Low endogenous neural noise in autism

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Abstract

'Heuristic' theories of autism postulate that a single mechanism or process underpins the diverse psychological features of autism spectrum disorder. Although no such theory can offer a comprehensive account, the parsimonious descriptions they provide are powerful catalysts to autism research. One recent proposal holds that 'noisy' neuronal signalling explains not only some deficits in autism spectrum disorder, but also some superior abilities, due to 'stochastic resonance'. Here, we discuss three distinct actions of noise in neural networks, arguing in each case that autism spectrum disorder symptoms reflect *too little*, rather than too much, neural noise. Such reduced noise, perhaps a function of atypical brainstem activation, would enhance detection and discrimination in autism spectrum disorder but at significant cost, foregoing the widespread benefits of noise in neural networks.

Autism spectrum disorder (ASD) is characterized by a broad range of psychological and behavioural features, spanning social, language, executive, motor and perceptual domains. Previous research within the three defining symptom domains (social communication, language and repetitive behaviours) has spawned several theories of autism, the most successful of which highlight broad commonalities between symptoms across domains and propose single cognitive or neural mechanisms for them. Here, we term these 'heuristic' theories, in reference to their application of a single, fairly simple principle across multiple domains (e.g. Theory of Mind Deficit, Baron-Cohen et al., 1985; Weak Central Coherence, Frith, 1989; Executive Dysfunction Theory, Pennington and Ozonoff, 1996; Russell, 1997; Enhanced Perceptual Functioning, Mottron et al., 2006; Reduced Generalization Theory, Plaisted, 2000, 2001; Theory of Hypo-Priors, Pellicano and Burr, 2012).

It is unlikely that any heuristic theory can account for the broader landscape of autistic features and symptoms. Indeed, the heterogeneity of the disorder would seem to preclude such an explanation, and the current general stance is one of caution in applying a single deficit theory to account for the disparate set of research findings and clinical symptoms of ASD (Happé et al., 2006). Nonetheless, single process theories can provide a clear starting framework by which to begin to explore seemingly intractable individual diversity and complexity; they remain a powerful stimulus for research, highlighting commonalities between aspects of autistic features that have no transparent relation (the Weak Central Coherence hypothesis proposed by Frith, 1989, provides a compelling and enduring example).

We focus here on another heuristic proposal, that there are high levels of endogenous neural noise in autism, rendering neural signals 'noisy' and unreliable (Rubenstein and Merzenich, 2003; Simmons et al., 2007, 2009). One appeal of this hypothesis, as of any that considers neural processes that may affect synaptic connectivity, is its potential application to understanding atypical long- and short-range structural and functional connectivity in autism (Belmonte et al., 2004; Domínguez et al., 2013; Minshew and Williams, 2007). The hypothesis of increased neural noise has undergone refinement recently by Simmons et al. (2009), who emphasized that, because neural noise can either enhance or disrupt stimulus detection and discrimination under different circumstances, excessive neural noise might explain both enhanced and impoverished performance in autism, a key hurdle for heuristic theories. Milne (2011) subjected the proposal that neural signatures in ASD are noisy and unreliable to its first direct test, and found higher trial-to-trial variability in electroencephalography (EEG) recordings in

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ASD individuals, concluding that this was consistent with high endogenous neuronal noise in ASD (see also, Dinstein et al., 2012).

The identification of neural noise, as a means to explain features of autism, is a potential breakthrough. However, we recently speculated (Greenaway et al., 2013) that an account of ASD might, in principle, be developed from a directly opposing foundation to previous work: *reduced* neural noise in autism. Here we develop such a view, illustrating how *low* endogenous neural noise in autism can provide an attractive explanatory heuristic for a range of ASD features, including its clinically evident symptoms and laboratory results. We assume that any lower noise will be present in all cortical processes throughout development, and that any group differences will reflect low noise directly, not compensatory responses or transient stages during development. These added assumptions are intended to make the view as simple to falsify as possible – an important feature of heuristic accounts as their primary utility is to motivate psychological and physiological experiments.

Neural noise

For practical purposes, neural 'noise' often refers to variation in neural responses that is of indeterminate origin, of complex spatial/temporal structure and that typically limits detection or discrimination by reducing signal-to-noise ratio (see e.g., Baker & Meese, 2012, McDonnell & Ward, 2011; Stein, Gossen & Jones, 2005, for recent discussions). In physiological terms, noise may crudely be considered either as exogenous (i.e. reflecting stimulus noise) or endogenous (spontaneous, internally generated, intrinsic to a neural mechanism). Endogenous noise is often modelled as multiplicative (proportional to the magnitude of a response to a stimulus) or additive (constant across stimulus magnitudes). This distinction will be crucial in modelling future experiments that explicitly target neural noise in autism, but for our current purposes is unnecessary. Here, for simplicity, we illustrate our case with regard to endogenous, additive noise that provides a fairly constant background to our cognitive, perceptual and motor processing, and assume that multiplicative noise will be similarly affected.

