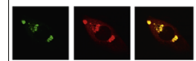


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Research Report

Event-related brain potentials reveal correlates of the transformation of stimulus functions through derived relations in healthy humans



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ABSTRACT

This research aimed to explore the neural correlates of relational learning by recording high-density EEG during a behavioural task involving derivation levels of varying complexity. A total of 15 participants (5 male; age range 18–23 years; mean age=20.0 years) completed contextual cue training, relational learning, function training and a derivation task while 128-channel event-related potentials (ERPs) were recorded from the scalp (Background). Differences in response latencies were observed between the two derived (symmetry and equivalence) and directly trained relations, with longest latencies found for equivalence and shortest for the directly trained relations. This pattern failed to reach statistical significance. Importantly, ERPs revealed an early P3a positivity (from 230 to 350 ms) over right posterior scalp sites. Significantly larger mean amplitudes were found at three channels (P6, E115 and E121) for the equivalence relations compared to the two other types (Results). We believe this may constitute a first demonstration of differences in brain electrophysiology in the transformation of stimulus functions through derived relations of hierarchical levels of complexity (Conclusions).

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1. Introduction

One of the cognitive hallmarks of the human species is the ability to process and retain abstract concepts, a capacity which arises due to our highly developed frontal lobes, and in particular the prefrontal cortices (Fuster, 1997; Damasio, 1998). Such abstract reasoning has conferred upon us significant evolutionary advantages, including the ability to retain information in short-term memory (Goldman-Rakic, 1990), to generate language (Fuster, 2002; Barbas et al., 2013) and to plan for

future actions and events (Quintana and Fuster, 1992; Hoshi and Tanji, 2004; Mushiaki et al., 2006; Barbey et al., 2009). A crucial element for the successful handling of abstract concepts and symbols is the ability to understand the relationships that may exist between them, such as category inclusion (A is a member of B) and relative magnitude (A is greater than B). While many such relationships can be explicitly learned or trained, other novel relationships between concepts have been observed to emerge, without training, as a result of exposure to an initial set of relations (for example, if the relations A–B and

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A–C are trained, the untrained relationships between A, B and C are reliably seen to emerge; Wang and Dymond, 2013).

Sidman (1994,1971) was among the first to formalise the study of such stimulus equivalences, defining the different types of derived relations as *symmetry* (e.g. if A–B then B–A) and *equivalence* (e.g. if A–B and B–C then C–A). Subsequent research into the nature and limits of these relations has revealed that, while adults, children and those with developmental difficulties appear to generate such equivalences spontaneously (reviewed in Dymond and Rehfeldt, 2000), evidence of derived relations of this sort in non-humans is elusive (see Dymond et al., 2003 for a review). Further, other human-based studies suggest that these relations are absent in pre-verbal children and those without the capacity for speech (Devany et al., 1986; Barnes et al., 1990; Augustson and Dougher, 1992). This has led some researchers to propose that the presence of this ability may be related to another uniquely human characteristic, the use of language (Bickerton, 1990; DeLisi, 2001), drawing parallels between the processes involved in derived and semantic relations (Barnes-Holmes et al., 2005; Haimson et al., 2009; Yorio et al., 2008). Indeed, data from event-related potentials (ERPs) studies of stimulus equivalence using the well-established N400 semantic mismatch paradigm (Kutas and Hillyard, 1980) would appear to support this view, as do findings from the literature on semantic priming (McNamara, 2005).

