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Category structure and the two learning systems of COVIS

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Abstract:

An influential multi-process model of category learning, COVIS, suggests that a verbal or a procedural category learning process is adopted, depending on the nature of the learning problem. While the architectural assumptions of COVIS have been widely supported, there is still uncertainty regarding the types of category structures that are likely to engage each of the COVIS systems. We examined COVIS in an fMRI study with two novel (in terms of COVIS research) categorizations. One of the categorizations could be described by a simple, unidimensional, rule that was expected to favor the verbal system. The other categorization possessed characteristics typically associated with the procedural system, but could also potentially be verbalized using a rule more complex than the ones previously associated with the verbal system. We found that both categorizations engaged regions associated with the verbal system. Additionally, for both categorizations, frontal lobe regions (including left ventrolateral frontal cortex) were more engaged in the first compared to the second session, possibly reflecting the greater use of hypothesis-testing processes in the initial stages of category acquisition. In sum, our results extend our knowledge of the conditions under which the verbal system will operate. These findings indicate that much remains to be understood concerning the precise interplay of the verbal and procedural categorization systems.

In recent years, the idea that categorization involves multiple systems has become increasingly popular. Perhaps the most influential multi-process account is COVIS (COmpetition between Verbal and Implicit Systems; Ashby et al., 1998). According to COVIS, category learning proceeds either through the development of an explicit, verbal rule (cf., Smith et al., 1998) or procedurally through the gradual association of exemplars with category labels (Squire, 1982).

In the verbal system, rules are hypothesized to arise through an explicit hypothesistesting procedure: guesses are made, and evaluated, for how the observed stimuli are categorized. The verbal system is supported primarily by the prefrontal cortex, anterior cingulate, and the head of the caudate nucleus. By contrast, in the procedural system, information from multiple dimensions is integrated pre-decisionally (Maddox & Ashby, 2004) and the knowledge acquired is difficult to verbalize. The procedural system involves inferotemporal cortex, the tail of the caudate nucleus and the nigrostriatal dopamine pathway (Maddox & Ashby, 2004). COVIS has benefited from extensive support not only in neuroscience studies (Nomura et al., 2007), but also in experimental ones (e.g., Ashby & Maddox, 2005).

A key issue to the further specification of COVIS concerns the conditions under which each system operates. The original COVIS proposal by Ashby et al. (1998) has been relatively uncommitting on this front. Ashby et al. (1998, p. 442) state that: "COVIS assumes that the verbal system initially dominates, presumably because it is controlled by consciousness." A further assumption is that the verbal system will operate to the extent that the categorization can be represented by a simple, verbal rule and that the procedural and verbal systems are in competition with each other: the system that provides more accurate

category responses eventually dominates. Ashby et al. also note that complicated rules are less salient than simple rules and consequently, the verbal system will rarely select such a rule. Previous research has shown that unidimensional and conjunctive rules are simple enough to engage the verbal system (Filoteo, Lauritzen, & Maddox, 2010; Nomura et al., 2007); a critical question, however, is whether more complex rules would also engage the verbal system, or, alternatively, require the procedural system.

Using fMRI, we investigate this by examining a novel category structure, which contains many of the properties associated with the procedural system (see Method), but has a complex rule that can, in principle, be verbalized. The extent to which this novel category structure activates regions associated with the verbal system or alternatively regions associated with the procedural system, will provide insight into the boundary conditions of the verbal system.

We also investigated whether neural processes differ between the acquisition of novel categories and the application of the same categories when the structure has been learnt. Previous imaging studies have typically focused on category acquisition and neglected the application of already learnt categories (but see Koenig et al., 2005; Poldrack et al., 2001). However, this is a key issue, as it informs our understanding of processes relating to category learning versus category representation.

Materials and Methods

Participants

26 right-handed participants from the University of Exeter, aged 18-35, were recruited. Participants received course credits or £10 on completion of the study. There were 13 participants in each of two between-subject conditions. Participants all gave informed consent according to procedures approved by the Psychology Ethics Committee, University of Exeter.

Stimuli

We employed stimuli varying along two dimensions of physical variation, so that the two dimensions could be seen as cohering together to give the impression of a single entity, without analytic processing (see Figure 1; cf., Milton & Wills, 2004, 2009; Pothos & Close, 2008). Equally, participants would ideally be able to perceive changes in one dimension of variation independently of changes in the other (that is, the two dimensions should be separable). For similar reasons, the dimensions were in different colors (as displayed in Figure 1) so that participants could, from the beginning of the experiment, detect that there were two independent dimensions. In addition, the stimuli were not related in any obvious way to exemplars from a real-world category in order to avoid any contamination of the categorization process by general knowledge. The two dimensions of physical variation were the height of the rectangle and the width of the ellipse. With both these dimensions we can assume a Weber fraction of 10% (Morgan, 2005). The ellipse varied in width between 32mm and 112.6mm and the rectangle varied in height between 35mm and 123.1mm. The visual angle of the stimuli varied between approximately 4° and 8.5°.