Our claim concerns noise that arises within small-scale neural networks, and noise in this sense does not necessarily translate into 'noisier' signals in functional imaging studies or into less reliable/more variable responses across trials. Indeed, spatio-temporally localized noise in small-scale networks likely *stabilizes* large-scale network responses in the brain across trials and other longer time frames (e.g. Ermentrout et al., 2008; Kirkpatrick et al., 1983; Sagués et al., 2007). We must search for the effects of noise in cognitive and perceptual performance rather than *large-scale* physiological patterns in the autistic brain; greater variability in event-related potentials (ERPs) of individuals with ASD (Milne, 2011) might reflect less (or more) noise in individual neurons and local networks (Ermentrout et al., 2008).

Our claim is distinct from Brock's (2012) proposal that autism may involve reduced variance in the Bayesian likelihood function – corresponding to sensory noise. First, our view holds that low noise is a *pervasive* feature of brain function in ASD, as opposed to Brock's claim, that implicates sensory noise only. Second, Bayesian suggestions regarding uncertainty in autism (see also Van de Cruys et al., 2013) have not distinguished trial-by-trial variability (large-scale − '*noise*', as measured by Milne (2011) from variability of responses within a single presentation in local networks ('*noise*' as we conceive of it here). *Either* will generally increase uncertainty by limiting how accurately bottom-up sensory processes specify the nature of a stimulus. However, increments in local, 'within-trial' noise may reduce rather than increase inter-trial variation (Ermentrout et al., 2008) underscoring the importance of distinguishing between claims about large-scale inter-trial variability autism versus smaller-scale, neural noise. Indeed, we suggest that the increased inter-trial variability observed in autistic compared to neurotypical individuals by Milne (2011; see also Dinstein et al., 2012) is consistent with and perhaps reflects reduced local noise. Optimal levels of local noise would tend to decrease large-scale inter-trial response variability and an absence of this stabilising influence in ASD would be expected to increase inter-trial variability. Thus, Milne (2011) and similar findings may speak against Brock's suggestion regarding the likelihood function, but need not impact the view espoused here.

Noise, whether externally present in a stimulus or inherent in neural mechanisms, typically impairs detection and discrimination of perceptual signals. However, a great deal of previous research has also addressed the potential benefits of, and indeed need for, some neuronal noise in perception, cognition and motor mechanisms (for reviews, see Braun and Mattia, 2010; McDonnell and Ward, 2011; Moss et al., 2004). Our proposal is that ASD symptoms reflect atypically *low levels of* neuronal noise, not high levels as has previously been supposed. We illustrate our argument by referring to three primary actions of neural noise on (1) enhancing or impairing stimulus detection/discrimination, (2) inducing transitions between alternative perceptual or cognitive states and (3) enhancing generalization across representations. While these separate benefits fundamentally reduce to the same action of noise, distinguishing their effects on performance is important to illustrate the influence of noise in autism. For reference, these three different actions of noise are cartooned in Figure 1.

Action 1: noise influences stimulus detection and discrimination

Noise typically reduces the ability of sensory systems to detect and to distinguish signals. However, computational models of neurons and their interactions suggest that a nar-
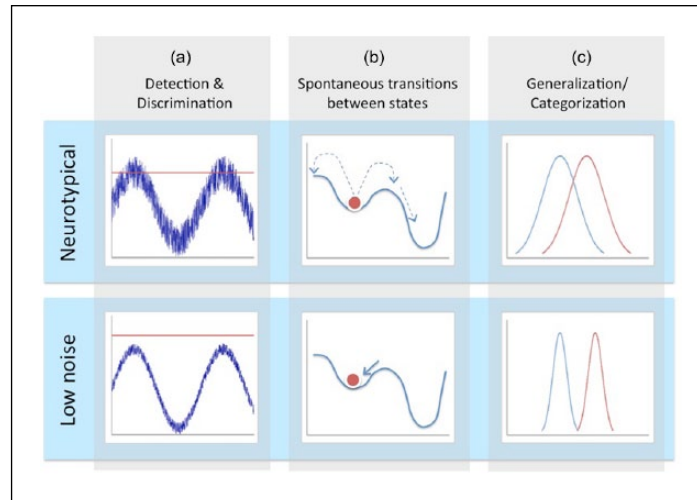
Figure 1. Three basic actions of noise in neural network, cartooned for a brain with notionally optimal noise (upper panels) and for a low-noise brain (lower panels). (a) The red line in the upper and lower panel represents a cell's threshold for responding. When a subthreshold stimulus is applied to the cell, threshold is not reached when little or no noise is added (lower panel). However, with the addition of sufficient white noise to the signal, the signal and noise intermittently sum to reach the cell's threshold and elicits a response. Hence, noise can facilitate detection of weak signals. (b) The blue lines in the upper and lower panels represent the landscape of potential states of a neural network and its current state is indicated by the red dot, which in the absence of noise will predictably tend to gravitate towards, and then remain in, the nearest stable state (depicted as a tendency to 'roll downhill' and to settle when it reaches a local minimum − see lower panel). However, noise (upper panel) randomly perturbs the network's state so that it can 'jump' to a state from which it will then tend to gravitate towards a different stable state. That is, noise can cause a network to shift from one state to another. (c) When two stimuli, differing along a single feature dimension, are represented by a network, the variability of these representations can be represented as two Gaussian distributions around the mean representations. When there is little noise in a network (lower panel), there will be little common activation between the two representations rendering them highly discriminable, but there will also be no basis for generalizing learning about one stimulus to the other stimulus. Conversely, in a higher-noise network (upper panel), the greater overlap between the representations will impoverish the network's discrimination of them, but will afford an intrinsic basis for generalizing learning about one stimulus to the other.

