive tasks. This then provides a conceptual basis from which to systematically uncover the most relevant processes in any task-ability correlation.

At the bottom of the cognitive hierarchy, in the realm of psychophysical tasks, PP suggests that task- and activity-ability relationships should be most directly a function of the types and level of uncertainty those tasks induce. This sets up competing hypotheses as to whether ERP-IQ relationships are largely generic, such that any given component should always bear the same relation to intelligence, or whether (as presently suggested) such effects are inherently task-specific, reflecting the more unique variance that a given task-related network shares with broader ability. Further, because PP can be operationalized in terms of both discrete ERPs (Kolossa et al., 2015; Wacongne et al., 2011) and more distributed, temporally-extended processes (e.g., the BOLD response; Kok et al., 2012; oscillatory modulation; Samaha et al., 2015), it allows for explicitly testing the contribution of top-down processes to these lower-level effects.

Near the top of the hierarchy, the indeterminacy concept accommodates several key features of complex highly *g*-loaded tasks, as well as the cortical structures most implicated in IDs therein. As increasing complexity renders correct responding more indeterminate, tasks will recruit increasingly distributed neural networks. This reflects the fact that unlike narrower, perceptual tasks, complex tasks are distinguished

by their relative demands on abstract relations and (often) the need for step-wise cognition—both of which require greater cognitive control. In those scenarios, the capacity of domain-general substrates (f–p networks) to coordinate processing across disparate sub-systems should be a more central factor in cognitive differences. Note also however that because complex tasks necessarily recruit specific and more elaborate networks in any one person, it is also possible that the neural substrates of intelligence may be somewhat idiosyncratic at the individual level. Thus, whereas f–p networks may be crucial to IDs in *g*, lower-order factors, and especially a person's more unique capacities, are apt to involve still broader networks (e.g., see Barbey et al., 2012 Fig. 2).

Finally, because indeterminacy and PP both address the continuum of the cognitive hierarchy, they may provide a means for bridging the speed-level distinction. While such a gap may always exist at the behavioral level, it may yet be possible to identify whether and when a shift occurs in the brain, such that task-ability effects come to reflect more domain-general versus domain-specific processes. Because active inference provides a framework for thinking about PEM as it applies to complex behavior and unfolds in real time, it might eventually be used to clarify not merely the structure of intelligence, but also its dynamic neural basis (e.g., see Haier, 2016, p. 114).

5.5. Broader implications: moderating factors in brain-ability relations

Finally, to turn back to neural efficiency, because PP and active inference furnish neuronal process theories, it also becomes possible to make predictions about the neuroimaging correlates of intelligence, and particularly as follows from the role of belief updating in a predictive account. In brief, a more complex task would generally involve a greater resolution of uncertainty and more belief updating, in the sense that such tasks not only require updating estimated perceptual states, but also evaluating and selecting the policies (i.e., mental routines) that will best minimize free energy, as well as subsequently integrating the relevant contingencies (Friston et al., 2017, pp. 2646–2647). Metabolically, from a neuroimaging perspective, this would normally be associated with an enhanced neuronal response – distributed over the appropriate elements of cortical hierarchies. The longer it takes to resolve uncertainty the greater the neuronal activation. Interestingly, a failure to resolve uncertainty goes hand-in-hand with the loss of statistical efficiency, where the latter is scored by free energy and can be decomposed into accuracy minus complexity (Friston et al., 2017, p. 2644). This means that an inefficient inference process corresponds to a higher level of complexity and more neuronal computational complexity costs. A second layer of this argument rests upon the fact that the brain has to estimate the precision (i.e., inverse uncertainty) of its various beliefs. Because precision is thought to affect the gain of neuronal message passing, one might expect to see pronounced neuronal correlates of precision (i.e., the encoding of uncertainty) that will vary inversely with the degree of intelligent processing.