The categorizations presented in Figure 2 extend previous related research with the COVIS model. First, they involve three categories instead of two. This is important because, when learning two categories, the cognitive system could conceivably learn one category and then classify all other instances as not members of the first category. The use of three categories avoids this potential interpretative complication. Second, the Figure 2 categorizations involve a relatively small number of training exemplars, which were presented multiple times during training. This is characteristic of the majority of categorization paradigms (e.g., Medin & Schaffer, 1978; Shepard, Hovland, & Jenkins, 1961) that have been employed in non-neuroscience studies. However, this is in contrast to most previous COVIS related studies, which typically use dozens of unique stimuli (but see Waldron & Ashby, 2001). Even if one believes that greater numbers of stimuli ultimately provide a more ecologically valid examination of human categorization processes, the above difference is a major issue in trying to understand the bulk of standard categorization research in terms of COVIS. We therefore used a limited number of perceptually similar stimuli and presented them multiple times (as in many categorization paradigms, cf., Medin & Schaffer, 1978).

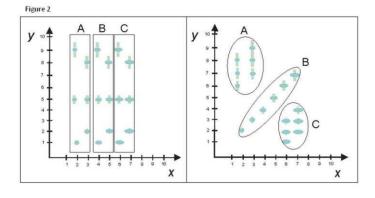
The category structure presented in the left panel of Figure 2 can be described by a simple unidimensional rule (the Simple condition) - items with a narrow ellipse go in category A, items with an intermediate ellipse go in category B, and items with a wide ellipse go in category C. The logical form of this categorization closely resembles that of rule-based categorizations that have typically been employed in other COVIS research (cf.,

Maddox et al., 2004; Nomura et al., 2007), which indicates that this categorization should be learnable by the verbal system.

The categorization presented in the right panel has been designed to be more complex and it will be referred to as such. Unlike the Simple condition, this category structure has not previously been used in COVIS related research. Whilst this is a category structure that seems to have many characteristics that favor the procedural system, one could equally argue that it would engage the verbal system instead. For example, the decision boundary separating the categories is diagonal and requires integrating information from both dimensions x and y. Furthermore, there is also no simple rule available. These factors are believed to make activation of the procedural system more likely (e.g., Nosofsky, Palmeri, & McKinley, 2005). On the other hand, whilst any verbal rule would have to be very complicated, as it would require multiple decision bounds, it is, in principle, possible to develop such a rule. For instance, one potential rule (but perhaps not the only possibility) would be that items that have a tall rectangle and a narrow ellipse go in Category A, items that have a wide ellipse and a short rectangle go in Category C, items that have both a wide ellipse and a relatively tall rectangle go in Category B, and the remaining items also go in Category B. In previous COVIS related work, the tested category structures which were meant to engage the verbal system have all involved rules (e.g., unidimensional, conjunctive or disjunctive rules, cf., Ashby & Maddox, 2005), which were much simpler than any multi-component rule that can be used to describe our Complex category structure. Nevertheless, Ashby et al. (1998) did not commit themselves regarding the possible complexity of the rules that participants can spontaneously generate, so it is plausible that more complicated rules than those previously tested could also engage the verbal system.

As such, examining a novel category structure that contains a rule more difficult to verbalize than has previously been shown to engage the verbal system should provide insight into the conditions under which this system operates.

Note that, even though there is a strong intuition that the Simple categorization would be easier to learn than the Complex one, we also assessed this pre-experimentally on the basis of the Simplicity model of categorization, whose purpose is to predict people's spontaneous impression of different classifications, on the basis of putative representations of the stimuli (Pothos & Chater, 2002; Pothos & Close, 2008; Pothos & Bailey, 2009). The simplicity model provides a quantitative measure of how intuitive different classifications are. The calculation is based on three terms. First, it is based on the information content of the similarity relations between a set of stimuli, D; this depends simply on the number of relations. The second term is the information content of the similarity relations given some categories, D|C; this term will be lower if the categories are such that within category similarities are generally greater than between category similarities (this is a standard intuition in categorization; e.g., Rosch & Mervis, 1975). Finally, the third term, C, is the informational complexity of specifying the categorization itself. Thus, according to the simplicity model categories are interpreted as hypotheses for the similarity structure of a set of stimuli. Given the above terms, we can apply a standard minimum description length framework (Rissanen, 1978) and select as most intuitive the categorization for which D -(D | C + C). In practice, predictions of the model are expressed as a percentage codelength, which reflects the informational saving of using categories. This is computed as $\{(D|C+C)\}/$ D, so that the lower it is, the more intuitive the corresponding categorization is predicted to be.



