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Shared neural processes support semantic control and action understanding

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Executive–semantic control and action understanding appear to recruit overlapping brain regions but existing evidence from neuroimaging meta-analyses and neuropsychology lacks spatial precision; we therefore manipulated difficulty and feature type (visual vs. action) in a single fMRI study. Harder judgements recruited an executive–semantic network encompassing medial and inferior frontal regions (including LIFG) and posterior temporal cortex (including pMTG). These regions partially overlapped with brain areas involved in action but not visual judgements. In LIFG, the peak responses to action and difficulty were spatially identical across participants, while these responses were overlapping yet spatially distinct in posterior temporal cortex. We propose that the co-activation of LIFG and pMTG allows the flexible retrieval of semantic information, appropriate to the current context; this might be necessary both for semantic control and understanding actions. Feature selection in difficult trials also recruited ventral occipital–temporal areas, not implicated in action understanding.

1. Introduction

Our conceptual knowledge encompasses a large body of information but only particular aspects of concepts will be useful in any given context or task: as a consequence, executive control processes are engaged to guide conceptual processing in a context-dependent manner (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Jefferies, 2013; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010). We can match objects on the basis of specific features, even when these are not prominent aspects of the items, and this is crucial for intelligent behaviour – for example, when trying to pitch a tent, we can understand that a shoe has properties that make it suitable for banging pegs into the ground, even though these properties are not directly related to its dominant associations. Semantic control processes in left inferior frontal gyrus (LIFG) are thought to be critical for this selection of task-relevant attributes (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) and the controlled retrieval of weak associations (Noonan, Jefferies, Visser, & Lambon Ralph, 2013; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). However, little is known about *how* control processes are deployed to focus neural activity on specific, task-relevant aspects of knowledge – and whether the same mechanisms are recruited for different types of features (e.g., action vs. visual properties).

Contemporary theories of semantic cognition agree that modality-specific sensory and motor areas, plus multi-modal regions capturing specific features, contribute to semantic representation (Meteyard, Rodriguez Cuadrado, Bahrami, & Vigliocco, 2012; Patterson, Nestor, & Rogers, 2007; Pobric, Jefferies, & Lambon Ralph, 2010; Pulvermüller, 2013). As a result, semantic judgements about manipulable objects are thought to draw on representations across the cortex, including inferior parietal, premotor and posterior middle temporal (pMTG) regions, which support motor and praxis features (Chouinard & Goodale, 2012; Liljeström et al., 2008; Pobric et al., 2010; Rueschemeyer, van Rooij, Lindemann, Willems, & Bekkering, 2010; Vitali et al., 2005; Watson, Cardillo, Ianni, & Chatterjee, 2013; Yee, Drucker, & Thompson-Schill, 2010; Zannino et al., 2010). Although some research suggests that sensory and motor regions are recruited rapidly and automatically following word presentation (Hauk & Pulvermüller, 2004; Shtyrov, Butorina, Nikolaeva, & Stroganova, 2014), recent neuroimaging studies have examined how activity within modality-specific areas might be modulated on the basis of task demands (Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008; Rüeschemeyer, Brass, & Friederici, 2007; Tomasino & Rumiati, 2013). Action words (e.g., kick) and their semantic associates do not necessarily activate

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motor regions when presented in isolation; this response is seen more strongly for literal sentences ('kick the ball') in which the action properties are relevant to the task (Raposo, Moss, Stamatakis, & Tyler, 2009; Schuil, Smits, & Zwaan, 2013; van Dam, van Dijk, Bekkering, & Rueschemeyer, 2012). Such findings challenge the assumptions of strong 'embodied' accounts of semantic cognition, in which neural connections between distributed sensory and motor features are sufficient for conceptual representation. Furthermore, they raise questions about how semantic representations are applied in a controlled way, to suit the particular task or context.

In addition to the role of distributed visual and motor/praxis representations in object knowledge, some theories suggest these disparate features are drawn together in an amodal semantic 'hub' in the anterior temporal lobes (ATL; Patterson et al., 2007). This proposal remains controversial (Simmons & Martin, 2009) because although data from multiple methods – including patients with semantic dementia (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000), TMS (Ishibashi, Lambon Ralph, Saito, & Pobric, 2011; Pobric et al., 2010) and PET (Devlin et al., 2002) – reveal a contribution of ATL to conceptual knowledge across modalities, fMRI is relatively insensitive to signals from ATL due to magnetic susceptibility artefacts that produce signal loss and distortion in this brain region (Visser, Jefferies, Embleton, & Lambon Ralph, 2012; Visser, Jefferies, & Lambon Ralph, 2010). Consequently the fMRI literature does not uniformly emphasise a role for ATL and instead focuses on the contribution of pMTG to multimodal tool/action knowledge, with some recent studies suggesting pMTG is a semantic hub for tool and action understanding (Martin, 2007; Martin, Kyle Simmons, Beauchamp, & Gotts, 2014; van Elk, van Schie, & Bekkering, 2014).