row band of *optimal* levels of noise may also enhance perceptual detection and discrimination via 'stochastic resonance', a property of non-linear systems in which addition of noise can facilitate detection and discrimination of subthreshold signals. Its effects have been observed in single unit recordings (e.g. Destexhe and Contreras, 2006; Hänggi, 2002; Lopes et al., 2013; Manjarrez et al., 2007; Sasaki et al., 2008) and, more controversially, are claimed to arise in human observers' perceptual thresholds (Goris et al., 2008).

To illustrate how stochastic resonance might operate, imagine a sensory neuron that only responds when stimulus intensity at any one time reaches a threshold value. Stimulating this cell with a repeating signal that is *subthreshold* (not sufficiently strong to reach threshold) will never yield a response. However, adding white noise to the signal can improve the cell's detection of it. The upper and lower panels on the left of Figure 1(a) represent this situation; a subthreshold stimulus is changing in intensity sinusoidally over time and, in the relative absence of noise, as in the lower panel, fails ever to reach the cell's threshold – the cell will show no response. In the upper panel, however, a greater magnitude of noise has been added to the signal. The mean value of the noise is zero so it does not increase mean stimulation over time: half the time, it will

effectively decrease the cell's stimulation, and half the time, it will increase stimulation. Nonetheless, when positive values of the added noise and a signal peak are summed, the total stimulation exceeds the cell's threshold and the cell responds (see Figure 1 legend). This illustrated mechanism will respond (i.e. will be able to detect signals) in the presence of noise, without which it could not. Crucially, the beneficial noise need not be present in the stimulus: It could be 'endogenous' noise added *by the cell itself*. Further, no hard threshold is required for a system to display such effects; the types of nonlinear increments in neurons' responses that pervade biological perceptual systems seem to permit stochastic resonance (Braun et al., 1994; Levin and Miller, 1996), including in-human perception (e.g. Goris et al., 2008).

Simmons et al. (2009) noted that if the autistic brain were noisier than the neurotypical brain, the principle of stochastic resonance could be applied to research findings to account both for superior and inferior performance in ASD. To illustrate this potential, they highlighted Bertone et al.'s (2005) finding that individuals with autism exhibited greater sensitivity for first-order (luminance-defined) stimuli yet reduced sensitivity for second-order (contrast-defined) stimuli, relative to neurotypical individuals. Simmons et al. (2009) argued that both enhanced and

impaired sensitivity in the ASD group of study might be explained by increased neural noise in ASD. For first-order stimuli, which are detected at very low luminance-contrasts with relatively little stimulus noise, slightly increased internal noise in autistic individuals could augment signal detectability through stochastic resonance, accounting for those individuals' higher sensitivity. In contrast, processing of second-order stimuli may be an intrinsically noisier process (due to extra processing stages). Accordingly, noise levels in both ASD and typically developing (TD) groups would have surpassed optimal levels that might yield stochastic resonance – any greater noise in ASD participants would only exacerbate the deleterious effects of too much noise in that task, yielding an ASD group disadvantage.

Our view – that ASD is characterized by *decreased* neural noise – may also accommodate these two opposing findings. On this alternative approach, the ASD detection *advantage* for Bertone et al.'s (2005) first-order stimuli would reflect improved signal-to-noise ratio due to *reduced* endogenous noise relative to the typical group. This account of the ASD advantage with *first-order* stimuli seems preferable to the high-noise view, as the latter requires ASD to have a narrow band of optimal noise levels for stochastic resonance. However, the *strength* of high-noise view lies in its account of Bertone and colleagues' *second-order* results and its neat account of why group-differences for first- and second- order signals differ. As originally conceived, our low-noise view postulated that ASD groups' deficits for perceiving second-order signals reflected *insufficient* neural noise in those brains to benefit from stochastic resonance (see Greenaway et al., 2013). We now consider this unlikely – a weakness in our initial thinking.

Following discussions as part of the review process, we have come to an alternative view of Bertone and colleagues' second-order stimulus results that does not invoke stochastic resonance. The carrier noise in such stimuli would have consisted in many relevant, but individually misleading (luminance-defined) orientation signals, among which participants must detect the second-order global signal. We know, from the ASD detection *advantage* for Bertone et al.'s (2005) first-order stimuli, that the ASD participants were much more sensitive to those misleading luminance signals. This greater sensitivity to irrelevant stimulus features would likely have hindered ASD participants' discovery of, and attention to, those parts of the perceptual signal necessary to perform the task – yielding the observed group difference.

