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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

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http://dx.doi.org/10.1016/j.brainres.2014.12.044 0006-8993/© 2014 Elsevier B.V. All rights reserved. future actions and events (Quintana and Fuster, 1992; Hoshi and Tanji, 2004; Mushiake 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 nonrelated 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).

2.2. Electrophysiological results

Visual inspection of the waveforms revealed four distinct posterior components: a right posterior P1 (100–200 ms) which was maximal at PO4, a left posterior N2 (170–250 ms) with maximal amplitude at PO3, a right posterior P3a (230–350 ms) and P3b (350–520 ms), both of which peaked at channel P6. Repeated measures ANOVA was carried out for each component to compare the three types of relation using Mean Amplitude as the dependent variable. No significant differences were observed across conditions for the P1, F(2,18)=1.54, p>0.05, N2, F(2,18)=0.81, p>0.05, or P3b, F(2,18)=0.81, p>0.05. A significant main effect of relation type was found for the P3a, F(2,18)=4.28, p<0.05. Bonferroni post-hoc comparisons revealed that the P3a elicited by equivalence relations had significantly larger mean amplitude compared to directly trained and symmetry relations (both p<0.05; see Fig. 2).

Further analyses were carried out on six electrodes surrounding the right posterior channel P6 (P4, P8, P08, E114, E115 and E121) to test for the presence of a main effect of relation type (see Fig. 3). This main effect was present at one of the six selected channels: E121, F(2, 18)=4.69, p<0.05, and was driven by significant differences between directly trained and equivalence relations (p<0.05). Furthermore, a significant difference between directly trained and equivalence and equivalence relations was also evident at electrode E115 (p<0.05) albeit in the absence of a significant main effect of type of relation, F(2,18)=1.97, p>0.05, Greenhouse–Geisser adjusted.

2.3. Explicit stimulus ratings

Mean group scores for each of the six brand stimuli indicated that participants established two accurate three-member equivalence groups and attributed each with the correct valence classifications; positively-valenced Ciney (2.7 ± 0.50), Witkap (2.7 ± 0.47) and Gageleer (2.5 ± 0.52), and negatively-valenced Pardal (-2.7 ± 0.50), Zatte (-2.4 ± 0.52) and Ettalas (-1.8 ± 0.79). A one-way repeated measures ANOVA confirmed that the difference in ratings across brands was significant, F(5,45)=22.76, p<0.0001. Bonferroni post-hoc analyses showed that the mean likeability scores for Ciney, Witkap and Gageleer were all significantly higher compared to Pardal (all p<0.05), Zatte (p<0.01, p<0.01, p<0.05, respectively) and Ettalas (p<0.01, p<0.01, p<0.05, respectively). Finally, all participants correctly categorised the meaning of the two contextual cues as 'Same' and 'Opposite' when explicitly asked.

3. Discussion

In this experiment, we first established two three-member stimulus equivalence classes, using contextual cue and relational learning paradigms. We then established a stimulus function (appetitive/aversive) for the first member of each class (i.e. A1-Same-Appetitive; A2-Same-Aversive; A1-Opposite-Aversive; A2-Opposite-Appetitive) using function training. Following this, behavioural and electrophysiological responses to the directly trained and emergent (derived) relations (i.e. symmetry and equivalence) were compared during a derivation test. Finally, explicit ratings for stimuli were obtained. While a trend was evident wherein response latencies were longer in response to the more complex equivalence trials, no significant differences in reaction times were found across the three conditions. Electrophysiologically, ERP waveform components were identified over posterior scalp, with significant amplitude differences present for the early P3a component over right parietal scalp sites. At three of the seven right parietal leads examined, significantly larger positive deflections were elicited by the equivalence relations compared to the directly trained and/or symmetry trials. This may indicate that the P3a component is at least partially sensitive to the level of complexity of hierarchical derived stimulus relations.

Behaviourally it was hypothesised that response latencies would increase in accordance with the complexity of the relations being tested (Hughes et al., 2012). Specifically, the shortest RTs were predicted for directly trained relations, where all that was required in the derivation test was a recapitulation of the previously learned relations (e.g. 'A1-Same-B1'); intermediate RTs were anticipated for symmetry relations, which involved a reversal of the trained relationship (e.g. 'A1-SameB1' becomes 'B1-SameA1') and the longest latencies were expected for the equivalence relations, where an additional processing operation was necessary to derive the relationship accurately (e.g. 'A-Same-B1' and 'B1-Same-C1' becomes 'A1-Same-C1'). Surprisingly, the observed behavioural data did not follow this pattern. While longer latencies (almost 2500 ms) were present for the equivalence trials, the RTs for the directly trained and symmetry trials were very similar, and none of these differences were statistically significant. This finding is at odds with previous studies which have shown latencies to increase with increasing relational complexity (for



Fig. 1 – Schematic diagram showing examples of trials used in the Contextual Cue Training, Relation Training and Function Training phases as well as the Derivation Task. Correct responses occasioned the appearance of the word 'correct' in the centre of the screen for 1000 ms. A 1000 ms interval followed, before the task progressed to the next trial. When an incorrect response was made, participants were required to make the correct response to move on to the next trial. The position of each contextual cue was varied between the bottom left- and bottom right-hand sides of the screen within each block of training trials. Cuelocation did not vary during the derivation task.



