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Disentangling signal and noise in autism spectrum disorder

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ABSTRACT

Predictive coding has recently been welcomed as a fruitful framework to understand autism spectrum disorder. Starting from an account centered on deficient differential weighting of prediction errors (based in so-called precision estimation), we illustrate that individuals with autism have particular difficulties with separating signal from noise, across different tasks. Specifically, we discuss how deficient precision-setting is detrimental for learning in unstable environments, for context-dependent assignment of salience to inputs, and for robustness in perception, as illustrated in coherent motion paradigms.

1. Introduction

As part of the wider trend in computational psychiatry (Friston, Stephan, Montague, & Dolan, 2014; Montague, Dolan, Friston, & Dayan, 2012; Stephan & Mathys, 2014), recent explanatory accounts of autism spectrum disorder (ASD) take inspiration from well-articulated information processing models of typical cognition (Hohwy, 2013; Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012; Qian & Lipkin, 2011; Quattrocki & Friston, 2014; Rosenberg, Patterson, & Angelaki, 2015; Sinha et al., 2014; Van de Cruys et al., 2014). Particularly influential in most of these new proposals for ASD is the predictive coding framework (Clark, 2013; Friston, 2010). Predictive coding assumes that the brain builds a so-called generative model about the environmental causes of the sensory inputs it receives. It infers these causes by making a best guess, or prediction, about incoming inputs at each point in time and evaluating whether the predicted sensory activity corresponds with that actually received through the senses. If not, the system will attempt to reduce this mismatch, or prediction error, by adjusting its prediction about the state of the environment and adapting its generative model for the current context accordingly. Within this scheme, these models are hierarchically structured (Rohe & Noppeney, 2015; Wacongne et al., 2011), where higher levels are capable of capturing patterns in sensory inputs that have larger spatial or temporal spans.

However, not all prediction errors are created equal. In order to appropriately weigh a prediction error, not only the mean (best estimate) is predicted at each level, also the precision (inverse variance) of the prediction error is estimated. The comparison with a statistical *t*-test makes clear why this is important: in a *t*-test a difference in means ("prediction error") is weighted by the variance or expected (standard) error (Friston, 2010). Otherwise, there is no way to interpret the importance (informative value) of the differences one finds. Technically, precisions are hyper-parameters which are estimated and learned with the same predictive coding machinery. Multiple types of uncertainties in the inputs we receive, make the task of predicting the world particularly challenging. There may be uncertainty because of our lack of knowledge about a particular regularity in the environment, either because we have not fully learned the regularity, or because the regularity has recently changed, which happens frequently in a volatile environment. Uncertainty can also be due to the probabilistic nature of a given regularity: By chance, an expected input pattern may not occur. All these types of uncertainties will result in prediction errors in the system. Unfortunately, we do not know a priori whether a given prediction error is actually relevant, i.e., corresponds to an actual learnable (change in) regularity in the environment, or not relevant, i.e., is due to probabilistic noise variability. In the first case the prediction error should be used to change inferences and learn new structure, but in the second case

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we should largely ignore it, using it only to improve future precision estimates. Optimally, precision or gain should be high (Yu & Dayan, 2005) when prediction errors correspond to reducible, learnable uncertainty or when confidence in the prediction is low.

In many of the recent proposals for ASD, deficient precision estimation is assumed to be key (Lawson et al., 2014; Palmer, Paton, Kirkovski, Enticott, & Hohwy, 2015; Pellicano & Burr, 2012; Van de Cruys, de-Wit, Evers, Boets, & Wagemans, 2013; Van de Cruys et al., 2014). Our own account, termed "HIPPEA" (for High, Inflexible Precision of Prediction Errors in Autism), assumes that bottom-up prediction errors are assigned a precision that is too high and not adapted (inflexible) to the uncertainty in the context (Van de Cruys et al., 2014). A crucial consequence of this is that prediction errors are taken at face value, hence there will be too little discounting of (prediction errors stemming from) noise or irrelevant variability in inputs. Non-repeating, accidental variations in the input will receive disproportionately high weight, resulting in overfitting to these irrelevant differences: models will be shaped by putative regularities that will not generalize. By setting precision invariably high, "training examples" will be more literally encoded (cf. veridical mapping, Mottron et al., 2013). According to HIPPEA, inefficient predictive updating will result in different top-down priors or predictions, namely overfitted, low-level ones that capture too much redundant inputs, and possibly an impoverished set of very high level ones that are not sufficiently informative. Such an incomplete hierarchical generative model would result from the fact that unduly high precision of inputs induces predictive matching that takes place on (and might not get beyond) very local (lower) levels. While this happens at the expense of detecting more abstract regularities, note that the basic capacity of forming predictions remains unaffected. Rather, encoding of noise hampers discovery of regularities when these are embedded in more complex, noisy inputs.