Notably, while those considerations largely parallel the classic framing of NEH, newer literature has of course highlighted various regional and contextual factors that have qualified that account (Basten et al., 2013; Neubauer and Fink, 2009). Thus, while PP offers a compelling neural process model of computational efficiency, it remains that for any given task, regional effects are apt to depend on the precise computations in question, as well as factors like motivation and overall ability (e.g., Dunst et al., 2014). Nevertheless, there is still another, broader way in which PP may relate to NEH. Namely, although NEH has now been qualified as a *primary* description of how brain activity varies with intelligence, these same qualifications exemplify its value in highlighting various factors that *moderate* activity-ability relations. This then is something else that PP and NEH share.

Specifically, because both accounts emphasize variation in neural activity, they each face the issue that activation is fundamentally dynamic and elicited in context. This means that individual differences will not only reflect variation in intelligence and effects of task features,

but potentially also idiosyncratic effects of the eliciting conditions (plus other external factors that may differentiate examinees). Within the NEH literature, such considerations have motivated studies investigating the moderating effects of sex and expertise (Grabner et al., 2003; Neubauer et al., 2005), and more recently, anxiety (Basten et al., 2011), and subjective task difficulty (Dunst et al., 2014). For PP, however, these issues are perhaps even more central, due to the role that experience and context play in its account of cognition. Namely, if all behavior results from the interplay of neurons that implement hierarchical priors with those that convey environmental changes, any differences in activation could reflect not only variation in response to the latter (i.e., task demands), but also the influence of context and priors.

For its part, context includes factors like testing conditions, time-of-day, and hunger and motivation, which insofar as they cancel out across people or are constant within studies, merely add noise to samples and to the overall literature. However, a somewhat more challenging possibility is that variation in experience, and thus priors, might cause examinees to *systematically* vary in a way that is confounded with intelligence. That is, PP suggests that individuals with different life histories may bring different priors to bear on solving cognitive tasks. In turn, any variability in responding to the resulting uncertainty could reflect not only "intrinsic" variation in momentary capacities, but also variation in previous experience (Linhares, 2000, p. 253). This of course undermines interpretations of any neural effects as solely reflecting differences in momentary processing. Instead, to the extent that examinees who perform better on IQ tests do so because they possess priors which differentially select and facilitate the very processes required, any effects will reflect an unknown combination of variation in more momentary capacities as well as those built up from experience.

This centrality of learning to PP represents both a major challenge and potential virtue of the present framework. One the hand, because indeterminacy is both inherently subjective and partly a function of experience, it is impossible to hold it completely constant across people. As a result, examinees who lack the relevant exposure might perform less well and exhibit more (or less) activation, not because they possess lower capacity, but due to the lack of priors. Differential experience could thus act as a confound, such that disadvantaged examinees might have equal *momentary* capacity but face unequal tasks, necessitating more neural resources to achieve equivalent performance. Further, a potentially more likely and difficult possibility is that experience actually influences the growth of intelligence, such that the two become intertwined. In this case, differences in performance and activation might legitimately reflect variation in intelligence per se, but with the proviso that the latter's development fundamentally depended on environmental inputs. Thus, unlike most prior neural accounts of intelligence, PP seems to inherently conflate ability due to learning with that due to intrinsic variation.

While this confound initially appears devastating for PP's viability, in actuality, it only contradicts the most absolute (and hence implausible) hereditarian views. To the contrary, it aligns well with accumulating evidence for the importance of environmental factors, and especially gene-environment (GxE) interactions, to intellectual development. In particular, while a major role for genes is essentially beyond dispute (Haier, 2016, Chapter 2), it is also now established that the heritability of intelligence varies according to developmental factors: Genetic variance in IQ increases both as children age and at higher SES (Nisbett et al., 2012b). In the case of age, it has been argued that the genes which children carry induce them to select and modify their environments in ways that further enhance those genetic impacts (Briley and Tucker-Drob, 2013; Haworth et al., 2010). For SES, advantaged environments appear to both enhance IQ as well its variance due to genes (Bates et al., 2013), whereas low-SES environments appear to attenuate positive genetic effects that might otherwise accrue (Tucker-Drob et al., 2011).