Fig. 2 – Mean response latencies (ms) for each category of relations (inset). Overall Grand Mean waveforms depicting: a P1 component at the PO4 electrode; an N2 component at the PO3 electrode; P3a and P3b components at the P6 electrode. Significantly larger mean amplitude was observed for the P3a component in response to equivalence relations, compared to directly trained and symmetry relations (*p* < 0.05). Scalp-topographies depict maximal amplitude positivities at the P6 and PO4 electrodes and negative activation at the PO3 electrode, for each category of relation.

example, O'Hora et al., 2002; Steele and Hayes, 1991). Crucially, explicit tests confirmed that participants successfully identified the meaning of the contextual cues, established the equivalence groups and attributed the correct valence to each of these classes. Therefore, it is unlikely that the absence of significant RT differences between relation types can be explained by participant misconception.

This failure to detect differences between relation types might be attributed to the testing procedure: whereas previous research (e.g. Wang and Dymond, 2013; O'Hora et al., 2002) has used a single test block containing mixed A, B and C trials, the current study separated these into three blocks of trials. Additionally, O'Hora et al. (2002) note that response latencies tend to be longer in the case of relations of relative magnitude (e.g. A1 is greater than B1 becomes B1 is *less than* A1) compared to equivalence relations (e.g. A1-Same-B1 becomes B1-Same-A1), due to the existence of a different relation at the level of symmetry to that which was directly trained. It can thus be argued that the lack of a different relation at the levels of symmetry and equivalence may not have allowed the hypothesised response latency differences to be statistically detectable. Additionally, research has shown that response latency tends to increase as a function of nodal distance (i.e. the number of stimuli by which two adjacent stimuli are related to one-another: Bentall et al., 1993, 1999; Fields et al., 1990). Since the maximum nodal distance in the three-member equivalence classes employed in the current experiment was equal to 1, we argue that our failure to observe significant latency differences may be attributed to this. It is also possible that the relatively small sample size of those passing criterion may have rendered such latency effects difficult to detect statistically. Furthermore, O'Hora et al. (2002) warn of other factors extraneous to the experimental paradigms used in stimulus equivalence research - such as participants' prior histories of reinforcement - that may also cloud genuine effects in the data.

A number of ERP components were observed over posterior scalp during the derivation test, specifically a right hemisphere P1, a left lateralised N2 and a right posterior positivity in the 230–550 ms range with two distinct peaks, and early P3a and



Fig. 3 – Overall Grand Mean waveforms depicting P3a positivity at six posterior electrodes surrounding the P6 electrode: P4, P8, P08, E144, E115 and E121. Significantly larger mean amplitude was observed for the P3 component in response to equivalence relations compared to directly trained and symmetry relations at E115 and E121 (p < 0.05).

later P3b. No significant differences in mean amplitude were found for the P1 and N2 waveform components, suggesting that these deflections are likely reflective of early sensory (in this case visual) processing of the stimulus features presented on screen (see Luck and Hillyard, 1994; Eimer, 1996). Yorio et al. (2008) also reported similar reflexivity-based P2 and N2 components in their task, and it is generally accepted that components observed within 200 ms of stimulus onset, while modulated by attention, are usually an index of stimulus processing in early sensory cortices (Ritter et al., 1982, 1983; Hillyard and Münte, 1984; Paz-Caballero and García-Austt, 1992). The later P3b component - which was maximal over electrode P6 from 350 to 520 ms - also failed to reveal any significant amplitude differences across the three stimulus conditions. Given that this was the latest of the components to be identified within the 1000 ms post-stimulus epoch, it is possible that this waveform may be indicative of pre-response processes such as response selection, decision making or motor preparation which were invariant across all conditions. Others have reported P3b-type components associated with similar processing activities (e.g. Coles, 1989; Verleger, 1997; Verleger et al., 2005; see Polich, 2007 for a comprehensive review of P3a and P3b), and areas such as frontal, premotor and supplementary motor areas have been implicated in the

generation of this scalp-recorded potential (e.g. Garavan et al., 2002). Finally, no evidence of an N400-like component was evident within the epoch, which may be explained by the fact that semantic or relational mismatch was not specifically manipulated in this task.

Significant amplitude differences were observed across the three conditions for the P3a component over right posterior scalp sites from 230 to 350 ms. At electrode P6, equivalence trials elicited larger mean amplitudes than both symmetry and directly trained, while differences between equivalence and directly trained blocks were also found at leads E115 and E121. Given that response latencies did not differ significantly, this ERP effect cannot be attributed to differences in response speed across blocks. Rather, this waveform difference may reflect an electrophysiological correlate of hierarchical complexity in the processing of derived stimulus relations, potentially indexing the additional processing stages and cognitive resources required to accomplish the more arduous equivalence relationships over the more straightforward operations required in directly trained and symmetry trials. These results are comparable to those of Wang and Dymond (2013), who reported larger late posterior P3 amplitudes for symmetry and equivalence relations over directly trained relations in their second experiment, while

others have shown a late P3 component which was sensitive to differentiating related from unrelated trials (Yorio et al., 2008; Haimson et al., 2009).

