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How should educational neuroscience conceptualise the relation between cognition and brain function? Mathematical reasoning as a network process

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Background: There is increasing interest in applying neuroscience findings to topics in education.
Purpose: This application requires a proper conceptualisation of the relation between cognition and brain function. This paper considers two such conceptualisations. The *area focus* understands each cognitive competency as the product of one (and only one) brain area. The *network focus* explains each cognitive competency as the product of collaborative processing among multiple brain areas.
Sources of evidence: We first review neuroscience studies of mathematical reasoning – specifically arithmetic problem-solving and magnitude comparison – that exemplify the area focus and network focus. We then review neuroscience findings that illustrate the potential of the network focus for informing three topics in mathematics education: the development of mathematical reasoning, the effects of practice and instruction, and the derailment of mathematical reasoning in dyscalculia.
Main argument: Although the area focus has historically dominated discussions in educational neuroscience, we argue that the network focus offers a complementary perspective on brain function that should not be ignored.
Conclusions: We conclude by describing the current limitations of network-focus theorising and emerging neuroscience methods that promise to make such theorising more tractable in the future.

Keywords: educational neuroscience; mathematics education; arithmetic; dyscalculia; magnitude comparison; large-scale cortical networks

Introduction

The relationship between education and neuroscience has been the subject of productive debate (Ansari and Coch 2006; Blakemore and Frith 2005; Bruer 1997; Byrnes and Fox 1998; Geake 2004; Goswami 2006; Varma, McCandliss and Schwartz in press). We supplement this discussion by describing two approaches to explaining how the brain gives rise to cognitive competence, and how they might contribute to educational thinking.

One appeal of cognitive neuroscience is that it is a 'place-based'. The topology of the brain yields the prospect of a spatial map that ties functions to areas. The place-based grounding of neuroscience theories makes them different from psychological theories, which are cast in terms of more abstract constructs like schemas, IQ and identity. It is literally possible to search databases by brain area to see which tasks cause them to

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activate – without ever entering a psychological keyword (e.g., Laird, Lancaster, and Fox 2005).

Figure 1 depicts two dominant approaches for understanding the place-based nature of cognition. The *area focus* typifies earlier theorising in cognitive neuroscience, and continues to characterise discussions in educational neuroscience. It decomposes cognition into a set of tasks and maps them to brain areas in a one-to-one fashion. Said differently, it seeks to identify *the* brain area that activates most selectively for each task competency. In contrast, the *network focus* explains task competency as the product of coordination among multiple brain areas. Network-focus research typically builds upon pioneering area-focus research that has identified initial landmarks. It expands the unit of analysis from the functioning of individual brain areas to the co-functioning of networks of brain areas.

Our concern is that the area focus currently dominates discussions in educational neuroscience, and it risks inappropriate inferences for improving educational practice. The one-to-one mapping of competencies to brain areas easily leads to the conclusion that students just need to exercise one part of their brain to develop or remediate a skill. It also naturally leads to the complaint that 'knowing where it sits in the brain does not tell us anything useful'. The problem with area-focus reasoning is that most tasks that educators care about are complex and multifaceted (especially compared with those studied by cognitive neuroscientists). These tasks are likely to map to brain areas in a many-to-many fashion. Said another way, most tasks activate multiple brain areas, and conversely most brain areas activate for multiple tasks. Moreover, the same task can be accomplished by different networks depending on experience (Tang et al. 2006). This paper argues that exclusively adopting an area focus risks the uptake of educational neuroscience in a seductive but premature form, and that a complementary network focus should also be emphasised. It grounds the argument primarily in the content area of mathematics.

This paper has the following structure. It first describes the area focus and illustrates its application to topics in mathematics education. Much of the discussion centres on two brain areas: intraparietal sulcus (IPS) and angular gyrus (AG). These areas are shown in Figure 2, along with a number of other areas that are mentioned below. Next, the area focus is incrementally broadened into the network focus through a broader consideration

