

in brain areas usually associated with both the trigger sensation and the secondary sensation. For example, activation in left colour-sensitive cortex occurred in word-colour synaesthetes hearing words [14] but not in non-synaesthetes trained to associate colour with words [15]. Many issues concerning the anatomy underlying information processing in synaesthesia remain to be elucidated but this method of using interference techniques to investigate whether synaesthesia involves the same sensory multimodal areas that support cross-modal integration in non-synaesthetes is an important approach. The two immediate questions that pose themselves are how Esterman *et al.*'s finding will generalize to other synaesthetes and whether the timing of the putative synaesthetic binding is similar to that of sensory integration in non-synaesthetes.

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### Letters

# Improving reverse neuroimaging inference: cognitive domain versus cognitive complexity

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In a recent TICS article, Poldrack [1] offers a highly informative analysis of the use and misuse of 'reverse inference' in neuroimaging, a common practice by which the engagement of a particular cognitive process is inferred from the activation of a particular brain region. Using a formal Bayesian analysis framework, Poldrack shows that the usefulness of reverse inference depends on the selectivity of activation in the region of interest (the ratio of process-specific activation to the overall likelihood of activation in that region across all tasks). However, it is important to note that the usefulness of reverse inference also depends on whether the relevant task characteristics for the region of interest are taken into account.

### Cognitive domain

Perhaps the most salient task characteristic is a task's cognitive domain. For example, distinctions are often made between attention, language and working-memory tasks.

Some regions appear to show selectivity with respect to such domains. For example, Broca's area [Brodmann area (BA) 44] is more likely to be activated by language than by non-language tasks [1]. Other regions, however, such as the rostrolateral prefrontal cortex (RLPFC; lateral portion of BA 10), appear to have much lower domain-selectivity. Thus, activations in the RLPFC have been observed with similar probability across tasks in the domains of reasoning, working memory and episodic memory [2], as well as attention [3]. This lack of domain-specificity is not surprising, given that the functions of this region probably include highly integrative, abstract cognitive processes [2,4,5]. If tasks that recruit this region were defined solely in terms of their cognitive domain, this lack of selectivity would seem to preclude reverse neuroimaging inference altogether.

### Cognitive complexity

On the other hand, if such tasks were defined in terms of their level of cognitive complexity, selectivity of RLPFC activation would be relatively high. Cognitive complexity

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has been defined in various ways, including the level of embedding in a goal–subgoal hierarchy during problem-solving [6], the number of relations being simultaneously processed during reasoning [7], or the number of items held in working memory [8]. Reviews of RLPFC recruitment across multiple domains [2,9] show that activations are more frequent when the complexity of cognitive processing is high than when it is relatively low. This selectivity would permit reverse neuroimaging inference to a much greater extent, especially when specific cognitive processes such as relational integration [7], the evaluation of self-generated information [4], or subgoal processing [5,10] are theorized at the highest levels of cognitive complexity.

### Implications and questions for future research

In summary, brain regions differ not only in their overall selectivity of response, but also in terms of the specific task characteristics they are selective to. This suggests that reverse inference can be improved by incorporating information about the relevant task characteristics into neuroimaging databases and meta-analyses. At present, databases generally classify tasks according to their cognitive domain and contain virtually no information about the level of task complexity, possibly because complexity of processing can be difficult to quantify and compare across tasks.

In addition, a number of other questions emerge: Are there other brain regions that show selectivity to the level of task complexity but lack selectivity to task domain? How can we compare levels of cognitive complexity across different cognitive domains? What other task characteristics, in addition to complexity and domain, might be relevant in determining the selectivity of brain regions? Clearly, much remains to be resolved. In the meantime, the framework

presented by Poldrack places clear constraints on the inferences that can be drawn with the limited information that is currently available.

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## Neuroeconomics and the metastable brain

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In a recent article Sanfey and colleagues [1] suggest that neuroeconomics should build upon the strengths of the ‘unitary perspective’ in economics and the ‘multiple-systems approach’ in neuroscience to challenge classic decision-making theories rooted in rationality. They entertain the notion that ideas from economics will shed light on one of the great riddles of neuroscience: how the many diverse regions of the brain are coordinated to produce goal-directed behaviour. In an attempt to bridge the conceptual gap between two such disparate fields Sanfey and colleagues offer an analogy between the *modus operandi* of the brain and of a corporation. In a nutshell, both are presented as

systems ruled by an executive control that interacts with more or less independent specialized agents that transform an input into an output [1].

An alternative approach to this purely hierarchical model is coordination dynamics [2,3]. Inspired by self-organizing principles specifically tailored to the informational demands of cognitive and brain function, coordination dynamics proposes that states-of-mind, manifested as coordination patterns in the brain, spontaneously arise from non-linear coupling among interacting components. Which patterns arise depends upon their stability under given constraints. As circumstances change, one pattern might lose stability and another emerge spontaneously because it better fits current demands. Such context-dependent decision-making and pattern selection have

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