Neuroimaging studies have identified a prefrontal-parietal network which is activated during a wide range of transitive inference and equivalence tasks. Using functional MRI, Acuna et al. (2002) reported activation in bilateral prefrontal and lateral posterior parietal cortex (PPC) during a transitive inference task, with further activations in motor-related areas, precuneus and insula. Dickins et al. (2001) also observed bilateral activation in PPC during a matching-to-sample task of equivalence relations, together with activity in dorsolateral prefrontal cortex (DLPFC), a similar network to that activated for semantic relations. Two studies by Schlund et al. (2007, 2008) compared directly trained relations with symmetry, transitive inference and equivalence, and again identified a fronto-parietal network, as well as a frontal-subcortical pattern of activation involving the striatum. In their 2008 study, the authors revealed medial temporal lobe activations, in the parahippocampal gyrus for symmetry, and bilaterally in anterior hippocampus for equivalence and transitive inference. The authors proposed that this may reflect a hippocampal role in the memorial maintenance of such relations once they are derived. Taken together, these studies point to a distributed network underpinning the processing of derived relations. This network appears to be strongly driven by fronto-parietal connections and supported by subcortical structures including the hippocampal formation.

Another class of derived stimulus relations involves hierarchical levels of complexity in terms of the emergent equivalences among a set of concepts. Relations of this sort often include ideas such as “same as” or “opposite to”. For example, if a relation “same as” is trained between A and B, then the derived relation “B is the same as A” is termed *symmetry* since “same as” is a bidirectional operator. When two relations – between A and B, and between B and C – are trained, a more complex relation emerges to characterise the nature of A’s relationship to C and vice versa; this is termed *transitive inference* or *equivalence*. In both of these cases, the exact nature

of the relationships will depend on the relations trained; for example, A greater than B, B greater than C would lead to C less than A. O’Hora et al. (2002) observed a significant increase in response latencies as the hierarchical complexity of relations increased from directly trained to symmetry to equivalence relations. Hinton et al. (2010) compared symmetry and equivalence relations in an fMRI study and again found activation in frontal and parietal areas, specifically inferior frontal cortex, DLPFC and bilateral parietal cortex. In addition, activation was observed in right prefrontal and parietal areas in response to the symmetry relations.

While the semantic mismatch-related N400 waveform has been the main focus of several of the previous ERP studies of derived relations, other waveform components have been reported in these studies as potential indices of relational processing. Yorio et al. (2008) reported, in addition to the dN400 mentioned above and early N2 and P2 reflexivity-based deflections, a posterior P3 component from 350 to 600 ms which was larger for equivalence trials compared to non-related stimuli. A P3 waveform which differentiated related and non-related stimuli was also present from 350 to 450 ms in the first experiment of Haimson et al., 2009, though the authors attribute its presence to a potential methodological confound and only fronto-central electrodes are reported. As Wang and Dymond (2013) also point out, no statistical analysis of the P3 component was carried out in Haimson and colleagues’ study, as the focus was the N400 waveform. Finally, Wang and Dymond (2013) compared directly trained, symmetry and equivalence relations and noted that a late (350–550 ms) posterior P3 was elicited which was larger for symmetry and equivalence stimuli compared to directly trained. These and other studies linking the late posterior P3 component with higher order functions such as categorisation (for example, Duncan-Johnson and Donchin, 1977) suggest that this late positivity could represent a potential marker of relational processing which might discriminate between relations at different levels of hierarchical complexity.

Here, we recorded 128-channel event-related brain potentials (ERPs) while participants completed a derivation test to compare response latencies and waveform components for directly trained, symmetry and equivalence relations. We predicted longest latencies for the equivalence relations and shortest for the directly trained, with intermediate response times for symmetry relations (consistent with O’Hora et al., 2002). Electrophysiologically, we hypothesise P3 waveform differences matching the response latency data, with larger amplitudes associated with relations of higher complexity.

2. Results

2.1. Behavioural results

Mean response latencies for each type of relation in the derivation test revealed no significant main effect, $F(2,18)=1.59$, $p>0.05$, Greenhouse–Geisser corrected. No significant differences were observed between latencies for directly trained relations (1993.43, ± 209.05 ms), symmetry relations (1914.03, ± 124.5 ms) or equivalence relations (2457.66, ± 489.97 ms; see Fig. 2, inset).

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