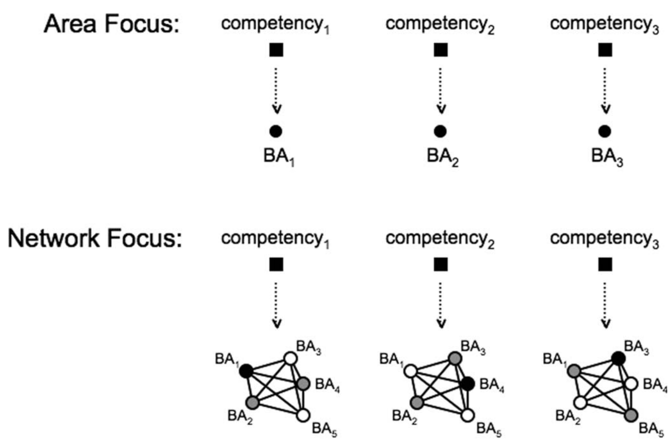

Figure 1. The area focus and network focus. The darker a circle, the more a brain area (BA) contributes to a competency.

of neuroscience findings on mathematical reasoning. Finally, the value of the network focus is illustrated by applying it to three topics in mathematics education: the development of mathematical reasoning, the effects of practice and instruction and the derailment of mathematical reasoning in dyscalculia.

The area focus for mathematical reasoning

The area focus has thus far dominated discussions in educational neuroscience. One reason for this dominance is that the methods of neuroscience have historically been well suited for isolating the brain areas necessary for a given ability. For example, in the nineteenth century, Broca encountered a patient with intact receptive language but impaired expressive language. Although the patient could comprehend language, he could only produce the utterance 'tan'. An autopsy revealed a lesion to a single brain area (left inferior frontal gyrus). Broca localised the expressive language competency to this area. A few years later, Wernicke applied the same logic to localise the receptive language competency to a different area (left posterior superior temporal gyrus). Another example of an area focus on brain function is the work conducted by the neurosurgeon Penfield in the early twentieth century. He electrically stimulated the brains of awake patients and observed their responses and impairments. A famous result of this research was the homunculi – topographical maps of somatosensory and motor cortex where adjacent brain areas coded sensation and action for adjacent regions of the body.

The area focus has been the dominant way to understand the results of neuroimaging experiments. Perhaps the most popular technique is functional magnetic resonance imaging (fMRI). When neurons fire, they make metabolic demands, consuming local stores of glucose and oxygen. This brings a haemodynamic response to replenish these

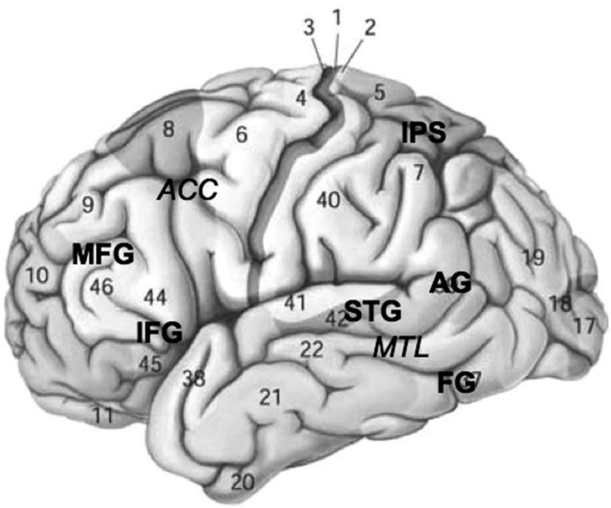

Figure 2. Important brain areas for mathematical reasoning: intraparietal sulcus (IPS), angular gyrus (AG), Broca's area/inferior frontal gyrus (IFG), Wernicke's area/prosterior superior temporal gyrus (STG), fusiform gyrus (FG), medial temporal lobe/hippocampus (MTL), middle frontal gyrus (MFG) and anterior cingulate cortex (ACC). Lateral areas (i.e., near the outside of the brain) are labelled in bold, medial areas (i.e., near the centre of the brain) in italics. The numbers are according to Brodmann's scheme.

stores: the vascular system carries oxygenated blood to the region via arteries and carries deoxygenated blood away from the region via veins. Oxygenated blood and deoxygenated blood have different magnetic susceptibilities. As a result, differences in their relative concentration in a region produce differences in the magnetic resonance signal emanating from that region, and these differences can be used to generate images. As this brief description makes clear, fMRI is a rather indirect measure of neuronal activity: it registers the vascular response to metabolic activity in support of neuronal activity (for a more comprehensive description of fMRI see Huettel, Song, and McCarthy 2004). fMRI is popular because it can non-invasively measure activity in behaving brains, and because it provides good spatial resolution (i.e., each picture element has a volume in the order of 10 cubic millimeters) and acceptable temporal resolution (i.e., an image can be acquired every second or so).