It follows that we should be careful in stating that individuals with ASD cannot form informative priors (only "weak" or low precision priors), as several authors seem to suggest (Manning, Tibber, Charman, Dakin, & Pellicano, 2015; Pellicano & Burr, 2012; Sinha et al., 2014; Zaidel, Goin-Kochel, & Angelaki, 2015). Surely, in lots of cases individuals with ASD can detect and learn to use regularities (in the form of informative priors). A recent study by Spanò, Peterson, Nadel, Rhoads, and Edgin (2015) convincingly showed that children with ASD use both low-level priors (on convexity and surface integration) and higher level priors (based on form/object memories) in a basic visual figure-ground segregation task, to the same extent as typically developing children. As pointed out before, even probabilistic and implicit regularities can be learned in ASD (e.g., Nemeth et al., 2010; Roser, Aslin, McKenzie, Zahra, & Fiser, 2015; Solomon, Smith, Frank, Ly, & Carter, 2011). If the task makes clear which stimuli or dimensions are relevant, people with ASD may even be more sensitive to changes in environmental patterns (Westerfield, Zinni, Vo, & Townsend, 2015) as seen in the P3 ERP component, consistent with our proposal of increased precision of prediction errors.

Still, there is important commonality between the HIPPEA account and the weak priors account (Pellicano & Burr, 2012), because both are talking about *relative* precisions of bottom-up and top-down information *on each level of the hierarchy* (see also Lawson et al., 2014). The weight of new evidence (and thus the change in prediction) is defined as the precision of input divided by the precision of the prior (see Mathys et al., 2014 for the full computational details). Hence, weaker (i.e., lower precision or less confidence in) top-down predictions would also lead to increased reliance on bottom-up information as in the "weak priors" account (Pellicano & Burr, 2012). The importance of relative precisions, however, also implies that studies that find reduced adaptation in behavior or reduced repetition suppression in fMRI responses in ASD (or high autism traits) (e.g., Ewbank et al., 2014; Molesworth, Chevallier, Happé, & Hampton, 2015; Turi et al., 2015) cannot simply be considered evidence for the weaker priors thesis, even though both adaptation and repetition suppression are thought to be the result of (top-down) predictive activity (Chopin & Mamassian, 2012; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008).

Both ways of shifting the balance in inference (higher bottom-up precision vs. lower top-down precision) should be dissociable, at least in principle, when considering the result of inference. Specifically, one would expect higher precision of the posterior estimate for ASD in case of higher precision prediction errors. At first sight, this seems to be a testable prediction, for example by directly or indirectly probing for decision confidence (Meyniel, Schlunegger, & Dehaene, 2015; Yeung & Summerfield, 2012). Additionally, one should expect less trial-by-trial fluctuations in confidence according to the current proposal. However, simple confidence measures may not be able to satisfactorily answer these questions, given that (1) they provide one measure for something (posterior) that takes place on multiple hierarchical levels, (2) they might be affected by (executive) post-perceptual processes, and (3) they require the capacity to explicitly reflect on one's own thought processes (explicit metacognition), which may be particularly deficient in ASD (Grainger, Williams, & Lind, 2014).

To make progress on these Bayesian accounts of ASD, it will be important to study the updating (learning) and application of priors on a trial-by-trial basis, precisely quantifying varying uncertainties and to what extent they are taken into account for future inference. In the next section, we will discuss studies in ASD that are beginning this enterprise, in the context of learning in unstable or volatile environments. We will see that forming higher order expectations on volatility are necessary to restrain the effect of noise.

In a second section, we will look at studies on salience in perception in ASD. Even if priors are learned, they may fail to adequately smooth out the variability that is inherent to all natural stimuli, because of the weight that deviations receive. This increased sensitivity to variability, irrespective of its origin or relevance, means that the informative value or salience of different pieces of input is not properly determined. Again, this can be seen as an inability to disentangle relevant (signal) and irrelevant (noise) inputs, dependent on a given context.

In a final section, we will discuss the sensitivity to variability in the input and how that leads to the lack of robustness in inference. We will discuss studies that suggest that coherent motion perception and motor behavior is more vulnerable to noise in ASD. Here too, second-order estimations of to be expected variability, learned across different experiences, would typically help rein in noise, but because of the precision-based mechanism described above this seems to be hampered in ASD.