While either the high- or low-noise account can explain Bertone and colleagues' findings, neither offers a natural account of why visual acuity (Bölte et al., 2012; Kéïta et al., 2010) and the contrast sensitivity function (Koh et al., 2010) should be normal in autism. One feature of both tasks is that they use stimuli with minimal noise. Our current speculation is that stochastic resonance may play a role in such findings

– a more subtle one than we initially supposed (Greenaway et al., 2013). In stimuli that have *very* low external noise, stochastic resonance may operate in neurotypical participants (due to their endogenous neural noise), tending to enhance their sensitivity relative to that of ASD participants. This effect would offset what would otherwise be an expected clear ASD group advantage due to those individuals' low endogenous noise levels, these opposing effects summing to no measurable group difference. However, at *slightly* higher external noise levels (Bertone et al., 2005), stochastic resonance effects may be equivalent for the two groups: neurotypical individuals may no longer benefit, or alternatively ASD individuals may also now benefit, from stochastic resonance. In the absence of stochastic resonance differences between the groups, the ASD individuals' benefit due to lower noise brains would once again be evident.

Looking beyond detection and discrimination thresholds for single stimuli, the research literature in ASD seems to favour the 'low-noise' account over the 'high-noise' view. For example, if high levels of neural noise were to characterize the brain in ASD, such noisy representations should be less readily discernible from flanking items. The low noise view would instead be congruent with reduced crowding effects of neighbouring items (Van den Berg et al., 2010), as has recently been observed in autism (Baldassi et al., 2009; Kéïta et al., 2010). Similarly, low endogenous noise should enhance discrimination of targets from nontarget stimuli in visual search tasks when many stimuli are presented simultaneously, as well as benefitting the fidelity of mental 'mapping' of one representation onto another. These expected outcomes again find broad support, for instance, within the visual search literature. For both single feature- and feature-conjunction searches, children with ASD are often found to distinguish targets from non-targets more readily than typical controls (Kaldy et al., 2011; O'Riordan et al., 2001; O'Riordan and Plaisted, 2001; Plaisted et al., 1998a). Joseph et al. (2009) have ascribed this advantage in ASD to increased perceptual 'clarity' (rather than more rapid attention shifts), resonating with the low-noise proposal, and Baldassi et al. (2009) provide evidence that the autism advantage relates, at least in part, to reduced crowding-type effects from non-target stimulus elements, as would be expected in lower noise brains.

Such enhanced discrimination abilities in ASD (though not always evident) have also been reported for novel dot patterns that vary quantitatively along a continuum (Plaisted et al., 1998b), pitch discrimination (Bonnel et al., 2003) and fine judgments of temporal simultaneity (Falter et al., 2012). High-fidelity mapping of low-noise representations also offers a simple account of superior performance by individuals with ASD on mental-image mapping tasks (e.g. Mottron and Burack, 2001; Soulières et al., 2011b). In contrast, such effects are not readily accommodated within a high neural noise view.

Given that low noise would tend to predict enhanced discrimination in relatively noisy stimuli, a particular challenge for the low-noise view is impaired (e.g. Annaz et al., 2010; Milne et al., 2002; Pellicano et al., 2005; Spencer et al., 2000) or typical (e.g. Jones et al., 2011) ability of ASD participants to detect the dominant motion of randomly moving dots with a net bias in one direction. This deficit (when it is found) is attributed either to poor perception of the motion direction of individual dots in the array, or impoverished integration across the dot field (Dakin et al., 2005; Dakin and Frith, 2005). However, the low-noise view would suggest a slightly different interpretation, in which the range of findings reflects two opposing influences on group differences in the motion coherence task. First, on our view, the perception of *individual* directions of motion in the task is likely to be intact or superior in autism, reflecting low-endogenous noise in the ASD group. Consistent with this claim are findings of superior (Chen et al., 2012; Foss-Feig et al., 2013) or typical (Manning et al., 2013) perception of motion ASD when all elements move in the same direction. Second, for a reason outlined later relating to a third action of noise (neural noise tends to increase representational overlap between stimuli, increasing apparent similarity), low-noise should impoverish integration of local element motions in these stimuli (as it seems to for static elements: Brosnan et al., 2004; Falter et al., 2010); this should act to impoverish performance in ASD. Sometimes, these two opposing effects will roughly cancel one another yielding no overall group differences in motion coherence thresholds (e.g. Jones et al., 2011), whereas, under typical conditions (when noise dots have only four or eight very distinct directions of motion), the reduced integration of dots' motions will outweigh any benefits of low noise, yielding a deficit in the ASD group.