The design and analysis of fMRI experiments have historically depended on the use of *tight subtractions*.[1] Participants complete two nearly identical tasks (e.g., naming digits versus naming letters). The fMRI scan produces a map of activation across the brain for each task. The map will include activation in areas of little theoretical interest, for example, due to moving the eyes or pressing a response button. To remove this 'noise', researchers subtract the activation map of the control task (e.g., letter naming) from the activation of the target task (e.g., digit naming). This leaves only the activation due to the competency of interest (e.g., accessing number). Over the past 15 years, thousands of fMRI experiments have used tight subtractions to map competencies to brain areas in a one-to-one manner.

In addition to the availability of suitable methods, another allure of the area focus is that it can be straightforwardly applied to understand the neural bases of complex forms of cognition. For example, consider the mathematical competency of being able to reason about numbers as magnitudes (Case et al. 1997) – what is also called 'number sense' (Dehaene 1997) and understanding 'numerosity' (Butterworth 2005; Landerl, Bevan, and Butterworth 2004). The area focus asks which brain area implements this competency. Neuroscientists have pursued this question by capitalising on the symbolic distance effect (SDE) – the finding that the time taken to compare two digits decreases as the distance between them increases; for example, people are faster to judge which of 1 versus 9 is larger than to judge which of 1 versus 3 is larger (Moyer and Landauer 1967). The SDE is commonly interpreted as evidence that people reason about numerical magnitudes using a 'mental number line' that is psychophysically scaled, so that, much like perceptual discriminations (e.g., loudness and softness), values that are closer together on the number line are harder to discriminate than values that are far apart. Neuroscientists have used the SDE to identify the 'numerical magnitude area' of the brain. A representative study is by Pinel et al. (2004). Participants compared pairs of digits, judging which was greater. A handful of brain areas showed an increase in activation that paralleled the increasing response times for closer comparisons. Most prominent among them was IPS.[2] From an area focus, this is evidence that this brain area is the primary correlate of the numerical magnitude competency – that it is the seat of the mental number line.

The area focus can also provide insights about individual differences, which present a natural bridge from neuroscience to education (Kosslyn and Koenig 1992). The area focus describes a deficit as a dysfunction of the brain area that implements the relevant ability. This is a variant of the reasoning that Broca and Wernicke applied to understand language impairments, augmented with the assumption that a structurally intact area can be rehabilitated by exercising it through repeated practice of the relevant task. The application of this reasoning produced the biggest success story in educational neuroscience to date, the remediation of one subtype of dyslexia. In a representative study, Eden et al. (2004) used fMRI to first identify the networks of brain areas recruited by typical readers and those with dyslexia. Dyslexic readers showed reduced activation in AG, which has been implicated in mapping orthography to phonology. Next, the dyslexic readers participated in a program developed by educational researchers for remediating phonological difficulties. Post-test fMRI scans revealed that successful remediation was associated with increased activation in AG. From an area-focus approach, this 'weak' brain area had been 'strengthened'.

An area focus is currently being applied to understand dyscalculia, the mathematical analog of dyslexia. Dyscalculia is defined as scoring in the lowest 5% (or so) on tests of mathematical achievement relative to age, education level and intelligence (Butterworth 2005). This is a coarse clinical definition, and dyscalculia is likely a blanket term that includes multiple subtypes. Molko et al. (2003) applied the logic of the area approach to understand the mathematical impairment of a relatively homogeneous group of dyscalculics – those with Turner syndrome. They focused on the mathematical competency of arithmetic problem-solving – the ability to compute or retrieve the answers to addition and subtraction problems (and, in other experiments, multiplication and division problems) where the operands are small positive integers. They capitalised on the *problem size effect*: the finding that the time to solve problems with large operands (e.g., $8 + 9$) is slower than the time to solve problems with small operands (e.g., $4 + 3$) (Ashcraft 1992). Stanescu-Cosson et al. (2000) had previously identified a neural analog of the problem size effect in normal adults, finding that operand size correlates positively with activation in IPS. Molko et al. (2003) found that patients with dyscalculia failed to show a problem size effect in IPS (or any other brain area).[3] An area-focus interpretation of this finding is that under-activation of IPS in this group of dyscalculics is correlated with their impaired arithmetic problem-solving. The next logical step would be a training study to exercise this 'mental muscle', with the expected result that performance would improve and IPS activation would come to resemble that of people without dyscalculia.