2. Learning in unstable environments

A mix of uncertainties (actual and accidental changes) is particularly present in a probabilistic learning task, where the governing rule (e.g., stimulus A is rewarded) has to be learned based on imperfect (probabilistic) feedback on your choices, and the governing rule can change unexpectedly (e.g., not A but B is rewarded from now on). If one accurately estimates the intrinsic level of uncertainty across multiple trials (i.e., the expected amount of prediction errors one will encounter), it is easy to weight feedback that exceeds this expected uncertainty, such that subsequent predictions about which rule holds, will be updated. Probabilistic reversal learning studies in ASD participants show that while they seem perfectly able to learn a probabilistic rule initially, performance is worse relative to neurotypical participants when the rule needs to be learned and updated in an unstable environment (D'Cruz et al., 2013; Robic et al., 2015; South, Newton, & Chamberlain, 2012). More specifically, there are different ways in which rule updating may be affected by aberrant precision setting, going from switching too often (when the newest evidence is continuously weighted too highly), to switching too little (for persistent low weighting of new trials). HIPPEA would predict the former, however, note that such differences may only become apparent when variability on an irrelevant dimension is present (i.e., orthogonal to the dimension of the rule).

Importantly, the type of meta-learning —learning when to learn and when not to learn— needed for this kind of learning in unstable environments also concerns a regularity, but one that is integrated across a longer time scale, namely about what type of variability can be expected in a given context. There is learnable structure in the presence of uncertainty as well (Hohwy, 2013), which means we can learn to expect varying amounts of uncertainty based on the context. These are estimated as higher order parameters that are modelled accordingly in a hierarchical Bayesian model (e.g., Iglesias et al., 2013; Mathys et al., 2014). They serve as learned top-down constraints (priors) that seem to be deficient in ASD. The regularity learned here may be that the conditions (causes) in this environment alternate frequently. In the experimental setting of reversal learning, this is somewhat contrived and arbitrary, but in real-life such a regularity may be indicative of different generative processes (e.g., different intentions of different agents) behind these alter(n)ations. Hence, being able to dissociate different types of uncertainty enables inference of new (higher order) causes in environment. Note that, apart from these types of explicit learning tasks, the mismatch negativity signal could also be exploited to infer the learning of these types of regularities from the amplitude (gain) of the mismatch responses (for an example in a typical population, see Todd et al., 2014).

3. Salience in context

Natural settings are often even more complex than the environment of a probabilistic reversal learning task: One is presented with multiple objects, each with numerous perceptual dimensions, which can take on a huge range of discriminable values. Which dimensions or values (features) are relevant is highly dependent on the context. While a man's moustache is a relevant piece of information (signal) when attempting to recognize that face, the same moustache is far less relevant (noise) when trying to read the emotional state of the face. Given this "task" context, i.e., predictions that are activated (or the top-down questions we "ask" from inputs), the weighting of those parts of the input should be different, such that our inferences are preferentially guided by the informative or consequential pieces of information. Again, a certain context will not only elicit certain predictions (after learning), it will also prepare us with certain expectations on the type of variability we can expect. These estimations are what should inform the weights (precision) of prediction errors.

This implies that setting precision has to do with a fallible dismissing of certain inputs as noise and highlighting others as relevant, in relation to the current predictions. Hence, noise is not defined independently of the particular predictive models in question (Jost, 2004). It is not an objective quality of input data. Rather, it is defined as input variability uncorrelated with the prediction or task at hand. A given datum is relevant, if this datum changes the inference given the current context. Hence, what will be signal and what will be noise has to be determined relative to a particular context and a given level of predictions. Contrary to other proposals that focus exclusively on the functional implications of different levels of endogenous noise, caused by physiological processes in neurons (Davis & Plaisted-Grant, 2015; Simmons et al., 2009), we draw attention to the fundamental challenge of disentangling signal from noise or relevant and irrelevant parts *of the input*.

One could also describe precision-setting in attentional terms. Particular learned statistical regularities induce an "attentional set" (Austen & Enns, 2003; Cosman & Vecera, 2014) characterized by differential weighting of different inputs. For example, part of what makes face processing holistic or global, is the high expected precisions for relevant or diagnostic features, for example the eyes, at the expense of others. Indeed, Chua, Richler, and Gauthier (2014) gathered data suggesting "that holistic (face) processing is an expression of learned attention to diagnostic face parts." At the same time, it is an expectation on the features that can vary and to what extent, without being consequential for the task at hand (cf. generalization). For instance, precise details of a font do not matter (are expected to vary) for the task of reading the text, but they might matter for a different task on the same inputs. This highlights the link between precision setting and a global versus local processing style. Global processing is a learned attentional strategy —by precision setting— to focus attention to those differences in the input that could answer "questions" (predictions) from a particular (high) level of processing. Hence, it is about using a spatial configuration (a predictable structure) to efficiently sample informative parts and eliminating non-diagnostic information.