Adoption studies provide further evidence for environmental

moderation, showing higher IQs among adopted children relative to their non-adopted siblings (van IJzendoorn et al., 2005), and especially for those adopted into more advantaged homes (Kendler et al., 2015). Finally, GxE interactions also help explain how the Flynn effect—the tendency of cognitive scores to rise in populations over time (Pietschnig and Voracek, 2015)—could co-exist with the high heritability of IQ. Specifically, initial genetic advantages might set-off a positive feedback loop, such that genes which promote higher cognitive performance would also promote access to environments that demand and reward cognitive activity (Dickens and Flynn, 2001). At the population level, increased cognitive demands in society over time (e.g., increased technological complexity) could promote better abstract reasoning and thus higher IQs in younger cohorts, in the absence of significant genetic changes from their recent forbearers (Armstrong et al., 2016; Flynn, 2007; Fox and Mitchum, 2012).

In summary, the upshot of these various effects is that intelligence increasingly appears to involve not only one's inborn capacity to marshal momentary resources, but also the development of that capacity contingent on experience. Thus, it is not that PP somehow erroneously conflates learning and intrinsic variability, but rather that their intermingling likely reflects how the brain actually develops and functions. This makes PP's emphasis on learning a potentially beneficial and distinguishing feature among neural theories. Moreover, not only does PP accommodate environmental effects at the conceptual level, but it suggests methods for verifying their mechanisms in the form of neural priors. Speculatively, plausible scenarios where such effects could be expected to manifest include comparisons between more basic perceptual vs. higher-order semantic ERPs, as well as in the influence of top-down modulatory signals in tasks with more constraining mental contexts. In turn, to the extent that such priors can actually be observed, they would provide an important new tool for addressing controversies in the development of intelligence.

6. Objections and limitations

Predictive processing is arguably the most ambitious theory in contemporary neuroscience, proposing that a single physiological principle underlies all neurocognitive activity. Yet, because it is articulated at this grand, overarching level, it under-specifies the precise mechanisms by which PEM is accomplished in any individual domain or behavioral circumstance. As a result, it faces a primary critique related to its scope and level of detail.

Following Marr's framework (Marr and Poggio, 1976), theories of information processing systems should ideally address three interlinked levels of explanation: the computational level, or what the system is trying to achieve and why; the algorithmic level, or the rules used to accomplish that goal; and the implementation level, or how those processes are physically realized (Eliasmith and Kolbeck, 2015). In the present case, although *predictive coding* has a relatively well-specified algorithmic structure (Bastos et al., 2012; Huang and Rao, 2011), PP really refers to a class of theories that vary in their details (Wiese and Metzinger, 2017), with PEM more properly referring to its actual theoretical commitments. Thus, although a growing number of studies are examining hypothesized mechanisms of PP (Section 2.2), when divorced from those more detailed contexts, both PP and PEM face charges of vagueness.

This concern has been raised in two related ways: First, are PP/PEM so under-specified as to make them unfalsifiable, and second, is PP stated so abstractly that it runs the risk of being empirically but trivially true (Hohwy, 2015; Rasmussen and Eliasmith, 2013; Sims, 2017)? As outlined by others, perhaps the best response to these concerns is by way of analogy to other theories with similarly broad scopes. In particular, both mechanical laws in physics and natural selection in biology have been invoked as instances of other very general principles that nevertheless motivate testable predictions at more detailed levels of description (Friston et al., 2012b; Hohwy, 2015). In each case, although

the principle alone merely describes a phenomenon, when applied to a particular context, it still predicts the relevant details. For the physical principle of least action, its particular manifestation will of course vary with the situation (e.g., planetary orbits, a river's course; Friston et al., 2012b), but lacking knowledge of the outcome, it still predicts the results. Similarly, while natural selection alone fails to specify the mechanisms of heritability (Klein, 2016), it nevertheless predicts their existence. In the case of PP/PEM, although many discussions gloss over their implementations (which may even vary by domain), any specific experiment will demand a more precise operationalization, and hence the chance for disconfirmation. Thus, while PP theorists face a legitimate challenge to better specify its assumptions and subject it to meaningful tests (Buckley et al., 2017; Spratling, 2013), in light of its overall promise, it merits pursuing while that process unfolds.