The network focus for mathematical reasoning

Although an area focus is important for initially mapping the functional terrain of the brain, it ultimately presents an oversimplified view of the neural bases of mathematical reasoning. That one area is necessary for a particular ability does not imply that it is sufficient. A broader consideration of neuroimaging studies reveals that many mathematical competencies are better viewed as emergent products of networks of brain areas. As a corollary, some impairments of mathematical reasoning may be better viewed as breakdowns in network function; consequently, remediation may require exercises that *coordinate* areas rather than strengthen them in isolation.

The network focus has been a minor theme in neuroscience theorising for decades. An early example comes from Lashley, who incrementally removed portions of rats' brains to identify 'the memory area'. His conclusion was that no such area existed, and that the rat brain instead worked by *mass action*: the more that was removed, the more performance declined. Though it ultimately proved to be an untenable account of memory, the proposed distribution of function served as a useful counterweight to the area focus. Another early example of a focus on network function is Luria (1966), who observed that focal brain lesions often impair not a single competency, but rather a range of competencies, some more than others. More recently, Mesulam (1990) has argued that attention and language are better understood as the products of partially overlapping, large-scale cortical networks. In this view, most competencies are implemented by multiple areas, and most areas contribute to multiple competencies.

fMRI studies are increasingly focusing on the network of brain areas that activates for a given task, rather than the single area that activates most selectively. For example, consider the neural bases of face recognition. Early studies found evidence that fusiform gyrus (an area in inferior temporal cortex) selectively activates for processing faces when activation associated with the processing of other visual categories, such as houses, is subtracted away (Kanwisher, McDermott, and Chun 1997). This led to the label 'fusiform face area' and the concomitant assumption that the ability to discriminate faces had enough survival value that the human brain evolved a dedicated area. However, subsequent studies revealed that fusiform gyrus activates not just for faces, but also for other visual categories such as houses and furniture, though to a lesser extant (Ishai et al. 1999). Conversely, other inferior temporal areas that activate selectively for other visual categories also activate for faces, though to a lesser extant. In this way, an initial area-based understanding of face recognition has been articulated into a more nuanced network-based understanding. The remainder of this section describes a similar (and ongoing) shift, where an initial area-based understanding of arithmetic problem-solving is being refined into a network-based understanding.

Early neuroimaging studies of adults found selective activation of IPS when subtracting single-digit operands. Within the area focus, this was interpreted as evidence that IPS implements the subtraction competency. Because other researchers had found activation in this area during visuospatial processing, Dehaene et al. (2003) proposed that subtraction problems are solved by imagining and moving along a mental number line. In contrast, early studies of multiplication found selective activation of AG. This was interpreted as evidence that this area implements the multiplication competency. Because other researchers had found AG activation during retrieval of phonological information, Dehaene et al. (2003) proposed that multiplication is performed by look-up in a verbally coded, mental multiplication table. In this way, the area focus made sense of early neuroimaging studies – subtraction involves visuospatial processing and multiplication verbal processing.

Though simple and elegant, the area focus can miss potential complexities revealed by a network focus. For example, Lee (2000) had participants solve subtraction and multiplication problems in the scanner and found network effects. Multiple brain areas activated more for subtraction than multiplication; IPS was one, but it was not the only one. Conversely, multiple brain areas activated more for multiplication than subtraction; AG was one, but it was not the only one. These results suggested that mathematical competencies might be better understood as the products of networks of brain areas, not single brain areas.

In the preceding examples, researchers used tight subtractions: activation during multiplication was subtracted from activation during subtraction, and vice versa. By definition, each activation peak was associated with one, and only one, arithmetic operation. This led naturally to the inference of *independent* brain areas in the case of Dehaene et al. (2003) and *independent* (i.e., non-overlapping) networks of brain areas in the case of Lee (2000). Other studies have used 'loose subtractions' to isolate activation patterns. In a loose subtraction, activation from a relatively low-level control condition, such as viewing a fixation cross, is subtracted from activations during the experimental conditions of interest. The result is a more complete picture of the network recruited by each experimental condition. Studies employing loose subtractions reveal that subtraction and multiplication activate a *common* network of brain areas, although they activate different areas to different degrees. For example, Chochon et al. (1999) subtracted activation when viewing a fixation cross from activation during subtraction and multiplication respectively. They found that subtraction activated a network of brain areas, one that included IPS. Critically, they found that multiplication activated almost the same network. This network included IPS, although it was activated less intensely.