The scalp distribution of the P3a component was predominantly right lateralised over posterior scalp, with maximal amplitude observed at electrode P6. While inferring cortical generators from scalp-recorded electrical potentials is notoriously difficult (see Hallez et al., 2007 for a review), this right posterior distribution could be interpreted as supportive evidence for the right hemisphere prefrontal-parietal network which has been implicated in a number of functional imaging studies of comparable tasks (Acuna et al., 2002; Hinton et al., 2010; Ogawa et al., 2010; Schlund et al., 2007). Others (Soltani and Knight, 2000; Polich, 2003) have suggested that aspects of the P300 component may reflect a circuit pathway between frontal and temporo-parietal areas. The type of processing required to compute the more complex equivalence relations would be consistent with several of the known functions of the posterior parietal region, which include spatial processing (see Duhamel et al., 1997; Rushworth et al., 1997), estimations of relative magnitude (Pinel et al., 2001; Walsh, 2003) and tasks involving transitive inference (Goel and Dolan, 2001). Further, the prefrontal-parietal circuit mentioned above has been shown to be involved in cognitive activities such as syllogistic reasoning (Osherson et al., 1998), arithmetic and mental spatial cognition (Roland and Friberg, 1985; Pinel et al., 2001). In addition, a right lateralised prefrontal-parietal network is also known to underpin sustained attention and vigilance during long task blocks (e.g. during the Sustained Attention to Response Task, SART; Manly et al., 2000; Cabeza and Nyberg, 2000; Posner and Petersen, 1990). Such a capacity is likely to be necessary in relational training paradigms given their typical duration and cognitive demands. Finally, as Schlund et al. (2007, 2008) point out, this prefrontal-parietal circuit may be augmented by subcortical structures including striatum and medial temporal lobe regions, and it is highly possible that the scalp recorded posterior P3a is resultant from multiple generators (see Wood, 1982), both cortical and subcortical, which may include some of these structures.

While the results reported here may show some preliminary evidence for an electrophysiological correlate of relational complexity among derived relations, they must be interpreted with caution for a number of reasons. Of particular concern is the relatively small sample size (n=10) following the exclusion of those participants who failed to reach the passing criterion on implicit training (n=5). Although this significantly reduces the statistical power of the analyses reported, such participant numbers are not uncommon in tasks of this nature: Yorio et al. (2008) reported data from a sample of 10 participants, Haimson's two experiments involved samples of 12 and 8, and the second study reported in Wang and Dymond (2013) included 13 participants. Given the rigorous accuracy criteria which must be passed in such experimental paradigms (i.e. >80%; see Table 1), a high failure rate appears inevitable, leading to reduced participant numbers for inclusion in final analyses. That notwithstanding, any results reported or conclusions offered here must be considered speculative and requiring of further experimentation with larger samples to be verified.

In addition, it would be of interest to compare the behavioural and electrophysiological responses during derivation tests of those who pass the criterion with those who fail to meet the passing level. It would be particularly instructive to explore whether a unique set of structures are activated for correct relational processing, or whether failure to derive is instead determined by failure to activate a common set of areas within a specific time window, as has been seen for other cognitive functions (e.g. response inhibition; see Garavan et al., 2002). Finally, functional neuroimaging during a comparable paradigm would be of benefit in elucidating the precise cortical network involved in this form of relational cognitive operation, while transcranial magnetic stimulation (TMS) over prefrontal and posterior parietal regions during such a task could help to ascertain which of these regions are necessary, rather than merely sufficient, for successful relational processing to occur.

In conclusion, here we report preliminary data suggesting that a right posterior P3a ERP waveform component may constitute an electrophysiological marker of relational complexity among directly trained and derived relations, with larger amplitudes associated with the more complex equivalence relations. This difference was observed in the absence of response latency differences, and may reflect the activity of a right hemisphere prefrontal-parietal circuit specialised for relational-type processing, though the results must be interpreted with caution given the small sample size. We believe this may constitute a tentative first demonstration of differences in brain electrophysiology in the transformation of stimulus functions through derived relations of hierarchical levels of complexity.

4. Experimental procedure

4.1. Participants

A convenience sample of 15 participants (5 male; age range 18-23 years; mean age=20.0 years) was recruited for this experiment. All participants were native English speaking, right-handed with normal or corrected-to-normal vision, and were free from any self-reported history of neurological disorders, brain injuries or family history of psychotic illness. Five participants (2 male) were excluded from the analysis due to failure to meet implicit training criterion (see Section 4.3.3). The remaining sample (n=10) fell within normal ranges for the National Adult Reading Test (Nelson, 1982) estimates of IQ (Full Scale IQ=112.3, Verbal IQ=110.5, Performance IQ=111.5). Participants were informed that they would be taking part in a study involving European brand products, about which they would be given the opportunity to learn. Each participant received 10 Euro on completion of the experiment. Written informed consent was obtained from all participants prior to the beginning of the study. Furthermore, all experimental work was conducted in accordance with the ethical standards set forth by the APA and the World Medical Association and was approved by the local ethics committee.