An alternative view about the contribution of pMTG to semantic cognition is provided by work on semantic control (for reviews, see Jefferies, 2013; Noonan et al., 2013). Although this research has largely focussed on the role of LIFG in selection and controlled semantic retrieval (Badre et al., 2005; Hoffman, Jefferies, & Lambon Ralph, 2010; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner et al., 2001), a recent meta-analysis revealed that manipulations of the executive demands of semantic tasks activate a distributed cortical network, including left and right inferior frontal gyrus (LIFG; RIFG), medial PFC (pre-SMA), dorsal angular gyrus (dAG) bordering intraparietal sulcus (IPS) and, most notably, pMTG (Noonan et al., 2013). These sites all show greater activation during difficult tasks that tap less prominent aspects of meaning, or require strongly related distracters to be suppressed (Rodd, Johnsrude, & Davis, 2010; Wagner et al., 2001; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). Moreover, inhibitory TMS to LIFG and pMTG produces equivalent disruption of semantic tasks tapping controlled retrieval, but has no effect on semantic judgements to highly-associated word pairs, which rely largely on automatic spreading activation (Whitney et al., 2011). This network for semantic control overlaps with the "fronto-parietal control network" involved in cognitive control across domains – which includes inferior frontal sulcus, intraparietal sulcus and occipital–temporal regions (Duncan, 2010; Woolgar, Hampshire, Thompson, & Duncan, 2011; Yeo et al., 2011), although some sites appear to make a relatively restricted contribution to control processes important for semantic cognition, particularly anterior parts of LIFG and pMTG (Devlin, Matthews, & Rushworth, 2003; Noonan et al., 2013; Whitney, Jefferies, & Kircher, 2011; Whitney et al., 2011, 2012).

In summary, separate literatures on executive–semantic processing and action understanding have linked similar left hemisphere networks – encompassing IFG/premotor cortex, IPL and pMTG – with diverse aspects of semantic cognition (Noonan et al., 2010; Watson et al., 2013). Since these regions are associated with understanding actions, tools, verbs and events, it has been suggested they might represent motion, action, or praxis features (Chouinard & Goodale, 2010; Liljeström et al., 2008; Spunt & Lieberman, 2012; Watson et al., 2013). However, left IFG, pMTG, and dorsal IPL are also activated during semantic tasks with high executive demands, suggesting they might support controlled retrieval/selection processes that shape semantic processing to suit the current context (Noonan et al., 2013). Damage to this network in semantic aphasia (SA) produces difficulty controlling conceptual retrieval to suit the task or context, both in verbal tasks like picture naming and non-verbal tasks like object use (Jefferies & Lambon Ralph, 2006; Noonan et al., 2010). These deficits can be overcome through the provision of cues that reduce the need for internally-generated control (i.e., phonological cues for picture naming; photographs of the recipients of actions in object use; Corbett, Jefferies, Ehsan, & Lambon Ralph, 2009; Corbett, Jefferies, & Lambon Ralph, 2011), suggesting that damage to this network does not produce a loss of semantic information about words or actions, but instead poor control over conceptual retrieval. However, both neuropsychological studies and neuroimaging meta-analyses have poor spatial resolution, and thus it is not yet known whether semantic control and action understanding recruit adjacent (yet distinct) or overlapping regions in pMTG and LIFG.

We addressed this question in an fMRI study with a 2 × 2 design that (1) contrasted decisions about action and non-action (visual) features and (2) compared easy, low-control judgements, in which participants selected a globally semantically-related item with more difficult, high-control judgements, in which the target was only related via a specific feature. We predicted that the recruitment of sensory/motor regions would vary according to the feature, with more activity within visual areas for visual decisions (e.g., lateral occipital cortex, occipital pole), and within motor/praxis areas for action decisions (e.g., precentral gyrus; IPL; pMTG). Executive–semantic regions were expected to show stronger responses for more demanding judgements irrespective of the feature to be matched. Furthermore, we examined whether brain regions recruited during the retrieval of action knowledge would overlap with those implicated in semantic control in both group analyses and at the single-subject level.

2. Method

2.1. Participants

20 right-handed, native English speaking participants were recruited from the University of York, UK. All subjects had normal/corrected to normal vision. Three participants had to be excluded from the final analysis due to head movement (>2 mm) and poor accuracy. A total of 17 participants were entered into the analysis (mean age = 22.7 years, 10 females).

2.2. Study design

A fully-factorial 2 × 2 within-subjects design was used. The two factors were *judgement type* (action or visual form matching) and *control demands* (contrasting easy decisions about globally related items with difficult decisions based on specific features).

In action judgement trials, participants were asked to match the probe and target words on the basis of shared or similar action features involved in stereotypical use (e.g., selecting SCREWDRIVER for the probe KEY, because both involve a precise twisting action). In visual judgement trials, participants performed a match on the basis of shared visual characteristics (e.g., SCREWDRIVER with PEN, because these objects both have a long, thin rounded shape). We also