for further advances in the field of seizure prediction.

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References

Riddle is to conundrum as the frontal pole is to...?

This scientific commentary refers to ‘Reasoning by analogy requires the left frontal pole: lesion-deficit mapping and clinical implications’, by Urbanski et al. (doi:10.1093/brain/aww072).

In this issue of Brain, Urbanski and co-workers make a key advance in respect of our understanding of how the prefrontal cortex (PFC) supports intelligent behaviour. It is one that may help solve a curious conundrum in research on the functions of rostral PFC. Rostral PFC is a very large brain region for which there are many names (including the ‘frontal pole’), all of which are rather imprecise, but generally approximate to Brodmann area 10 of the human brain. The conundrum is this: many human lesion studies over the past 60 years or so have suggested that large uncomplicated removals of this region, or damage to the connections to it, can cause little or no impairment on IQ tests (for review see Burgess et al., 2012). Indeed, there are detailed reports of individual patients who have had almost complete excisions of rostral PFC and yet still score within the top 1% of the population on the most commonly used clinical IQ test (e.g. Patient AP; Shallice and Burgess, 1991). But more recently, several authors have suggested that this brain region is in fact involved in ‘intelligence’ (Colom et al., 2007; Gläscher et al., 2010), based on evidence from both human lesion studies and functional neuroimaging. How are these discrepancies to be reconciled?

One possible solution lies in the way that ‘intelligence’ is measured (Duncan et al., 1995). There are, in broad terms, two predominant ways of conceiving of intelligence in the study of brain and behaviour. The first is to think of ‘intelligence’ as little more than an average of performance across a wide range of tasks that tap a wide range of abilities, and have little in common with each other. This view is typified by the various instantiations of the Wechsler Adult Intelligence Scale. This is probably the most widely used IQ test in neuropsychological practice, and is the kind of task that Patient AP performed so well. However, a completely different way of measuring intelligence is typified by various tests that attempt to measure so-called ‘fluid intelligence’. They rely for their rationale upon belief in an inference made about ‘positive manifold’. Positive manifold is the tendency within a correlation matrix of performances on a wide range of disparate tasks for there to be more positive correlations than would be expected by chance. Fluid intelligence tests tend to use test items that are quite similar to each other (or are selected from a narrow range of them), but have been shown to correlate highly with performance in a wide range of tests that are quite different in format. There are many examples of IQ tests in common usage that
have been developed through this second kind of approach, and many of them contain items that require extracting a principle from one set of stimuli and then applying it to a new set of stimuli. For instance, the AH6 IQ test (1970 version) contains many items of the form ‘Tool is to hammer as animal is to...’ with four response options to choose from. Other items, for instance, present a line containing two words on the left, and five on the right, and ask ‘which one of the five words on the right bears a similar relation to each of the two words on the left’. These problems are examples of analogical reasoning, which is the process of extrapolating from similarity or regularity in one situation to similarity in another.

So, the discovery by Urbanski et al. (2016) that lesions to rostral areas of PFC can lead to a specific deficit in analogical reasoning offers one potential solution to the conundrum described above, in that analogical reasoning is a key component of many ‘fluid intelligence’-type tests, but not of IQ tests that measure intelligence as an average across disparate tasks.

This possible explanation becomes more plausible when one considers other aspects of the data that Urbanski et al. present. They administered, in addition to the experimental tasks of analogical reasoning, several tests of so-called ‘executive function’ as background tasks (Fig. 1). Background tests are administered in these sorts of experiments to show the broader context of the patients’ cognitive abilities. The total patient sample performed poorly on them. Urbanski et al. (2016) also administered a control condition as part of the experimental tasks which required analysis of the same kinds of visual stimuli that were used in the analogical reasoning conditions, and also required such skills as seeing and attending to the stimuli, understanding instructions, making motor responses, and even matching complex stimuli to each other. The entire patient sample, considered as a group, was unimpaired in these control conditions, so we can exclude problems with these more basic processes as an explanation of any deficit.

If the impaired processes that caused these executive difficulties in the total sample are also involved to a significant degree with analogical reasoning, then the method that Urbanski et al. use to determine brain regions critical to analogical reasoning (voxel-based lesion-symptom mapping, VLSM) will be conservative. In VLSM, each voxel from MRI brain scans is classified according to whether the lesion affects the analogous reasoning conditions, and also required such skills as seeing and attending to the stimuli, understanding instructions, making motor responses, and even matching complex stimuli to each other. The entire patient sample, considered as a group, was unimpaired in these control conditions, so we can exclude problems with these more basic processes as an explanation of any deficit.

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Not only were Urbanski et al. able to identify quite circumscribed parts of the PFC as being critical to deficits in analogical reasoning, they also showed that patients with lesions involving the most important of these did not fail the background tasks. Nor did those who were impaired at analogical reasoning fail them either. (There is a complexity in their data as regards Stroop interference in the VLSM group but for current purposes this interesting issue will be put aside.) In other words, patients with lesions in the frontal pole may be impaired at analogical reasoning but not impaired at many other mentally taxing tasks.