This is nicely illustrated in heat maps of eye movements, showing how people "forage" information in object-specific trajectories (Yang, Lengyel, & Wolpert, 2016). Friston, Adams, Perrinet, and Breakspear (2012) model these saccades based on expected precisions, given certain predictive models (e.g., for the presence of a face). Given the task of discriminating a face (from a non-face or inverted face), eye movements visit certain regions of the input that have the highest expected precision, meaning they have the most discriminative power to reduce uncertainty about the input. In light of the role of expected precisions in deciding where to look, it is clear why studies in ASD often report aberrant, more variable saccade patterns compared to those of typical participants, for example for faces (Boraston & Blakemore, 2007; Pelphrey et al., 2002). However, in line with the current view, this atypical salience estimation is not limited to faces or other social stimuli. Wang et al. (2015) recently demonstrated that saccade hot spots (across various natural images), were more determined by low-level salience (e.g., contrast) in ASD than semantic-level salience as was the case for typically developing individuals.

Note that people with ASD seem perfectly able to assign salience, when explicitly guided by top-down knowledge. This is supported by their intact or superior visual search performance for simple displays (Gliga, Bedford, Charman, Johnson, & BASIS Team, 2015). Here, the relevant feature ("signal") is known in advance and does not need to be autonomously determined, based on extensive learning. It actually pays off to amplify the odd one out in this task. However, as a recent study by Keehn and Joseph (2016) pointed out, when the target is not known in advance people with ASD lose their advantage and actually perform worse, consistent with the current conception.

4. Robustness in perception and action

Appropriate precision-estimation not only provides salience, but also robustness to perception and action by suppressing noise or irrelevant variation. This may directly link to frequent reports of increased interindividual and intraindividual heterogeneity in neural and behavioral measures in ASD (e.g., Hahamy, Behrmann, & Malach, 2015; Haigh, Heeger, Dinstein, Minshew, & Behrmann, 2015). Again, the expectation about the variability itself needs to

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be acquired across multiple fluctuations (experiences), to allow for proper learning and reshaping of priors. In a meticulous individual-level study on micro-movements, Torres et al. (2013) showed that, in action as well, subjects with ASD did not properly learn about the variability or unreliability intrinsic in their own motions, making their micro-movements more random or "memory-less". Even though they were able to perform according to the goals of the motor task, Brincker and Torres (2013, p. 2) observed that "the movement variability from experiencing the "here and now" seemed to be the only useful kinesthetic information to them".

Coherent motion (CM) has been frequently used to study robustness in perception, including many studies in ASD. Most CM studies use random dot kinematograms (RDKs), for which participants are required to discriminate the overall dominant motion direction of a field of dots, while a certain percentage of the dots moves randomly across the display. However, rather than being a direct test for global processing capacities, as frequently thought, CM tasks actually confound the capacity to integrate local inputs into global percepts with one's sensitivity to noise (Dakin, Mareschal, & Bex, 2005; Manning, Dakin, Tibber, & Pellicano, 2014). While RDK performance in ASD is predominantly interpreted in relation to possible global integration deficits (or weak central coherence), the results could also be interpreted in terms of the participants' ability to cope with *noise* inherently present in the displays. Interestingly, studies with noiseless motion paradigms (e.g., Chen et al., 2012; Foss-Feig, Tadin, Schauder, & Cascio, 2013) have shown intact global motion perception in ASD.

In an exciting recent study, Manning et al. (2015) present data that speak directly to this issue by investigating the sensitivity to directional differences in motion display in children with and without ASD (matched on age and IQ). Children completed a direction integration task with two interleaved conditions (no-variability and high-variability) in addition to a traditional motion coherence task. In the direction integration task, dot directions were sampled from a normal distribution with a specified mean and standard deviation (SD). In the no-variability condition, the SD of dot directions was 0° and the mean direction of dots varied in order to find the finest direction discrimination possible. In the high-variability condition, the mean direction of dots was fixed but the SD of dot directions was varied to find the maximum level of variability that could be tolerated while successfully identifying the signal direction. In the motion coherence task, a proportion of dots moved in a coherent direction, while the remaining dots moved in random directions. The authors used an adaptive staircase method in all three tasks to estimate thresholds.