Participants might attempt to solve the Simple/ Complex categorization tasks by focusing on either of the two stimulus dimensions, or both dimensions. Regarding the Complex classification, the codelength for the categorization using both dimensions was 76.2% and using only one dimension 84.9% (on average). Thus, the a priori prediction is that this classification is a little bit more intuitive using both dimensions but, in both cases, the classification is relatively unintuitive. Regarding the Simple classification, the codelength on the basis of both dimensions was 98.4% and on the basis of the ellipses dimension only 58.6%. In this case, the prior prediction is that the required classification should be easy to learn if one considers only the ellipses dimension and ignores the rectangle dimension (cf. Ashby, Queller, & Berretty, 1999).

In summary, the main objective of employing the simplicity model is to have some a priori confidence regarding the most likely strategy for the two category structures we employed. The application of the simplicity model shows that, for the Simple category structure, it is much more intuitive to group the stimuli on the basis of one dimension than on the basis of both dimensions. By contrast, for the Complex category structure, the simplicity model prediction was that categorizing on the basis of both dimensions would be slightly more intuitive than categorizing on the basis of just one dimension. Since the stimuli were created in a way that the two dimensions were fairly well integrated with each other (though still perceptually separable) we therefore anticipated that categorization of the Complex category structure would be multidimensional (cf., Milton, Wills, & Hodgson, 2009).

fMRI Image acquisition

Images were collected using a 1.5-T Phillips Gyroscan magnet, equipped with a Sense coil. A T2*-weighted echo planar sequence was used (TR = 3000ms, TE = 45ms, flip angle = 90°, 32 transverse slices, $3.5 \times 2.5 \times 2.5$ mm). Participants completed two scanning sessions. In both sessions, 210 scans were acquired in each of the three runs per subject. An additional 5 "dummy" scans were performed before each run prior to the start of the stimulus sequence. Standard volumetric anatomical MRI was performed after functional scanning by using a 3-D T1-weighted pulse sequence (TR = 25ms, TE = 4.1ms, flip angle = 30° , 160 axial slices, $1.6 \times 0.9 \times 0.9$ mm).

Procedure

Participants were randomly assigned to either the Simple or Complex condition. Each condition involved two scanning sessions, run on separate days. Both sessions had an identical procedure. Visual stimuli were presented on a back-projection screen positioned at the foot end of the MRI scanner and viewed via a mirror mounted on a head coil. Button-press responses and reaction times were measured using two fiber-optic button boxes held in the participants' right and left hands. E-Prime (PST, 2002) was used for the presentation and timing of stimuli and collection of response data.

The current study employed an event-related design. Trials began with a blank screen lasting a random interval between 250ms- 3750ms, followed by a black fixation cross for 150ms. A stimulus from the set (Figure 2) then appeared in the middle of the screen for 2500ms. During this time, participants classified the stimulus into category A, category B, or category C by pressing the appropriate response button (the response buttons corresponding to each category were fixed, with categories A and B recorded with the response box in the left hand and category C recorded with the response box in the right hand). The stimulus remained on the screen for the whole 2500ms, regardless of when participants responded, in order to control for the perceptual characteristics of the trials across conditions and blocks. This was followed by feedback ("Correct", "Incorrect") lasting 1000ms. If participants did not respond in time, a message saying "Time out!!! Please respond quicker" appeared during this interval.

In both sessions, participants were presented with a total of 324 trials in nine blocks of 36 stimuli. In each block, all 18 stimuli in the set were presented twice in a random order. At the end of a block there was a break of 12 seconds during which time participants were informed of their accuracy in that block and told to take a break. A message then appeared for 1000ms telling participants to "Get ready to start the next block". Sessions were divided into three runs, each lasting 630 seconds, with 3 blocks presented in each run.

Analysis of fMRI data

Data analysis was carried out using the SPM5 software (www.fil.ion.ucl.ac.uk/spm). Functional images were corrected for acquisition order, realigned to the first volume and resliced to correct for motion artifacts. After realignment, spatial normalization was immediately performed. This involved coregistering a mean image created from the

realigned images to the structural T1 volume. From there, the images were then spatially normalized into the stereotactic space of the Montreal Neurological Institute (MNI). The spatial transformation was applied to the realigned T2* volumes that were spatially smoothed using a Gaussian kernel of 8mm full-width half maximum. Data were high-pass filtered (128s) to account for low frequency drifts. The BOLD response was modeled by a canonical hemodynamic response function (HRF) and the six head movement parameters were included as covariates. First-level linear contrasts of parameter estimates for each voxel were taken to the second-level and a random effects analysis was performed.