These findings may suggest that it would be useful to disentangle the notion of ‘fluid intelligence’ from that of analogical reasoning. If analogical reasoning is a key component of fluid intelligence, and fluid intelligence underpins performance on virtually all mental ability tasks, then Urbanski et al.’s patients who had analogical reasoning deficits should have failed a wide range of tasks. But they did not. So, how might analogical reasoning ability be correlated with a wide range of mental abilities in the healthy brain, and yet be impaired relatively independently in neurological patients? One possibility is that analogical reasoning may be an ability whose development is facilitated by development of other processes, but thenceforward is not directly causally related to them. In other words, there is correlation but not causation. Whatever, the implications of the Urbanski et al. study reach beyond our understanding of analogical reasoning alone.

One issue that the Urbanski et al. study did not address, however, concerns the critical processing impairment in those who fail the analogical reasoning task. (Volle et al., 2010) have shown, using functional MRI, that lateral rostral PFC is activated by an analogical reasoning task both during study of the source (i.e. before the source can be compared with a target) and also when the target appears. Hence the processing contribution made by at least some rostral PFC structures appears not to be specific to one particular problem-solving stage. (Burgess et al., 2007) suggest one possibility for a process of this kind in the ‘gateway hypothesis’. This holds that rostral PFC supports a brain region involved in ‘XN control’ (Burgess and Wu, 2013), which is the ability to voluntarily alter the degree to which we either attend to the environment (known as stimulus-oriented attending), or to the thoughts in our heads (known as stimulus-independent attending). Such an ability might be required both in attending to analogical stimuli and extracting important features from them, and then in making a ‘workspace’ in our heads to try out various hypotheses we generate about possible matches to the target stimuli. This explanation has been shown to be plausible for deficits in prospective memory following rostral PFC lesions (Benoit et al., 2012). However, its plausibility for explaining analogical reasoning deficits remains to be determined. The analogical reasoning test that Urbanski et al. present in this study may prove not only useful for that purpose, but also may add very usefully to our ability to detect in the clinic the kinds of impairments that follow rostral PFC damage.

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Multiple cues support speech perception

This scientific commentary refers to ‘Universal and language-specific sub-lexical cues in speech perception: a novel electroencephalography-lesion approach’, by Obrig et al. (doi:10.1093/brain/aww077).

Understanding spoken language, an activity in which we are engaged for a large part of our waking lives, is generally an effortless, automatic process. This apparent ease stands in contrast to the complexity of the processing required to extract meaning from sound waves. The sound structure of speech is based on multiple frequencies, changing rapidly, requiring an ultrafast analysis over different timescales. In this issue of Brain, Obrig and co-workers provide novel information about a crucial source of cues that help the brain to cope with this formidable challenge, namely the sublexical structure of words (Obrig et al., 2016).

One of the fundamental tenets of modern linguistics is that there is no boundless variation in language structure (Chomsky, 1981; Moro, 2015). While this idea has been particularly developed (and discussed) in the case of syntax, it applies also to the phonological level. Of course, in the latter case there are clear physical determinants of the sounds that the human vocal system can and cannot produce, given its anatomical and physiological features. In addition to these general constraints, there is also evidence for universal preferences in the selection of phonemic sequences. One well-known principle was described by Clements (1990) and is based on the concept of hierarchy in sonority. The ideal syllable has a ‘peak’ in a vowel, with an increase in sonority from the syllable onset to the peak, and then possibly a decrease. It must be specified that in this case, ‘universal’ indicates a general preference, rather than a law. ‘Fra’ is a common syllable across languages; ‘Mzda’ is a violation of the ascending-peak-descending hierarchy, yet it is realized as a word in Russian. Universal preferences, in general, interact with language-specific restrictions in the permissible combinations of phonemes at specific positions within words. For example, in English, /g/n/ does not occur at the beginning of words, whereas it is fairly common in Serbian. These combinatorial rules are the ‘phonotactics’ of a specific language. The perceptual correlates of the universal and language-specific aspects are clear-cut. If a sound sequence markedly deviates from ‘universal’ rules, it does not sound like real language; on the other hand, if we listen to a meaningless sequence of phoneme strings, which obey language-specific phonotactics, we may say ‘this sounds like Italian’ or ‘this sounds like German’.

The idea of a division of labour in cortical auditory processing is more recent than in the case of the visual system (Ungerleider and Mishkin, 1982), but has generated a large body of research in the last few decades (see, for example, Rauschecker, 2012). The traditional neural model of speech perception posited information transfer from Heschl’s gyrus, responsible for primary auditory analysis, to Wernicke’s area, conceived as a specialized region for phonetic processing. This view has been replaced by a complex mosaic of cortical structures supporting the analysis of the sound signal, the extraction of phonological information and the mapping to lexical semantics (Hickok and Poeppel, 2007).

Functional imaging studies have played a crucial role in the development of this concept (Scott et al., 2000). The aim of the Obrig et al. study is to map the neural systems responsible for the analysis of the important phonological cues described above, by combining the classical anatomo-clinical method with state of the art EEG analysis. The rationale is quite straightforward. The waves associated with the deviations from ‘normal’ words can be detected as event-related responses, both in controls and in patients with focal brain lesions. The results of this analysis indicated that violations of universal phonological structure (reversed pseudowords) were associated with event-related potential (ERP) differences at several latencies, including an early positive response around 250 ms. In contrast, the language-specific phonotactic contrast was associated with a selective increase in negativity for illegal pseudowords at a latency around 400 ms.

A second step analyses the correlation between the neurophysiological responses and the location of brain damage. This elegant approach is an...