A novel prediction of this account is that if individual elements' directions in motion-coherence displays were to be made less distinct, by adding noise to each element's direction over time, or sampling elements' directions from a continuous population over a smaller *range* of directions, group differences in *integration* of the elements would be minimized. With this factor equated between the groups, one would expect intact or even superior performance in ASD. Thus, the low-noise view can accommodate motion coherence findings and also makes some specific predictions for future experiments.

This apparent tendency for enhanced local perception to adversely affect attention to, and processing of, global aspects of a stimulus, is reminiscent of an effect observed in studies using hierarchical shape stimuli (Navon, 1977). When presented with a global shape constructed from many local, identical elements, children with ASD often seem to attend more to the local elements and less to the global shape than do typical controls (Wang et al., 2007). This seems not to reflect an *inability* of children with autism to process global information per se (Plaisted et al., 2006);

they can do so efficiently when instructed to attend selectively to the global shape (Mottron et al., 2003; Plaisted et al., 1999). Rather, as in our explanation of group differences in the motion coherence task and second-order perception, we suggest that enhanced clarity and distinctiveness of local-elements in autism biases processing to those local elements and at the expense of global processing.

We have highlighted aspects of the autism literature here that seem amenable to explanation in terms of low endogenous neural noise: Other findings may prove more difficult to explain. For example, as noted above, both high and low noise views struggle to explain *intact* contrast sensitivity across a broad range of spatial frequencies (e.g. Koh et al., 2010) in individuals with deficits in colour vision (Franklin et al., 2010). Indeed, no extant theory offers a natural account of such effects. These limitations aside, in terms of influences on detectability/discrimination, the low-noise view seems to offer a feasible account of ASD perception. Moreover, the strengths of the low-noise perspective become more evident when other actions of noise are considered.

Action 2: noise encourages transitions between neural states

To make decisions, shift attention, switch between tasks and complete tasks involving multiple steps, neural networks must be able to move readily between stable states. These states and transitions are often modelled as attractor networks in which first one, and then another, attractor (a self-sustaining state) dominates (see, e.g. Braun and Mattia, 2010). The behaviour of these networks can be illustrated by considering perception of a bistable stimulus, such as Rubin's famous vase-faces figure: The stimulation remains constant but the observer's perception fluctuates between one of two interpretations. Often these transitions are experienced as spontaneous and unintentional (e.g. the unbidden 'flipping' from one side to the other of the front-end face of the Necker cube). Let us assume that the two interpretations are equally likely to dominate – to be consciously perceived. When the stimulus is first presented, minor trial-by-trial variation (in allocation of attention, for example) will likely result in a bias towards one of the two interpretations. This initially preferred interpretation (functioning as an attractor) will continue to dominate until the network's state is shifted towards the alternative interpretation. The primary factors responsible for such shifting are typically modelled as perceptual adaptation (that reduces responses coding the dominant interpretation until it is less active than the alternative interpretation) and endogenous noise (which injects random jumps into the network's state, increasing the likelihood of a switch to the non-dominant interpretation; Braun and Mattia, 2010; Papageorgiou et al., 1998). The behaviour of attractor networks is commonly illustrated as

in Figure 1b, where the red circle indicates the network's current state and the curved line its potential states. In such energy landscapes, the state of the network will, in the absence of noise (lower panel), take a predictable, locally 'downhill' path towards a minimum point and remain in that state until the landscape changes shape (e.g. due to adaptation effects in perception). However, the addition of noise (upper panel) can perturb the network's state causing it to settle in other minimum (see Figure 1 legend for further details).

A network with low neural noise will shift between interpretations largely on the basis of adaptation; it will settle in one state (e.g. one interpretation of a bistable stimulus) until that attractor becomes sufficiently weak (as a result of adaptation) to permit transition to the other possible interpretation. Other things being equal, a neural system of this nature would exhibit prolonged settling in one state and more rhythmic switching between states than a system with greater levels of neural noise. In terms of perception, it would settle quickly (but not necessarily optimally) on a single interpretation of a stimulus and, without additional prompting, take longer to discover alternative interpretations. Too much noise should have the opposite effect: The injection of random perturbations would prompt constant shifts between states and an inability to settle on one interpretation, attentional focus or task. These effects of noise have already been used to model a range of cognitive and perceptual phenomena, such as memory (Ermentrout et al., 2008; Usher and Feingold, 2000), decision making (Hsu et al., 2005), motor cognition (Schöllhorn et al., 2009) and binocular rivalry (Brascamp et al., 2006).

Some primary, clinically evident features of ASD, in particular repetitive behaviours and narrowed interests, are highly consistent with reduced switching between states due to pervasively reduced levels of neural noise. Before discussing those, however, we note that the broad direction of relevant perception and attention findings in autism is also consistent with our proposal. For example, when presented with ambiguous stimuli of the kind mentioned above, children with ASD show fewer 'spontaneous' (unintended and not stimulus-controlled) shifts between perceptual interpretations than controls and a tendency to settle on one interpretation (Sobel et al., 2005). Note that this appears to be a lack of *spontaneous* shifting, a failure to benefit from the action of noise that would be evident in the neurotypical brain. It does not reflect a general inability to shift to another interpretation because, when prompted explicitly to do so by the experimenter, children with ASD show comparable levels of shifting between interpretations (Ropar et al., 2003). Together, these findings offer support for the low-noise perspective.