The regions correlated with successful categorization were identified by contrasting correct to incorrect responses within a session (as in, for example, Nomura et al., 2007). This baseline has the advantage of controlling the perceptual properties of the stimuli, motoric responses, and general task demands. One potential disadvantage of this approach, however, is that due to the nature of the canonical HRF, processing of feedback which, according to COVIS, differs between correct and incorrect trials may have been partly included in the signal, which could complicate interpretation of the results. To supplement our principle comparisons, we also analysed the data using a different baseline which contrasted correct responses to the interval between trials. At the second-level, data was analyzed using a category structure (Simple, Complex) x session (session 1, session 2) factorial design. A whole-brain analysis using a statistical threshold of p <.001 (uncorrected) and a voxel cluster threshold size of 10 were used for all analyses. In other words, only clusters where at least ten contiguous voxels each reached the threshold of p<.001 were considered significant. Monte Carlo simulations have shown that the combination of both statistical and cluster thresholds is an effective way to help safeguard against false positives

whilst ensuring sensitivity to detect genuine activity (e.g., Forman et al., 1995). For the Complex – Simple contrast we also conducted a Region of Interest (ROI) analysis (p<.01, uncorrected), using the WFU Pickatlas (Maldjian, Laurienti, Burdette, & Kraft, 2003), comprising the tail and body of the caudate nucleus together with the substantia nigra as these areas have been previously implicated in the procedural system (Ashby et al., 1998; Nomura et al., 2007).

In addition, a conjunction analysis was performed to explore the common activation between the Simple and Complex groups. This involved contrasting correct Simple responses to incorrect Simple responses and correct Complex responses to incorrect Complex responses. These contrasts were then combined using a logical "And" function via the minimum statistic to the conjunction null hypothesis (MS/CN; Nichols et al., 2005). This means the analysis revealed only those regions significantly activated for both the Simple categorization AND those activated for the Complex categorization. Both tests were thresholded at p<.001 with a cluster threshold of 10. Coordinates were transformed from normalized MNI space to Talairach space

(http://imaging.mrccbu.cam.ac.uk/imaging/MniTalairach) to establish the site of activation in relation to the atlas of Talairach and Tournoux (1988).

Results

Behavioral analysis

Mean accuracy for the Simple and Complex groups across the training blocks are shown in Figure 3. A mixed design ANOVA (collapsed across session) revealed a significant effect of block, F(17,408) =31.12, p < .0001, η_p^2 = .57, indicating higher accuracy as the task

progressed. There was a significant interaction between block and category structure, F(17,408) = 3.20, p = .022, $\eta^2_{p} = .12$, suggesting that participants in the Simple condition were less accurate than those in the Complex condition in the first block, but afterwards the learning curve for participants in the Simple condition rises more sharply and reaches the asymptote faster than for participants in the Complex condition. There was, however, no difference in accuracy across sessions between the Simple and Complex groups, F(1,24) =.004, p = .95, $\eta^2_p < .001$.

-----FIGURE 3-----FIGURE 3------

Modeling analysis

In order to acquire some insight into the classification strategies adopted by participants, we applied the Unsupervised Generalized Context Model (UGCM; Pothos & Bailey, 2009; Pothos et al., in press). The UGCM has been developed from the GCM (Nosofksy, 1984) and has been widely employed to study the psychology of categorization. Both the UGCM and the GCM cannot directly tell us whether the verbal or the procedural systems were engaged by participants (although given the potential flexibility of the verbal system this is ultimately a problem for all model-based approaches, which is why neuroscience methods have dominated the relevant debate). However, the UGCM can tell us whether participants are more likely to be categorizing on the basis of both stimulus dimensions or just one stimulus dimension. There are two ways in which this information is useful. First, it allows us to establish whether participants performed the categorization task in the way they were intended to. Second, on the basis of existing COVIS work, a categorization on the basis of a single dimension is likely to indicate activation of the verbal system whilst categorization on the basis of both dimensions may engage the procedural system (although please note

again the qualifications regarding the development of complex rules we noted above). The advantage of employing the UGCM in this context is that exactly the same model with the same number of parameters can be used for both the Simple and the Complex categorizations.