Duffau et al. (2002) conducted a neurosurgical study of a patient with a tumour in AG. Before removing the tumour, electro-stimulation was used to map competencies within AG. Among other tasks, the patient solved different kinds of arithmetic problems. Electrical stimulation was directly applied to different sites within AG, so it was possible to see which competencies were disrupted. Consistent with an area focus, the researchers found a multiplication site within AG. Critically, they also found a subtraction site in the same brain area, as well as a site common to both operations. These results suggest that it is a mistake to narrowly construe AG as *the* multiplication area. Rather, it is a component of a larger arithmetic network, and it plays a role not just in multiplication, but also in subtraction (and likely other aspects of mathematical reasoning as well).

These network findings indicate that the mapping of behaviour to the brain is more complex than that suggested by an area focus and frequently communicated to educators and educational researchers. The different pictures of arithmetic painted by the area and network approaches are important for education because they may have different implications for how best to teach. The area focus suggests that subtraction should be taught using spatial referents such as number lines to capitalise on the functional specialisation of IPS; and that multiplication should be taught verbally, for example, by rehearsing times tables, to recruit AG. In contrast, the network approach is consistent with instruction that targets the development of number sense (Baroody 1985). Children should be given opportunities to integrate different meanings and operations of number by engaging in activities that yield coordinated networks (Case et al. 1997). Note that this prescription does not preclude development of a mental number line, nor large doses of mathematical fact memorisation. However, it does suggest that a number line representation is not sufficient for achieving flexible subtraction competence, and memorisation is not sufficient for achieving flexible multiplication competence. As we describe below, there is a place for both meaning and memorisation in arithmetic.

Using the network approach to understand topics in mathematics education

The area focus currently dominates how neuroscience findings are packaged for educational researchers. As a result, the potential of the network focus remains largely untapped. This section illustrates this potential. It applies the network focus to three topics of interest to mathematics education: the development of mathematical reasoning, the effects of practice and instruction and the derailment of mathematical reasoning in dyscalculia. The examples show how a network focus can refine the broad-stroke neuroscience models one might use to explain educationally relevant phenomena.

Qualitative shifts underlying continuous behavioural changes

Developmental neuroscientists were among the first to adopt a network focus (e.g., Johnson et al. 2002). Consider the development of the understanding that digits name quantities or magnitudes. The SDE (i.e., the difference in response times for comparing near digits versus far digits) is indicative of whether people have developed an interpretation of number that includes its magnitude interpretation. In a cross-sectional study, Sekuler and Mierkiewicz (1977) documented that the SDE (i.e., the difference in response times for comparing near digits versus far digits) is present as early as kindergarten and decreases continuously into adulthood (but never completely). The area focus predicts that this continuous change in the degree of the SDE should be accompanied by a continuous change in the activation of IPS.[4] Ansari et al. (2005) tested this prediction by having adults and 10-year-old children make numerical comparisons. The adults showed an SDE in a network of brain areas that included IPS, replicating prior studies. Critically, for the children, an activation pattern differentiating near versus far comparisons was not observed in IPS, though it was observed in other brain areas. In the case of numerical magnitude, a continuous developmental change at the behavioural level belies a qualitative shift at the neural level.

Another example, from the domain of arithmetic problem solving, comes from a cross-sectional study by Rivera et al. (2005). Children between the ages of 8 and 19 solved simple addition and subtraction problems. Although accuracy was constant across development, there was a continuous improvement in solution speed with age. Recall that the area focus predicts that a continuous change in behavioural performance with development should be accompanied by a continuous change in the activation level of the corresponding neural correlate. However, the Rivera et al. (2005) results were more consistent with the network focus. Some areas of the arithmetic network were more active early in development. These areas have been implicated in domain-general forms of cognition (i.e., prefrontal areas associated with controlled processing and executive function and medial temporal areas associated with declarative long-term memory). Other areas became more active with development, including those known to be associated with visuospatial processing (IPS) and verbal processing (AG). These are more domain-specific forms of cognition. Once again, a continuous developmental change at the behavioural level – faster addition and subtraction – is better understood as a qualitative shift in the underlying network, in this case, reflecting a transition from domain-general to domain-specific processing.[5] This qualitative shift raises the question of whether educational activities should change over time to help students move from early domain-general processing to later domain-specific processing. Whether a constant dose of thought-provoking problems is the best way to encourage the shift, or whether practising the same types of problems repeatedly better encourages the shift, are interesting empirical questions raised by a network focus.