Lack of spontaneous shifting in ASD has also been reported for binocular rivalry, in which two disparate images are presented, one to each eye; under these conditions, the binocular, conscious percept typically switches

between the two eyes' inputs. Using coloured stimuli with small pictorial images, Robertson et al. (2013) found that children with ASD switched less frequently between inputs than neurotypical controls, consistent with a low noise account. An earlier study by Said et al. (2013), using orthogonal grating stimuli, concluded that binocular rivalry is normal in ASD. However, the dependent measure in Said et al.'s (2013) first experiment (proportion of time in 'mixed' states when neither eye's input dominates) showed a trend towards greater mixed states for ASD individuals as would be expected on a low-noise account (though is not exclusively predicted by our view). Their second experiment, measuring travelling-wave speeds as one eye's input becomes dominant, found no group differences; however, models of binocular rivalry suggest that this is would be expected on noise-based accounts (Webber and Bressloff, 2013).

Beyond perception, reduced neural noise would tend towards fewer spontaneous shifts from one dimension of a cognitive task to another and between tasks. Reduced cognitive flexibility and particularly becoming 'stuck-in-set' (Hill, 2004) has been regarded as one of the more commonly-observed executive dysfunctions (EDFs) in ASD that more broadly are thought to underpin the repetitive and restrictive behaviours. There has, however, been substantial debate about the universality and specificity of EDF in ASD (see Pellicano, 2012), and it has been established that there are wide individual differences in ASD in performance on classic neuropsychological executive functioning (EF) tests, with some individuals showing entirely intact performance. Yet, when executive functioning is assessed in 'open-ended' tasks that more closely mimic the less restrained context of real life scenarios than classic EF task batteries, even individuals with autism who 'pass' laboratory EF tasks perform worse on open-ended EF tasks (Hill and Bird, 2006; White et al., 2009).

The key difference between the classic EF and open-ended tasks is that the former are more highly constrained, raising the possibility that the correct answer is prompted by the format of the task and the instructions given to the participant. In contrast, open-ended tasks by their nature provide the opportunity to observe how individuals generate strategies and reach decision states independently of task instructions and prompts, that is, spontaneously. In the case of open-ended problems that offer no obvious solution, we assume that switching from one decision state to another can be achieved not only by controlled strategic processes, but also by spontaneous noise-induced 'jumps' until the network settles in a final attractor decision state (see Braun and Mattia, 2010). Of particular interest to this suggestion is the observation by White et al. (2009) that autistic children not only showed worse performance on open-ended than constrained tasks but also produced fewer spontaneous strategies in the open-ended tasks, indicating a greater propensity to settle on an incorrect answer rather

than shifting to other possible solutions. Again, this mirrors the pattern of findings from perceptual studies: While the cognitive ability in question can be well within or above typical norms, individuals with ASD show a tendency to settle on an initial and sometimes suboptimal decision state in the absence of external prompts. This tendency is well modelled by a network with reduced endogenous noise.

The discrepancy between performance in unconstrained scenarios and laboratory tasks in individuals with autism is seen in other cognitive domains such as decision-making. Although a relatively small literature, research on reasoning and decision making in ASD suggests laboratory tests present little challenge for individuals with ASD in contrast to everyday decision-making. For example, De Martino et al. (2008) observed a greater resistance to the misleading frames and greater levels of formal reasoning in individuals with ASD compared to typical controls when making choices in a laboratory gambling task. In contrast, parents, teacher and clinicians frequently report difficulties in everyday decision-making in children and adults with ASD. Luke et al. (2012) assessed self-rated experiences of everyday decision-making in adults with ASD and typical adults using a novel questionnaire designed to tap problems and difficulties when making decisions. Ratings of frequency of experiencing 12 different decision-making problems were higher adults with ASD, with the single exception of 'frequent changes of mind about the decision' (Luke et al., 2012: 616). The other 11 items included problems such as uncertainty, inability to reach a decision and exhaustion. Ratings of difficulty with 10 different types of decision-making context revealed greater difficulty for the adults with autistic spectrum conditions (ASC) when the decision had to be made quickly, involved changing a routine and talking to others.

These specific types of problem and difficulties in everyday decision-making are consistent with the idea that low endogenous noise results in prolonged settling in one state. Further, the ASD group's higher ratings of exhaustion in decision-making suggest that in the absence of noise-induced shifts towards one alternative or another, decision-making in ASD must recruit top-down executive control driven by rules of logic and probability (e.g. De Martino et al., 2008). The effortful, deliberate nature of such decisions likely also reflects a reduced tendency in ASD to make decisions on over-applied 'rules of thumb' (Brosnan et al., 2014), something that may follow from a third action of noise discussed next: enhancing generalization.