4.2. Implicit training tasks

4.2.1. Apparatus and stimuli

Two arbitrary shapes ($9.5 \text{ cm} \times 9.5 \text{ cm}$ in size; see Fig. 1) were employed to establish two contextual cues; 'Same' and 'Opposite', using a modified version of the 'Picture-Picture' paradigm (Levey and Martin, 1975; see Hughes, 2012,

unpublished data) during the contextual cue training phase of the experiment. For the relational training phase, six foreign brand names (Ciney, Witkap, Gageleer, Pardal, Zatte and Ettalas) were trained as two three-member stimulus equivalence classes (i.e. Ciney–Witkap–Gageleer and Pardal– Zatte–Ettalas; cf. Hughes, 2012, unpublished data). Five positively-valenced (appetitive) adjectives (delicious, fresh, tasty, sweet, yummy) and five negatively-valenced (aversive) adjectives (disgusting, stale, nasty, sick, rotten) were used in the function training phase and in the derivation task. All stimuli were presented in Visual Basic 2010. Participants were given access to a QWERTY keyboard for responses. Finally, explicit stimulus-rating scales were employed to obtain participants' ratings of the likeability of each of the brands.

4.3. Procedure

The study consisted of six distinct experimental stages: a control task (the National Adult Reading Test; Nelson, 1982), contextual cue training, relation training, function training, a derivation test (during which high-density EEG was recorded), and explicit stimulus ratings. The National Adult Reading Test was administered to ensure that participants were matched in terms of IQ (cf. Wang and Dymond, 2013; O'Hora et al., 2008).

4.3.1. Contextual cue training

During this phase, two contextual cues ('Same' and 'Opposite') were established by preferentially reinforcing the selection of one of two arbitrary stimuli (Fig. 1) in the presence of two pictures (9.5 cm \times 9.5 cm in size), in a desired context. Onscreen instructions prompted participants to "choose the symbol that describes the relationship between the two pictures at the top of the screen". The two arbitrary symbols appeared on screen in the bottom left-hand and right-hand corners, respectively (Fig. 1). Participants were instructed to press the 'D' key to select the symbol on the left or the 'K' key to select the symbol on the right. Selection of the correct contextual cue in a given trial was necessary for participants to progress to the next trial. Trials were separated by an intertrial-interval of 500 ms. When an incorrect response was made, participants were required to make the correct response in order to continue. Within each block of trials, the location of the 'Same' and 'Opposite' cues was varied between the bottom left- and right-hand sides of the screen. Once participants reached a level of 100% accuracy across 20 successive trials (of a possible 150 trials), they were exposed to a single test block to ensure that the cues had acquired the correct meaning, i.e. 'Same' and 'Opposite'. Correct responses were required on at least 80% of testing trials (24 in total) for participants to progress to the relational training phase.

4.3.2. Relational training

Once learned, the 'Same' and 'Opposite' cues were used to establish two three-member equivalence classes using brand names; Ciney-Same–Witkap-Same–Gageleer (i.e. A1–B1–C1) and Pardal-Same–Zatte-Same-Ettalas (A2–B2–C2); (cf. Hughes, 2012, unpublished data). Relational training consisted of three distinct phases: (i) AB relation training, (ii) BC relation training, and (iii) AB and BC relation training combined. The AC relation was not directly trained (i.e. Ciney-Same-Gageleer, CineyOpposite-Ettalas, Pardal-Same-Ettalas and Pardal-Opposite-Gageleer were not presented together) at any point during the training task. Each phase of relational training consisted of a maximum of three separate blocks of 50 trials. Participants were asked to learn about the series of brand names, using the two arbitrary symbols. During the first training phase (i.e. A-B), participants were instructed to learn about four of the six brands. Four relations were established by preferentially reinforcing the selection of the correct contextual cue in the presence of given stimulus pair (i.e. Ciney-Same-Witkap; Pardal-Same-Zatte; Witkap-Opposite-Pardal; Zatte-Opposite-Ciney). Participants were asked to "choose the symbol which describes the relationship between the two brand names at the top of the screen". For example, when A1-A2 or B1-B2 was presented, the selection of the 'Same' cue constituted a correct response and permitted progression to the next trial.

Conversely, when A1-B2 or A2-B1 was presented together, a correct response involved the selection of the 'Opposite' cue. Responses were made using the 'D' and 'K' keys on the keyboard, as before. When a correct response was made, the word 'correct' appeared at the bottom of the screen for 1000 ms, followed by a 1000 ms interval, before the task progressed to the next trial. When an incorrect response was made, participants were required to make the correct response to move on to the next trial. The location of the 'Same' and 'Opposite' cues was, again, varied between the bottom left- and bottom righthand sides of the screen within each block. The second training phase proceeded in a manner identical to the first, with the exception that four additional relations were established (A2-Same-A3; B2-Same-B3; A2-Opposite-B3; B2-Opposite-A3). In the third training phase, participants were re-exposed to the eight relations which had been established in phases one and two. In order to proceed from one training phase to the next, participants were required to meet a mastery criterion of twenty consecutive correct responses on each training (with corrective feedback) phase, followed by a minimum of 80% correct responses on each test phase. Participants who failed to reach this criterion (five in total) were thanked and debriefed, dismissed and their data omitted.