These concerns about PP as a general theory also have parallels in its application to intelligence. Most significantly, although uncertainty unifies the cognitive hierarchy and potentially integrates much of the literature, this again comes at the cost of some inherent vagueness. On the one hand, by making indeterminacy primary, PP can limit unnecessary (and possibly erroneous) appeals to still other constructs in explaining intelligence. Moreover, it motivates the intriguing and potentially transformative hypothesis that intelligence might be somewhat idiosyncratically organized from one brain to another. On the other hand, it also widens the range of contributing factors to intellectual performance, and especially conative variables like effort and motivation. As a result, the current framework seems to require either acknowledging a wider role for those variables in how intelligence is expressed, or restricting the construct to only cognitive processes in a potentially arbitrary way.

More challenging still, placing uncertainty at the center of intelligence forces a reexamination of the construct's conceptual limits. Following Marr again (1976), while the computational goal of more circumscribed constructs can be readily specified (e.g., object recognition), for intelligence, this has proved exceedingly difficult. Indeed, intelligence has famously defied definition in a way that few other constructs have, with some of its most eminent theorists either avoiding the term altogether (Jensen, 1998a), or defining it through reference to numerous other processes (Gottfredson, 1997a; Nisbett et al., 2012b). Accepting the primacy of uncertainty avoids the unsatisfying laundry-list approach, but at the cost of acknowledging the conflict that may motivate such definitions in the first place—the possibility that intelligence resists definition because it truly reflects a composite of all cognitive constructs[9], rather than a specific capacity with a cohesive neural basis (van der Maas et al., 2014). Whereas the present framework entertains a unitary *g* built around a single neural network, it also argues for some inherent ambiguity in those that mediate the more momentary, individualized expressions of everyday intelligence.

7. Conclusions

Despite considerable progress in the neuroscience of intelligence, the field as a whole faces several challenges, and perhaps most importantly, a need for greater integration. In this regard, the present account may be unique among candidate neural theories. In addition to ostensibly offering a paradigm for all of cognitive science, PP meets the needs of intelligence research for a theory of brain functioning that accommodates the construct as a somehow unitary yet multifaceted capacity (Deary, 2000, p. 95), and which appears to play a role in all mental tasks. It accomplishes this by outlining how the whole of the neural hierarchy, from low-level perceptual processes up to those that mediate conscious reasoning, represents a dynamic, integrated system that operates in the service of a single functional goal—successfully managing uncertainty. By applying that logic to the intelligence

literature, it appears possible to derive a plausible, parsimonious explanation for the presence and size of any given task-ability correlation, as well as a systematic approach for probing the underlying networks.

As an explicitly hierarchical theory, PP naturally accords with a broad swath of the psychometric intelligence literature, and by integrating this with contemporary neuroanatomical thinking, it suggests a compelling physiological explanation for how top-down processes might constrain the expression of otherwise dissociable capacities. Yet, at the same time, it also accommodates the tensions inherent to the intelligence construct, by providing a principled explanation for how IDs in lower-order and more domain-specific capacities might uniquely contribute to individual intelligence, as well as its momentary expression in narrower tasks. Thus, the present account also shows promise for integrating the current extremes of more reductive and higher-level neural research on intelligence. Finally, because PP and its current evidence base also support the existence of dissociable neural markers for prediction errors versus priors, it may provide new tools for investigating the neural basis of environmental effects on intelligence, as well as those of other moderators.

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[9] Though see Jensen's (2002) counterargument.

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