Action 3: increasing generalization, reducing stimulus distinctiveness

Figure 1(c) cartoons a third influence of noise responses – on generalization. Consider responses of a population of neurons to two stimuli, each stimulus presented once, and suppose that they differ along a single dimension. Within a single presentation, endogenous noise will cause variation across time in response to each stimulus. This variation in response to each stimulus is depicted as a Gaussian distribution around the network's mean response to each stimulus. The lower panel of Figure 1(c) represents the case when there is little noise and the upper panel of Figure 1(c), the case when there is a greater level of noise. In the low-noise case, there is no overlap in responses to the two stimuli, rendering the stimuli highly discriminable (presumably perceived as entirely distinct); in the high-noise case, there is much greater overlap, rendering the two representations less distinct – less discriminable, more similar. However, by the same token, the overlap between responses to the two stimuli in the high-noise network will mean that associations established in regard to one stimulus will spontaneously be applied when the other stimulus is presented. That is, the network will spontaneously *generalize* learning across the two stimuli, forming a single response *category.* This generalization will not arise in the low-noise case due to the absence of an overlap in responses to the two stimuli.

Impaired generalization of learning in ASD is a marked, clinically evident feature of the disorder and possibly relates to 'insistence on sameness' (Plaisted, 2000, 2001). Indeed, limited generalization is one of the key factors decreasing the effectiveness of behavioural intervention programmes, and accordingly is an important feature for any heuristic theory of ASD to address. Both properties expected of the *low* noise network – an increased tendency to discriminate between stimuli (to perceive them as different rather than similar) and a corresponding impaired tendency to generalize across exemplars – broadly resemble findings in autism (Brown and Bebko, 2012). The high-noise view does not seem consistent with these findings (see Greenaway et al., 2013, for a similar argument).

However, the low-noise view is by no means the only heuristic view to account for such findings. Reduced Generalization Theory (RGT; Plaisted, 2000, 2001) proposes that poor generalization is a pervasive feature of processing in ASD, affecting perception, cognition and action, and reflects a fundamentally enhanced processing of one stimulus's unique elements and poor processing of features shared between stimuli. Indeed, RGT and the low-noise view advocated here are only distinguished in terms of their proposed sources of enhanced representation of distinctiveness in ASD. Nonetheless, if a low neural noise account assumes independent actions of noise across stimulus dimensions, the two accounts may be empirically distinguished. Whereas RGT assumes enhanced discrimination and impoverished generalization for all stimulus types, the low-noise view makes a more selective claim – that reduced generalization and enhanced discrimination in ASD should be observed only in stimulus sets that vary continuously, and not with compound stimuli that differ in terms of complex, but more discrete, feature conjunctions (e.g. Plaisted et al., 2003). Noise within feature representations could result in overlap between representations of features lying sufficiently close

to one another along a continuum and hence enhance perceived similarity of those features, facilitating their combination into a category (as described above). However, when items to be categorized differ in terms of combinations of features, each of which varies discretely, noise will likely have minimal impact on generalization.

Experimental studies of generalization in ASD have generally considered categorization learning. Plaisted (2000, 2001) argued RGT predicts both enhanced discrimination *and* reduced categorization ability in autism. Most studies of categorization in autism have found slower initial learning of categories, as predicted by RGT, but have been less clear with regard to whether normal categories (and prototypes) are established after sufficient training in the ASD group. There is wide variation among these studies in methodology and participant characteristics that could account for some of this discrepancy. However, one broadly consistent distinction that may be drawn between those studies demonstrating typical categorization performance in ASD and those reporting slower learning, poorer generalization to more extreme exemplars of a category and reduced prototype abstraction is the nature of the stimuli employed. Poorer categorization performance (in terms of slower initial category learning, classification of distorted exemplars, or prototype formation) by individuals with ASD has been observed in studies using continuously varying stimuli (Bott et al., 2006; Church et al., 2010; Froehlich et al., 2012; Gastgeb et al., 2009, 2011, 2012; Plaisted, 2000). Two other categorization studies, using discretely different exemplars, have found no categorization differences in ASD (Molesworth et al., 2005) or slower learning but comparable ability to utilize a categorization rule (Soulières et al., 2011a).

One study by Vladusich et al. (2010) is perhaps particularly instructive in this regard. They performed two categorization experiments, each with dot stimuli. However, in a first experiment, yielding impoverished performance in ASD, the dots' positions varied continuously across exemplars; in a second study, the number of dots that changed position varied and this experiment yielded typical performance in ASD. This elegant design contrasted perceptual discrimination across continuous variations versus discrete variations in multiple dimensions, holding other aspects constant. These differential findings for poorer categorization of continuous compared to discrete stimuli in ASD appear to support the low-noise perspective.