4.3.3. Function training

Following successful establishment of the two stimulus equivalence classes, a 'Positive/Negative' function (appetitive/ aversive) was generated, using a modified 'Picture-Picture' paradigm (Levey and Martin, 1975; cf. Hughes, 2012, unpublished data) once again. The positive function was established for A1 (Ciney) and the negative function established for B1 (Pardal). A single trial consisted of either A1 or B1, presented with one of ten adjectives (five appetitive, five aversive) at the top of the screen. As before, the two contextual cues appeared on the bottom half of the screen (Fig. 1). The relations 'A1-Same-Appetitive', 'A1-Opposite-Aversive', 'B1-Same-Aversive' and 'B1-Opposite-Appetitive' were established by preferential reinforcement of the correct contextual cue in the presence of given stimulus pairs. As before, participants were provided with corrective feedback on each trial, and the same mastery criterion used in the relational training phase was applied. Upon successful completion of function training, participants underwent EEG preparation before progressing to the derivation task.

4.3.4. Derivation task

Participants completed a derivation task in order to determine if the two stimulus equivalence classes were formed as predicted and also to determine if the functions established for Ciney and Pardal were transformed through Witkap and Pardal to Ettalas and Gageleer. Each trial presented one of the six brand names with either an appetitive or aversive adjective along with the two contextual cues (Levey and Martin, 1975; cf. Hughes, 2012, unpublished data). The derivation task consisted of three blocks, each containing 100 trials. Each brand was presented in the presence of each adjective on five occasions (2 brands \times 10 adjectives \times 5 trials \times 3 blocks = 300 trials). Participants were, again, asked to "choose the symbol which describes the relationship between the brand name and the adjective (descriptive word) on-screen". In the first block, only two of the brands (C1 and C2) were presented with the valenced adjectives (i.e. the equivalence relation). In the second block, two more of the brands (B1 and B2) were presented with the valenced adjectives (i.e. the symmetry relation). In the final block of trials, the remaining two brands (A1 and A2) were presented with the valenced adjectives (i.e. the directly trained relation). No feedback was provided for any response produced during the derivation task and the order of presentation of the three derivation test blocks was counter-balanced across participants, but failure to meet accuracy criteria resulted in 7 participants allocated to the C-B-A condition and 3 participants in the A-B-C condition.

4.3.5. Explicit stimulus ratings

In this phase of the experiment, participants were asked to rate how likeable the six brands were, using a series of 9-point Likert scales, which ranged from -4 (negative/not likeable) to +4 (positive/likeable), where zero denoted a neutral response. Participants were also asked to state the meaning they had ascribed to the two contextual cues at the beginning of the experiment (to ensure that the correct meanings had been established). Following completion of these ratings participants were fully debriefed, thanked for their participation, paid a sum of 10 euro and dismissed.

4.4. Electrophysiological recording

EEG activity was recorded from 128 silver/silver chloride electrodes (BrainVision[©]; BrainProducts GmbH, Germany) over the surface of the scalp mounted within an elastic cap fastened with a chin strap (Easy-Cap[©]), in accordance with the extended version of the International 10-20 system for electrode placement (American Encephalographic Society, 1994). Electro-conductive gel (Abralyt 2000; Easy-Cap[©]) was placed into the 128 electrode sites with a 10 ml flat-tipped syringe. The reference electrode was located on the nasion at the tip of the nose and four EOG electrodes were positioned around the eyes to record blinking. Two electrodes were placed at the external canthi of the eyes to record horizontal movements, and one on the inferior and superior ridges of the orbit of the left eye to record vertical movements. Blinks were averaged off-line and a blink reduction algorithm was applied to the data. This algorithm involved automatic artefact correction (Scherg and Berg, 1991; Ille et al., 2002).

The impedance level was kept to below $10 \text{ k}\Omega$ in all cases. The voltage differences between the 128-channel electrodes and the reference electrode were extracted as electrical waveforms, which were then amplified using a band-pass of 0.16-100 Hz and a gain of 1000. The conversion rate was 2000 Hz per channel and the range was 150 V. The amplifier used was supplied by BrainVision. Recordings were notch-filtered offline at 50 Hz. EEG data were digitised at a sampling rate of 500 Hz and were averaged offline using BESA software. After electrophysiological preparation, participants were seated approximately 50 cm from an LCD computer screen, on their own in a darkened, copper-plated shielded and sound attenuated testing cubicle, measuring $150 \text{ cm} \times 180 \text{ cm}$ with access to a mouse for responses. Participants were asked to keep movements to a minimum due to potential artifacts induced by blinks, facial and head movements.