Effects of memorisation and strategy training

The network approach helps clarify the effects of practice on mathematical reasoning. Delazer et al. (2003) trained participants on complex multiplication problems, where a two-digit operand is multiplied by a one-digit operand. They were then scanned as they solved the same problems they had studied, plus a set of new problems of similar difficulty. This design makes it possible to identify the learning effects of memorising specific mathematical facts through practice versus computing them. Activation in AG (and some other areas) increased for the trained problems, suggesting that answers were being accessed from a verbal store. In addition, activation in IPS (and some other areas) decreased for trained problems, suggesting that less computation was performed for familiar problems. One interpretation of these results is that practice produced a shift in the arithmetic network that reflected a transition from a more computational visuospatial strategy to a more retrieval-based verbal strategy for the trained problems.

The Delazer et al. (2003) study is important because it addresses the effects of practice, an issue of interest to mathematics education. Delazer et al. (2005) took the next step in a study that examined the effects of pure memorisation versus learning an algorithm for computing solutions. They taught participants a novel arithmetic operation using two kinds of instruction. The memorisation group memorised the answers to problems with specific operands. They never learned how to compute the operation. By contrast, the strategy group was taught an algorithm for computing the answer given the same operands. Both groups then solved familiar and novel problems in the scanner.

The results showed that participants in the memorisation condition organised one network of brain areas to perform the operation and participants in the strategy condition another. For example, the memorisation network included AG, which has been implicated in the retrieval of verbally coded knowledge, whereas the strategy network included the anterior cingulate cortex, which has been implicated in controlled cognitive processing. This difference is important for two reasons. First, it is a difference at the brain level that matters at the behavioural level, and is thus relevant for education. The network organised by participants in the strategy condition supported transfer to novel problems (78% accuracy), whereas the network organised by participants in the memorisation condition did not (15% accuracy). Memorisation and calculation strengthen different networks rather than strengthening the same one, and thus the network analysis helps explain the differential effects of memorising versus learning to calculate. A second important contribution of this study for the prospects of educational neuroscience is that it demonstrates that fMRI can be used to study the consequences of instruction delivered outside the scanner over a relatively long period of time.

Dyscalculia as network under-activation

Recall that Molko et al. (2003) contrasted a group of normal controls with a group of dyscalculics as they solved addition problems. The critical finding was that normal controls displayed a problem size effect in the activation of IPS, whereas dyscalculics did not. Although the results of this study are comprehensible from an area focus, those of a more recent study of dyscalculia are better understood from a network focus. Kucian et al. (2006) imaged a group of dyscalculics and a group of normal controls as they performed a range of mathematical tasks. In one task, approximate addition, they found under-activation of the entire arithmetic network in the dyscalculic group relative to the normal control group. The implicated areas included bilateral IPS, inferior frontal gyrus, middle frontal gyrus and anterior cingulate cortex. These results suggest that understanding dyscalculia will require focusing on both the dysfunction of individual brain areas and the dysfunction of networks of brain areas.[6] It is an open question of what kinds of instruction may be able to organise a dysfunctioning network (as opposed to a dysfunctioning brain area, which we saw above in the dyslexia example: Eden et al. 2004)? We return to this question below.

Conclusion

This paper has considered two approaches to understanding the relationship between cognition and brain function. The area focus maps cognitive competencies to brain areas in a one-to-one fashion. The network focus understands each cognitive competency as the emergent product of information processing in a network of brain areas. Although the area focus has historically dominated discussions, we argued the network focus offers a complementary perspective on brain function that educational neuroscience should not ignore.