While the major explanatory power of reduced generalization in ASD relates to categorization and stimulus discrimination, we also note that reduced overlap of stimulus representations in a low-noise brain could account elegantly for a reduced tendency to group elements together on the basis of their mutual similarity (Brosnan et al., 2004; Falter et al., 2010). A similar logic might also apply to grouping of dots with differing local motion trajectories in the motion coherence task. In their elegant study, varying percentage motion coherence and slow and fast motion of dots, Manning et al. (2013) demonstrated motion coherence deficits only in a coherence condition where dots moved slowly. If integration by direction similarity requires noise, and slow motion stimuli contain less extrinsic noise than high motion stimuli, this differential pattern of motion coherence sensitivity in ASD would be predicted on a low endogenous noise view. We note this is highly speculative, and no previous work has systematically varied stimulus similarity. However, our point is to demonstrate that the low noise proposal predicts counterintuitive, testable alternative explanations to phenomena that have so far eluded explanation.

Concluding comments

Our proposal is that individuals with autism exhibit enhanced detection and discrimination under conditions of moderate *exogenous* noise compared to typical controls due to low *endogenous* noise. Additionally, such low noise may limit spontaneous (unbidden) changes of task-set and attentional focus, benefitting performance in ASD when a task requires prolonged focus or repetitive sequences of behaviour. These benefits of a low-noise brain, however, may come at significant cost. In the typical brain, neural noise likely enhances processing in perception, cognition and executive function. It can provide a mechanism for generalizing between stimuli that differ along a continuum, speeding the formation of categories and equipping an organism to ignore subtle changes to objects and their contexts. By perturbing networks from stable states, noise can also encourage exploration of different neural states, limiting perseveration and continued focus on one train of thought. Finally, noise will also enhance the reliability of responses to stimuli across presentations. A low-noise brain will not reap these benefits, may fail effectively to generalize learning from one context or stimulus to others, may become 'stuck' in a particular mode of thought or action, yet may not respond reliably to a stimulus across presentations.

Whether our perspective can account for a greater range of data than the high-noise perspective offered by Simmons et al. (2009) remains to be seen. Certainly, it offers a markedly different perspective, though it resonates with, and may underpin mechanisms implicated by some other views, such as Enhanced Perceptual Functioning theory (Mottron et al., 2006), Weak Central Coherence Theory (Frith, 1989) and RGT (Plaisted, 2001). In particular, the low-noise proposal provides a potential neural substrate for earlier conclusions that similarity processing differences underlie several perceptual and cognitive strengths and weaknesses in ASD (Brosnan et al., 2004; Falter et al., 2010; Mottron, et al., 2006; Plaisted, 2000, 2001). Similarly, the low-noise proposal offers a parsimonious mechanism for some aspects of Executive Dysfunction Theory's (Pennington and Ozonoff, 1996; Russell, 1997) explanation of higher

level and pervasive difficulties in ASD, such as insistence on sameness, becoming 'stuck in set' and slower, more effortful and less spontaneous decision-making (Ciesielski and Harris, 1997).

On the other hand, such continuities with existing theories could equally be seen as its major limitation. That is, any view based on such a malleable concept as 'noise' undoubtedly suffers from being too powerful. Further, we have only considered *some* broad characteristics associated with autism here and not, for instance, theory of mind deficits. While one could speculate that noise is likely to enhance generalization from self to other in learning to model others' mental states online, we have not discussed this possibility here as there seems no obvious way to study such influences of noise using stimulus manipulations (in contrast to the vision, attention and learning literatures that have been our focus). Nonetheless, a low noise view of autism, although initially counterintuitive, offers a parsimonious account of the disorder's key features that are evident either in clinical practice or the laboratory.

A further key challenge for this view will be to present a feasible account of the aetiology of a low-noise disorder. While polygenic disorders such as ASD lend themselves intuitively to high-noise accounts, the same cannot be said of the low-noise view. One potential route to an explanation is that low-noise in autism may reflect atypical activation by brainstem structures. For example, low tonic and relatively high phasic noradrenergic activation of the cortex by the locus coeruleus (LC) may play a role. Such 'hyperphasic' responses have been suggested to contribute to ASD symptoms (e.g. Blaser et al., 2014), have been found to affect cortical signal-to-noise ratios, and have been suggested to influence cognitive-flexibility (e.g. Nieuwenhuis et al., 2005). Though the low-noise view does not depend upon any single such speculation holding true, establishing feasible routes to low neural noise will be crucial to the view's broader acceptance.

For now, the low noise view does make novel testable predictions for experiments. If these experimental and mathematical predictions are borne out, it will be critical to elucidate the developmental implications of a low noise brain from birth. This will almost certainly be closely allied to the emerging and important discoveries concerning over-and under-connectivity in structural and functional magnetic resonance imaging (MRI) studies in ASD and their developmental causes (Uddin et al., 2013). These discoveries re-emphasize the urgent need to study the behaviour of local neural circuits to elucidate the underlying reasons for different larger scale connectivity patterns and differences in developmental modularization in the autistic brain (Karmiloff-Smith, 2007, 2012). The low-noise proposal offers one such possible neural atypicality that might contribute to these pervasive differences in formation of neural networks in autism over development.

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