4.5. Electrophysiological data processing

Epochs that exceeded the maximum amplitude of $50 \,\mu V$ were discarded from the analysis. Stimulus-locked average ERPs were created by averaging the EEG using stimulus presentation as the trigger. ERPs time-locked to the onset of the stimulus presentations were computed for each subject at all scalp sites, with epochs of -200 ms to 1000 ms. Three conditional ERPs were created based on stimulus presentation; directly trained, symmetry and equivalence relations. These three types of relation were compared across participants. Only correct responses were included in ERP analysis. ERP component structure was defined in an a priori manner with no prior knowledge of the pattern of effects the data may present. An overall grand-mean waveform was generated for each electrode by collapsing across all conditions. Visual inspection was used to identify the major components of interest in an a priori manner and BESA was used to conduct selected waveform analyses.

4.6. Statistical analyses

4.6.1. Behavioural data

The experiment employed a one-way repeated-measures ANOVA with three levels of the within-groups variable Type of relation: directly trained, symmetry and equivalence. Reaction Time (RT; in ms) constituted the primary dependent variable for all behavioural analyses. Bonferroni-corrected paired t-tests were carried out to examine behavioural differences between conditions on the derivation task. Accuracy data were used only to determine if the performance criteria were reached. Subject level percentage accuracy data are presented in Table 1.

4.6.2. Electrophysiological data

The electrophysiological paradigm comprised three independent variables: directly trained, symmetry and equivalence relations. The dependent variable was measured using mean amplitude. An overall grand mean waveform for each condition at each electrode was obtained and visual inspection identified the latency windows and electrode sites of interest. Electrode sites were chosen based on maximal activity in areas, and mean amplitude and/or latency data for each condition were recorded from these electrodes. The mean amplitude for Table 1 – Percentage correct responses to the relations present on each of the three test phases during which ERPs were recorded.

Participant number	% Correct	% Correct		
	A block (directly trained)	B block (symmetry)	C block (equivalence)	
1	91	91	92	
2	99	100	99	
3	92	97	99	
4	100	99	97	
5	99	100	88	
6	97	97	94	
7	99	99	100	
8	96	99	95	
9	96	98	98	
10	100	99	99	

Note: Table includes participants who met accuracy criteria on all phases of the training and testing only.

certain components was extracted and repeated-measures ANOVAs were conducted to compare conditions. Bonferronicorrected paired t-tests were employed to examine paired comparisons and elucidate results from the ANOVAs.

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REFERENCES

- Acuna, B.D., Eliassen, J.C., Donoghue, J.P., Sanes, J.N., 2002. Frontal and parietal lobe activation during transitive inference in humans. Cereb. Cortex 12 (12), 1312–1321.
- American Encephalographic Society, 1994. Guidelines for standard electrode position nomenclature. J. Clin. Neurophysiol. 11, 40–73.
- Augustson, K.G., Dougher, M.J., 1992. Teaching conditional discrimination to young children: some methodological successes and failures. Exp. Anal. Hum. Behav. Bull. 9, 21–24.
- Barbas, H., García-Cabezas, M.Á., Zikopoulos, B., 2013. Frontal-thalamic circuits associated with language. Brain Lang. 126 (1), 49–61.
- Barbey, A.K., Krueger, F., Grafman, J., 2009. Structured event complexes in the medial prefrontal cortex support counterfactual representations for future planning. Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci. 364 (1521), 1291–1300.
- Barnes, D., McCullagh, P.D., Keenan, M., 1990. Equivalence class formation in non-hearing impaired children and hearing impaired children. Anal. Verbal Behav. 8, 19–30.
- Barnes-Holmes, D., Regan, D., Barnes-Holmes, Y., Commins, S., Walsh, D., Stewart, I., Smeets, P.M., Whelan, R., Dymond, S., 2005. Relating derived relations as a model of analogical

reasoning reaction times and event-related potentials. J. Exp. Anal. Behav. 84 (3), 435–451.