For each participant, we considered his/ her responses during the first three blocks in Session 1 (i.e., the first scanning run) and (separately) in the last three blocks of session 2 (i.e., the last scanning run). These responses allowed us to infer the categorization participants were using at those particular times in testing. We achieved this through a simple majority rule, resolving any ties (which were rare) with the flip of a coin. For example, suppose that in Session 1 one participant classified the first stimulus four times in Category A and twice in Category B, we would consider this stimulus as a Category A member. Given a particular classification for a set of stimuli, the UGCM can then be applied to infer the attentional weights participants are likely to be employing. We applied the UGCM with a procedure nearly identical to that of Pothos and Bailey (2009). The form of the similarity function was allowed to vary between exponential and Gaussian, the Minkowski power metric between City Block and Euclidean, and the category biases between 0 and 1, subject to the constraint that they summed to 1. All these parameters are essential to ensure that the UGCM is applied properly, but our previous research indicates that they are not particularly significant. By contrast, this is not the case for the sensitivity parameter and the attentional bias parameters. In brief, the sensitivity parameter can have considerable impact on UGCM predictions and, moreover, it affects the values of the other parameters as well. Therefore, we carried out our analyses across a range of suitable upper limits for the sensitivity parameter (0.01, 0.1, 1, 5, 10), noting that typically the value of the

sensitivity parameter identified by optimization is its upper limit. Finally, for each classification, optimization involved 1000 iterations of the UGCM with random starting values for its parameters.

We averaged the attentional weight for the dominant dimension across participants for Session 1 and Session 2, for the Simple and Complex conditions separately (we considered the dominant dimension, rather than the optimal dimension for the Simple category structure, since the verbal system would be activated even when participants are employing incorrect rules). Note that the relative attentional weighting of the two dimensions is not expected to be exactly equal in the Complex condition, even when participants have perfectly learned the required categorization. This is because it is natural that different participants will perceive the relative salience of the two dimensions differently. But, the UGCM results can still inform the extent to which the categorizations participants are inferring from the stimuli are consistent with the unidimensional or multidimensional strategies. In brief, the evidence from the UGCM suggests this to be the case. Participants in the Complex condition had a significantly greater spread of attention across the two dimensions than those in the Simple condition (for all simulations p <.01 except when the sensitivity parameter was at 0.01; but note the validity of UGCM results with such a low value is unclear). These model-based analyses confirmed our reasonable expectations given the category structures we employed.

We can next examine whether there were any participants deviating from this average pattern of results (and so perhaps adopting classification strategies which were not intended, although as discussed this implies little regarding the processing system used). Some care is needed here, since, as noted, there are some unresolved issues regarding the most appropriate limit for the sensitivity parameter. We did not consider the results for an upper limit for the sensitivity parameter of 0.01 (see above). Regarding results with other values for the upper limit of the sensitivity parameter, we employed two criteria for identifying participants for whom there was evidence of adopting a categorization strategy that differed to the intended one. First, for the Simple condition, we looked at participants for whom the weight for the dominant dimension decreased from Session 1 to Session 2, since if participants were adopting the intended unidimensional strategy this weight ought to be increasing (and vice versa for the Complex condition). However, a decrease for the weight of the dominant dimension from 0.95 to 0.90 does not necessarily indicate a shift to a multidimensional strategy (it could just reflect minor attentional adjustments without a change in strategy). Therefore, the second criterion for identifying problematic participants in the Simple condition was that the weight for the dominant dimension in Session 2 would be less than 0.75 (and vice versa for the Complex condition). Looking at the results of this analysis for different values for the sensitivity parameter, in the Simple condition there were no problematic participants. For the Complex condition, depending on the upper limit of the sensitivity parameter, there would be as few as one problematic participant and as many as six. The greater (on average) number of problematic participants in the Complex condition is hardly surprising, given that it was more difficult to develop a rule for this categorization (and this could potentially indicate that participants in the Complex condition experimented a bit more with the possible strategies). While it should be clear that our modelling approach based on UGCM attentional weights requires some further development, it still enables two clear conclusions. First, participants in the Simple condition uniformly behaved as intended. Second, whilst participants in the Complex condition had a significantly greater spread of attention across the two dimensions than in the Simple condition, there was more variability in the precise strategy used for the Complex categorization. This perhaps

indicates more 'frontal' processing, in which participants were experimenting with different strategies (i.e., indicating use of the RB system). As it turns out, the fMRI results support this assumption.

Imaging analysis

Activation for the Simple condition (Table 1; Figure 4a), across both sessions, revealed an extensive pattern of activation including the left superior frontal gyrus (BA 8 and 10), right middle frontal gyrus (BA 10), left precentral gyrus (BA 6), the parahippocampal gyrus, and the posterior cingulate (BA 30). The Complex category structure, analysed across both sessions, evoked a similar pattern of activation (Table 2; Figure 4b). Specifically, we observed activation in bilateral medial frontal gyrus (BA 10), right superior frontal gyrus (BA 8), left inferior frontal gyrus (BA 45), bilateral precentral gyrus (BA 6) the left hippocampus and bilateral parahippocampal gyrus, and the posterior cingulate (BA 30).¹ The striking overlap between these conditions is demonstrated by a conjunction analysis which revealed extensive common activation between the two category structures (Figure 4c). Supplementary Figure 1 shows the same three analyses contrasted against the interval between trials (rather than against incorrect trials). Aside from the increased engagement of visual and motor areas the broad conclusions remain unchanged with both conditions engaging regions of the frontal lobe (albeit slightly reduced in scope, which may reflect task preparation and hypothesis generation processes that take place during this interval between trials).