Two of the examples presented above bring the area focus and network focus into particularly sharp contrast. The first concerns the arithmetic problem-solving of typical adults. Initial studies adopted an area focus. Their findings suggested that subtraction selectively activates IPS, and thus involves visuospatial processing, whereas multiplication selectively activates AG, and thus involves verbal processing (Dehaene et al. 2003). Subsequent studies adopted a network focus. In contrast, they found evidence for a common arithmetic network whose component brain areas are taxed differently by different operations (Chochon et al. 1999; Duffau et al. 2002; Lee 2000). The second example where both the area focus and network focus have been adopted is dyscalculia. Although the study of this impairment is still in its infancy, an early study by Molko et al. (2003) adopted an area approach. It found that a neural correlate of dyscalculia was dysfunction of IPS. By contrast, the more recent study by Kucian et al. (2006) adopted a network focus. It found under-activation not of a single brain area, but rather the entire arithmetic network. The network-focus conclusions are consistent with the views of many in mathematics education (Baroody 1985; Case et al. 1997), namely that arithmetic problem-solving is the product of an interrelated set of mathematical competencies, and that the failure to properly coordinate these competencies results in poor mathematical achievement. For this reason, we expect the network focus to become increasingly important as educational neuroscience matures.

We conclude by describing the current limitations of network focus theorising and emerging neuroscience methods that promise to make such theorising more tractable in the future. An important limitation of the network focus for education is that it posits a complex, many-to-many mapping of mathematical competencies to brain areas. This makes it difficult to make predictions about the effects of network function and dysfunction, and therefore to draw implications for questions of interest to educational researchers. By contrast, the area focus maps mathematical competencies to brain areas in a one-to-one fashion, with a deficit in a particular competency understood as a dysfunction of the corresponding brain area. This has a natural educational implication: to design instruction that 'strengthens' that 'weak' area, presumably improving performance. Although this approach has had a few limited successes (e.g., Eden et al. 2004), its prospects are ultimately limited by the fact that the brain is *not* carved at the same functional joints that make sense at the behavioural level. Rather, brain areas appear to be specialised for lower-level functions, and it is only through their organisation in large-scale networks that these functions coalesce into mathematical competencies that matter at the behavioural level, and are thus of interest to educational researchers.

However, there are methods that make network-style theorising more tractable. They should enable studies that ask how brain areas become connected and coordinated in networks, as when children learn to coordinate cardinal and ordinal conceptions of quantity (Case et al. 1997). One example is *functional connectivity analysis*, which looks for correlated activity in different brain areas during task performance (e.g., Friston 1994). The inference is that correlated brain areas are communicating as part of a large-scale network. For example, Büchel, Coull, and Friston (1999) found that learning gains were associated not with changes in the activation of a single brain area, but rather with increases in correlated activity among brain areas. Functional connectivity analysis may be useful for understanding the network-wide under-activations in dyscalculia documented by Kucian et al. (2006). This deficit may be better understood as a dysfunction of how well brain areas communicate with, and therefore co-activate, one another. Another promising neuroscience method is *diffusion tensor imaging* (DTI), which directly images the anatomical connections – the white matter tracts – over which brain areas communicate (e.g., Le Bihan et al. 2001). The potential of DTI to inform topics in education is illustrated by a recent study by Niogi and McCandliss (2006), who found that the integrity of left temporo-parietal white-matter tracts is correlated with reading ability in elementary school children. Future functional connectivity and DTI studies of mathematical reasoning, literacy and other forms of cognition of interest to educational neuroscientists promise to benefit from a network focus.

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Notes

1. The use of subtraction has declined over the years as other experimental designs and methods of analysis have been developed. We describe two of these advancements in the 'Conclusion' section.
2. Pinel et al. (2004) also had participants compare stimuli along physical dimensions, such as size and luminance. These comparisons also produced SDEs in IPS. Comparisons of numerical magnitude and physical size activated roughly the same peak coordinates in IPS, whereas the comparisons of physical luminance activated different peak coordinates, though in the same area.
3. The dyscalculic patients did show a behavioural problem size effect, but it was exaggerated relative to normal controls, suggesting use of a different strategy (e.g., verbal counting versus magnitude-based processing).
4. Whether the change is an increase or decrease in activation depends on one's conception of what develops (Poldrack 2000). If one believes that representations get richer, then the prediction is increasing activation. If one believes that representations are shaped or tuned (i.e., made more efficient), then the prediction is decreasing activation.
5. There are other ways to interpret this shift. Rivera et al. (2005) favour an attentional interpretation, from more controlled to more automatic processing. Importantly, this interpretation is also a network explanation.
6. The Kucian et al. (2006) results do not strictly compel a network interpretation. It is possible to interpret them from an area focus if one assumes that the dyscalculia is not a homogeneous deficit, but rather is composed of multiple subtypes; and that each subtype is associated with dysfunction of a single competency, and thus a single brain area.

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