- Bentall, R.P., Dickins, D.W., Fox, S.R.A., 1993. Naming and equivalence: response latencies for emergent relations. Q. J. Exp. Psychol. 46B, 187–214.
- Bentall, R.P., Jones, R.M., Dickins, D.W., 1999. Errors and response latencies as a function of nodal distance in 5-member equivalence classes. Psychol. Rec. 49, 93–115.
- Bickerton, D., 1990. Language and Species. University of Chicago Press, Chicago.
- Cabeza, R., Nyberg, L., 2000. Imaging cognition II: an empirical review of 275 PET and fMRI studies. J. Cogn. Neurosci. 12, 1–47.
- Coles, M.G.H., 1989. Modern mind-brain reading: psychophysiology, physiology, and cognition. Psychophysiology 26, 251–269.
- Damasio, A.R., 1998. Investigating the biology of consciousness. Philos. Trans. R. Soc. Lond – Ser. B: Biol. Sci. 353 (1377), 1879–1882.
- DeLisi, L.E., 2001. Speech disorder in schizophrenia: review of the literature and new study of the relation to uniquely human capacity for language. Schizophr. Bull. 27, 481–496.
- Devany, J.M., Hayes, S.C., Nelson, R.O., 1986. Equivalence class formation in language-able and language-disabled children. J. Exp. Anal. Behav. 46 (3), 243–257.
- Dickins, D.W., Singh, K.D., Roberts, N., Burns, P., Downes, J.J., Jimmieson, P., Bental, R.P., 2001. An fMRI study of stimulus equivalence. NeuroReport 12 (2), 405–411.
- Duhamel, J., Bremmer, F., BenHamed, S., Graf, W., 1997. Spatial invariance of visual receptive fields in parietal cortex neurons. Nature 389, 845–848.
- Duncan-Johnson, C.C., Donchin, E., 1977. On quantifying surprise: the variation in event-related potentials with subjective probability. Psychophysiology 14, 456–467.
- Dymond, S., Rehfeldt, R., 2000. Understanding complex behaviour: the transformation of stimulus functions. Behav. Anal. 23, 239–254.
- Dymond, S., Roche, B., Barnes-Holmes, D., 2003. The continuity strategy, human behavior, and behavior analysis. Psychol. Record 53, 333–347.
- Eimer, M., 1996. The N2pc as an indicator of attentional selectivity. Electroencephalogr. Clin. Neurophysiol. 99 (3), 225–234.
- Fields, L., Adams, B.J., Verhave, T., Newman, S., 1990. The effects of nodality on the formation of equivalence classes. J. Exp. Anal. Behav. 53 (3), 345–358.
- Fuster, J.M., 1997. The Prefrontal Cortex-Anatomy Physiology and Neuropsychology of the Frontal Lobe, third ed. Lippincott-Raven, Philadelphia.
- Fuster, J.M., 2002. Frontal lobe and cognitive development. J. Neurocytol. 31 (3–5), 373–385.

- Garavan, H., Ross, T.J., Murphy, K., Roche, R.A., Stein, E.A., 2002. Dissociable executive functions in the dynamic control of behavior: inhibition, error detection, and correction. NeuroImage 17, 1820–1829.
- Goel, V., Dolan, R.J., 2001. Functional neuroanatomy of humor: segregating cognitive & affective components. Nat. Neurosci. 4 (3), 237–238.
- Goldman-Rakic, P.S., 1990. Cellular and circuit basis of working memory in prefrontal cortex of nonhuman primates. Prog. Brain Res. 85, 325–335.
- Haimson, B., Wilkinson, K.M., Rosenquist, C., Ouimet, C., McIlvane, W.J., 2009. Electrophysiological correlates of stimulus equivalence processes. J. Exp. Anal. Behav. 92, 245–256.
- Hallez, H., Vanrumste, B., Grech, R., Muscat, J., De Clercq, W., Vergult, A., D'Asseler, Y., Camilleri, K.P., Fabri, S.G., Van Huffel, S., Lemahieu, I., 2007. Review on solving the forward problem in EEG source analysis. J. Neuroeng. Rehabil. 4, 46.
- Hillyard, S.A., Münte, T.F., 1984. Selective attention to color and location: an analysis with event-related brain potentials. Percept. Psychophys. 36, 185–198.
- Hinton, E.C., Dymond, S., von Hecker, U., Evans, C.J., 2010. Neural correlates of relational reasoning and the symbolic distance effect: involvement of parietal cortex. Neuroscience 168 (1), 138–148.
- Hoshi, E., Tanji, J., 2004. Area-selective neuronal activity in the dorsolateral prefrontal cortex for information retrieval and action planning. J. Neurophysiol. 91, 2707–2722.
- Hughes, S., 2012. Why We Like What We Like: A Functional Approach to the Study of Human Evaluative Responding. National University of Ireland, Maynooth, County Kildare, Ireland (unpublished doctoral dissertation).
- Hughes, S., Barnes-Holmes, D., Vahey, N., 2012. Holding on to our functional roots when exploring new intellectual islands: a voyage through implicit cognition research. J. Context. Behav. Sci. 1 (1–2), 17–38.
- Ille, N., Patrick, B., Scherg, M., 2002. Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. J. Clin. Neurophysiol. 19 (2), 113–124.
- Kutas, M., Hillyard, S.A., 1980. Reading senseless sentences: brain potentials reflect semantic incongruity. Science 207, 203–208.
- Levey, A.B., Martin, I., 1975. Classical conditioning of human "evaluation" responses. Behav. Res. Therapy 13, 221–226.
- Luck, S.J., Hillyard, S.A., 1994. Spatial filtering during visual search: evidence from human electrophysiology. J. Exp. Psychol.: Hum. Percept. Perform. 20 (5), 1000–1014.
- Manly, T., Datta, A., Heutink, J., Hawkins, K., Cusack, R., Rorden, C., Robertson, I.H., 2000. An electrophysiological predictor of imminent action error in humans. J. Cogn. Neurosci. 21E (Suppl), S111.
- McNamara, T.P., 2005. Semantic Priming: Perspectives from Memory and Word Recognition. Psychology Press, New York. Mushiake, H., Saito, N., Sakamoto, K., Itoyma, Y., Tanji, J., 2006.
- Activity in the lateral prefrontal cortex reflects multiple steps of future events in action plans. Neuron 50, 631–641.
- Nelson, H.E., 1982. National Adult Heading Test (NART): Test Manual. NFER-Nelson, Windsor.
- Ogawa, K., Abe, T., Nittono, H., Yamazaki, K., Hori, T., 2010. Phasic brain activity related to the onset of rapid eye movements during rapid eye movement sleep: study of event-related potentials and standardized low-resolution brain electromagnetic tomography. J. Sleep Res. 19, 407–414.
- O'Hora, D., Pelaez, M., Barnes-Holmes, D., Rae, G., Robinson, K., Chaudhary, T., 2008. Temporal relations and intelligence: correlating relational performance with performance on the WAIS-III. Psychol. Record 58, 569–584.
- O'Hora, D., Roche, B., Barnes-Holmes, D., Smeets, P.M., 2002. Response latencies to multiple derived stimulus relations:

testing two predictions of relational frame theory. Psychol. Record 52, 51–75.

- Osherson, D., Perani, D., Cappa, S., Schnur, T., Grassi, F., Fazio, F., 1998. Distinct brain loci in deductive versus probabilistic reasoning. Neuropsychologia 36, 369–376.
- Paz-Caballero, M.D., García-Austt, E., 1992. ERP components related to stimulus selection processes. Electroencephalogr. Clin. Neurophysiol. 82 (5), 369–376.
- Pinel, P., Dehaene, S., Riviere, D., LeBihan, D., 2001. Modulation of parietal activation by semantic distance in a number comparison task. Neuroimage 14, 1013–1026.

Polich, J., 2003. Overview of P3a and P3b. In: Polich, J. (Ed.), Detection of Change: Event-related Potential and fMRI Findings. Kluwer, Boston, MA.

- Polich, J., 2007. Updating P300: an integrative theory of P3a and P3b. Clin. Neurophysiol. 118 (10), 2128–2148.
- Posner, M.I., Petersen, S.E., 1990. The attention system of the human brain. Annu. Rev. Neurosci. 13, 25–42.
- Quintana, J., Fuster, J.M., 1992. Mnemonic and predictive functions of cortical units in a memory task. NeuroReport 3, 721–724.
- Ritter, W., Simson, R., Vaughan, H.G., 1983. Event-related potential correlates of two stages of information processing in physical and semantic discrimination tasks. Psychophysiology 20, 168–179.
- Ritter, W., Simson, R., Vaughan, H.G., Macht, M., 1982. Manipulation of event-related potential manifestations of information processing stages. Science 218, 909–911.
- Roland, P.E., Friberg, L., 1985. Localization in cortical areas activated by thinking. J. Neurophysiol. 53, 1219–1243.
- Rushworth, M., Nixon, P.D., Eacott, M.J., Passingham, R.E., 1997. Ventral prefrontal cortex is not essential for working memory. J. Neurosci. 17, 4829–4838.
- Scherg, M., Berg, P., 1991. New concepts of brain source imaging and localization. Electroencephalogr. Clin. Neurophysiol. 42, 24–37.
- Schlund, M.W., Cataldo, M.F., Hoehn-Saric, R., 2008. Neural correlates of derived relational responding on tests of stimulus equivalence. Behav. Brain Funct. 4 (6), 1–8.
- Schlund, M.W., Hoehn-Saric, R., Cataldo, M.F., 2007. New knowledge derived from learned knowledge: functional-anatomic correlates of stimulus equivalence. J. Exp. Anal. Behav. 87, 287–307.
- Sidman, M., 1971. Reading and auditory-visual equivalences. J. Speech Hear. Res. 14, 5–13.

Sidman, M., 1994. Equivalence Relations and Behavior: A Research Story. Authors Cooperative, Boston.

- Soltani, M., Knight, R.T., 2000. Neural origins of the P300. Crit. Rev. Neurobiol. 14 (3–4), 199–224.
- Steele, D.L., Hayes, S.C., 1991. Stimulus equivalence and arbitrarily applicable relational responding. J. Exp. Anal. Behav. 56, 519–555.
- Verleger, R., 1997. On the utility of P3 latency as an index of mental chronometry. Psychophysiology 34, 131–156.
- Verleger, R., Jakowskis, P., Wascher, E., 2005. Evidence for an integrative role of P3b in linking reaction to perception. J. Psychophysiol. 19, 165–181.
- Walsh, V., 2003. A theory of magnitude: common cortical metrics of time, space and quantity. Trends Cogn. Sci. 7 (11), 483–488.
- Wang, T., Dymond, S., 2013. Event-related potential correlates of emergent inference in human arbitrary relational learning. Behav. Brain Res. 236, 332–343.
- Wood, C.C., 1982. Application of dipole localization methods to source identification of human evoked potentials. Ann. N. Y. Acad. Sci. 388, 139–155.
- Yorio, A., Tabullo, Á., Wainselboim, A., Barttfeld, P., Segura, E., 2008. Event-related potential correlates of perceptual and functional categories: comparison between stimuli matching by identity and equivalence. Neurosci. Lett. 443, 113–118.