-----FIGURE 4, TABLES 1 and 2-----

A second level analysis based on a category structure (Simple, Complex) x session (session 1, session 2) factorial design was conducted. No regions were significantly more activated for the Simple group than the Complex one. Comparing the Complex group to the Simple group produced one small cluster located in the left frontal lobe (Table 2; Figure 4d). In supplementary analyses, however, when the Complex and Simple conditions were contrasted against the interval between trials at the individual subject level (rather than against incorrect trials) there were no differences between conditions. For the Complex – Simple contrast, we also conducted an ROI analysis (p<.01, uncorrected) comprising the tail of the caudate nucleus and the substantia nigra, on the basis that these areas are involved in the procedural system (e.g., Ashby et al., 1998), together with the caudate body which was activated by an information-integration category structure in Nomura et al. (2007). This analysis, however, also failed to produce any significant activation (this was also the case when the interval between trials was used as the baseline at the individual subject level). Lastly, we focused on the right caudate body region that was identified by Nomura et al. (2007, their Figure 4) as producing greater activation in the information integration than the rule-based categorization (x = 17, y = -11, z = 28). For the peak voxel, the differential activation for successful categorization between the Complex and the Simple categorization was non-significant, t(24) = 1.20, p > .2, d = .47, and in the direction of greater activation for the Simple categorization.

Turning to the effect of session, a contrast analysis revealed that Session 1 relative to Session 2 (Figure 5a; Table 3) resulted in greater activation in the right insula (BA 13), the left ventrolateral frontal cortex (VLFC; BA 47), the right thalamus, and the left inferior temporal lobe/fusiform gyrus (BA 37). In contrast, the Session 2 – Session 1 comparison elicited no significant activation.

------ FIGURE 5, TABLE 3 ------

Further analyses, assessing the interaction between group and session, were performed. Simple activation in Session 1 compared to Simple activation in Session 2 (Table 4; Figure 5b) produced significant activation in the right frontal lobe (BA 6) and the right insula (BA 13). The Complex Session 1 – Complex Session 2 comparison (Table 4; Figure 5c) elicited activation in the bilateral VLFC (BA 47), the left insula (BA 13), the right thalamus, and the left temporal lobe (BA 21).

----- TABLE 4------

For the Simple condition participants, contrasting activation in Session 2 to Session 1 (Table 4; Figure 6a) revealed activation in the left superior frontal gyrus (BA 9), and left medial frontal gyrus (BA 10). The Complex group (Table 4; Figure 6b) produced greater activation in Session 2 than in Session 1 in the left frontal lobe, the right precentral gyrus (BA 6), and the anterior portion of the right caudate body, close to the anterior cingulate.

-----FIGURE 6-----FIGURE 6-----

Discussion

This study revealed that both the Simple and Complex categorization conditions recruited a number of common regions including the left medial frontal gyrus (BA 10), the left superior frontal gyrus (BA 8), and the right superior frontal gyrus/paracentral lobule (BA 6). These regions are involved in executive functioning and have previously been identified as components in the verbal system of COVIS (e.g., Nomura et al., 2007). Related to this, the left superior frontal gyrus has also been shown to be more engaged for deterministic rules than probabilistic classifications (Seger & Cincotta, 2005). Additionally, similar frontal regions have commonly been found in rule based categorization studies (e.g., Buchsbaum et al., 2005; Grossman et al., 2002; Helie, Roeder, & Ashby, 2010; Koenig et al., 2005; Milton et al., 2009; Patalano et al., 2001; Rao et al., 1997; Seger & Cincotta, 2002; Tracy et al., 2003). Furthermore, consistent with the activation Nomura et al. (2007) observed in rule-based categorization, we found activation in the posterior cingulate and the medial temporal lobes for both categorizations. The posterior cingulate and medial temporal lobes are both involved in declarative memory processes (e.g., Eldridge et al., 2000; Milton et al., 2011); activation in these regions, therefore, supports the recent extension of COVIS that proposes that the declarative memory system acts, in conjunction with prefrontal structures, to identify and maintain verbalizable rules (Ashby & Valentin, 2005).