Manning et al. (2015) found that children with ASD, compared to the typically developing children, were as sensitive to directional differences when all elements moved in the same direction (no-variability). Crucially, the children with ASD proved more sensitive to the average direction in the presence of directional variability (high-variability) than the typically developing children. Despite the improved averaging ability, however, the children with ASD performed comparably to typical children in the standard motion coherence task. Manning et al. (2015) drew two main conclusions from these data. Firstly, children with ASD outperformed typically developing children in the high-variability motion direction task, suggesting enhanced integration of local motion in ASD. Several other studies have also indicated that individuals with ASD can process global spatial information at least as well as typical controls (e.g., in contour integration, Almeida, Dickinson, Maybery, Badcock, & Badcock, 2014; or in contextual cueing studies, Barnes et al., 2008). Taken together, these results present a major challenge for any account of ASD proposing a core deficiency of global, integrative processing of perceptual inputs (e.g., "weak central coherence"; Happé & Frith, 2006).

Secondly, Manning et al. propose that ASD is characterized by reduced segregation of signal from noise in motion signals, as the CM performance did not benefit from the enhanced motion integration demonstrated in the direction discrimination task. Hence, the study by Manning et al. is particularly revealing in its direct comparison of these two global motion paradigms.

Although the CM findings of Manning et al. support the hypothesis that individuals with ASD have problems in dealing with noise, their additional analyses suggest that these problems cannot be attributed to different levels of endogenous noise in the perceptual system, contrary to theories of ASD that argue for higher (Simmons et al., 2009) or lower (Davis & Plaisted-Grant, 2015) internal noise as core deficit. Hence, an alternative explanation based on the (inadequate) weighting of different local inputs, seems more attractive. In the high-variability direction discrimination task, all variability in the dot cloud is informative, so all dots are signal dots that can and should be weighted indiscriminately in order to make a decision on the (average) motion direction. Crucially, while the high-variability discrimination stands to gain from uniform, indiscriminate weighting of all dot directions (to estimate the mean), the no-variability would not gain (or lose) from this, consistent with their findings in ASD. In other words, the increased sensitivity to variability in ASD will not hurt performance in this task (because it is relevant). Finally, in the motion coherence task, signal dots should be weighted more strongly compared to randomly moving (noise) dots, which should be ignored as much as possible, hence differential weights are essential.

Remarkably, converging evidence was recently provided by Zaidel et al. (2015), using a paradigm in which participants had to discern the direction of simulated self-motion through random dot clouds (optic flow). Specifically, adolescents with ASD were slightly better for the condition in which 100% of dots moved in a coherent way, while their performance was disproportionately negatively affected when a proportion of dots moved randomly (noise), producing higher thresholds than controls. Zaidel et al. also included a vestibular cue that could be used (with lower reliability) to detect self-motion direction, and found that multisensory integration was intact in ASD, despite their increased sensitivity to visual noise. Most interestingly, subjects also performed several consecutive blocks of the task in the 0% coherence condition (complete visual noise), allowing the authors to study whether participants could actually learn to ignore the (uninformative) visual cue and rely only on the vestibular cue. While control participants quickly learned to down-weight the visual noise to perform more optimally, performance of individuals with ASD remained the same across blocks, showing that they were not flexible in the weighting of visual inputs.[1] Together, these CM studies suggest that individuals with ASD have problems in giving appropriate, differential weight to inputs in conditions of uncertainty (noise).

5. Conclusions

With these three examples above, we have argued that the real challenge of disentangling signal and noise in ASD lies in forming higher-order expectations about the type and quantity of variability that one should expect in given context, based on multiple experiences or trials on a longer timescale, not just single instances. In those cases, prior information should also be learned and used inefficiently, as findings by Skewes, Jegindø, and Gebauer (2014) suggest. However, extracting a mean estimate for a single display (e.g., contrast detection, average motion discrimination,

[1] Given recent evidence for deficient interoception in ASD (e.g., Garfinkel et al., 2016), future research will need to figure out whether generally poorer (low expected precision) vestibular perception could help explain these findings.

or numerosity estimation) should not pose a problem in ASD when the display does not include noise that should be weighted differently than the rest of the input, nor will learning a prior cause difficulties in such conditions. Hence, a viable hypothesis seems to be that individuals with ASD weigh inputs higher and indiscriminately, which leads to problems in certain settings, illustrated above, but not in others. Taking full advantage of the quantifying potential and nuance of Bayesian frameworks, future studies will need to bear out whether predictive capacities in ASD are indeed affected in this way.

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