Given the striking overlap of common activation between the Simple and Complex conditions, it is perhaps not surprising that differences between the conditions were limited. No areas resulted in greater activation for the Simple group than the Complex group, whilst additional activation for the Complex group relative to the Simple group was restricted to a small region of the left frontal lobe. Even when a liberal threshold of p<.01 (uncorrected) was applied, there was no evidence of greater activation in the Complex group than in the Simple group in the tail of the caudate nucleus, the caudate body, or the substantia nigra, regions that have been regarded as key components of the procedural system (Ashby et al., 1998; Nomura et al., 2007). Instead, there was greater activation in the left frontal cortex, perhaps reflecting the greater executive effort entailed in applying a

more complex rule or, alternatively, greater shifts in the precise rule used (Maddox, Filoteo, Hejl, & Ing, 2004; although note that this difference disappeared when categorizations were contrasted against the interval between trials at the individual subject level).

Our results, therefore, appear to suggest that participants in both the Simple and Complex conditions categorized via the verbal system. One caveat to this conclusion is that it relies on inferring processes on the basis of fMRI data which can be problematic. Having said this, the striking neural overlap between the Simple and Complex conditions suggests that (whatever processes are involved) there is much common ground between categorizations in the two conditions. Furthermore, our claim that the categorizations engaged the verbal system is strengthened by neuropsychological evidence which shows that patients with frontal damage (similar to the areas we identified) often demonstrate problems with rule-based tasks requiring working memory resources (e.g., Barcelo & Knight, 2002; Kimberg, D'Esposito, & Farah, 1997; Milner, 1964; Reverberi, D'Agostini, Skrap, & Shallice, 2005; Robinson, Heaton, Lehman, & Stilson, 1980). As noted above, our inference is also consistent with much previous imaging work that has identified similar regions in tasks known to evoke rule-based processes (e.g., Buchsbaum et al., 2005; Grossman et al., 2002; Helie, Roeder, & Ashby, 2010; Koenig et al., 2005; Patalano et al., 2001; Rao et al., 1997) and the clearly defined anatomical regions that are assumed to support the verbal and procedural systems of COVIS (e.g., Maddox & Ashby, 2004). Nevertheless, with this caveat in mind, it is worth considering the implications of this conclusion. On first consideration it may seem surprising that the Complex category structure appears to engage the verbal, rather than the procedural system, given that it possesses a number of characteristics that might have been expected to encourage use of the procedural system. Specifically, in the

Complex condition, two factors were present that have been argued to lead to category learning on the basis of the procedural system. These were the presence of diagonal decision bounds (e.g., Maddox & Ashby, 1993) and the large number of decision boundaries that were required to partition the space appropriately (e.g., Nosofsky et al., 2005). Furthermore, there was no simple verbal rule available (i.e., a unidimensional or simple conjunctive rule) to categorize the stimuli, instead, participants would have had to rely on a multi-componential rule. As such our findings demonstrate the flexibility of the verbal system and extend the conditions under which it has been shown to operate.

Our results do not mean, of course, that the verbal system will always be favored. Previous work suggests that there are situations where the procedural system will be preferentially recruited such as when a concurrent load is introduced (e.g., Zeithamova & Maddox, 2006), when participants learn overlapping categories for which perfect accuracy is not possible (e.g., Maddox & Ashby, 1993), under certain types of category structures (Nomura et al., 2007), and in patients for whom the verbal system is impaired (e.g., Maddox, Aparicio, Marchant, & Ivry, 2005; Pothos & Wood, 2009). Other manipulations, such as particular kinds of task instructions or stimulus materials, may also preferentially recruit the procedural system. A greater understanding of the conditions under which the procedural system is used appears an important avenue for future research.

In sum, these results broaden our understanding of the conditions under which the verbal system of COVIS operates. Our results show that the verbal system has considerable flexibility and can spontaneously generate complicated rules that are less salient than those previously shown to be supported by the verbal system (Ashby et al., 1998; Ashby & Maddox, 2005). Specifying the boundary conditions for the operation of the verbal system

with greater precision appears an important priority in the further development of the COVIS model.

An additional guestion addressed by our study was the extent to which neural processes are modified as categorization progresses from a hypothesis-driven acquisition stage (Session 1) to when category representations are assumed to be more fully established (Session 2). This issue has been somewhat neglected in previous neuroimaging studies of categorization (but see Koenig et al., 2005; Poldrack et al., 2001), even though it has been extensively considered in related behavioral work (e.g., Helie, Waldschmidt, & Ashby, 2010; Johansen & Palmeri, 2002; Nosofsky et al., 1994). One relevant paper, however, is that by Helie, Roeder, and Ashby (2010) who tested a Simple-1D rule (similar to the one we used) and a disjunctive rule over more than 10,000 trials including four separate scanning sessions. Like us, they found initial, rule-based, categorization recruited extensive frontal activations with no subcortical activations except for the thalamus. In later scanning sessions, whilst cortical activation remained stable, subcortical regions, including the caudate, became engaged, as automaticity emerged. We added to this previous work by comparing activation in the first scanning session to that in the second session. We identified a number of frontal regions, previously linked to executive functioning, that were more engaged in Session 1 than in Session 2. These included the right insula (BA 13), the left VLFC (BA 47), and the right superior frontal gyrus (BA 9). The right insula is involved with goal maintenance and working memory demands (Dosenbach et al., 2006), the left VLFC (BA 47) with working memory and response selection (e.g., Duncan & Owen, 2000), and the right superior frontal gyrus (BA 9) with outcome monitoring and decision making (e.g., Hayama & Rugg, 2009).

For the Simple group, successful categorization in Session 1 relative to in Session 2 resulted in activation in the right insula (BA 13) and the right superior frontal lobe (BA 6). The Complex group recruited a number of extra regions in Session 1 than in Session 2, including right VLFC (BA 47). The right VLFC has been linked to inhibitory processes (Hodgson et al., 2007), rule use (Grossman et al., 2002) and working memory demands (Aalto et al., 2005). It has also recently been implicated in multidimensional rule-based spontaneous categorization (Milton et al., 2009). Our finding extends this previous work by suggesting that this region is particularly involved in the initial stages of multi-dimensional rule categorization and becomes less engaged with increasing practice.

In contrast to the relatively extensive frontal regions preferentially recruited in Session 1, no regions emerged as more active when comparing Session 2 to Session 1. When considered separately, however, both the Simple and Complex conditions had small regions that were more activated in Session 2 than in Session 1. In the case of the Complex group, these included the right precentral gyrus (BA 6) and a region of the left frontal lobe. For the Simple group, these comprised activation in left superior frontal gyrus (BA 9) and left medial frontal gyrus (BA 10). The role of these activations is unclear. One explanation is that they may reflect goal maintenance or task monitoring processes to ensure that experimental conditions, such as the categorization rule, have not changed. In any case, the recruitment of additional frontal regions was much less pronounced for Session 2 than Session 1.

An additional region that was more active in Session 2 than in Session 1 for the Complex condition was the right body of the caudate nucleus. This may possibly suggest that the procedural system plays a greater role with increasing practice for the Complex categorization. This would also be consistent with Ashby et al.'s (1998) contention that in

the initial stages of categorization the rule-based system dominates whilst engagement of the procedural system emerges over time. Whilst intriguing, this explanation must be treated as speculative, given that this activation was in the anterior part of the caudate body and that it is the posterior region of the body that is specifically linked to the procedural system (e.g., Nomura & Reber, 2008). An alternative explanation is that this activity signals the initial emergence of automaticity. This would be consistent with Helie et al. (2010) who, as detailed above, showed that the caudate becomes more active with increasing practice at a disjunctive rule-based task.

Overall, we found a number of regions in the frontal cortex, linked with working memory and executive functioning, that were more engaged in the initial stages of category formation than when the category representation can be assumed to be more fully developed. Activation of these regions during category acquisition is likely to reflect greater learning effort in Session 1 than Session 2. This process of category learning is likely to involve a number of inter-related elements such as hypothesis formation, rule testing, error signaling, feedback monitoring, uncertainty, and increased attentional demands.

In conclusion, this study showed an extensive overlap of activation between Simple and Complex category structures. Both categorizations recruited diverse regions of the frontal cortex, such as the left medial frontal gyrus, the left superior frontal gyrus and the right superior frontal gyrus, that have previously been linked to the verbal system of COVIS (Nomura et al., 2007). Furthermore, we found evidence for activation of the medial temporal lobes, supporting the recent proposal that these regions are an important part of the verbal system (Ashby & Valentin, 2005). In addition, we observed greater recruitment of frontal regions during category acquisition (Session 1) than when the category

representation had been more fully formed (Session 2). This extra activation in the early stages of categorization may reflect the effort of learning a categorization with a rule-based, hypothesis-testing procedure. Our results clearly indicate that engagement of the verbal system extends to a broader range of situations than has previously been demonstrated and show that much additional work is required before we develop a precise understanding of the interplay between the verbal and procedural systems.

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References

- Aalto, S., Bruck, A., Laine, M., Nagren, K., & Rinne, J.O. (2005). Frontal and temporal dopamine release during working memory and attention tasks in healthy humans: A positron emission tomography study using the high-affinity dopamine D₂ receptor Ligand [¹¹C] FLB 457. Journal of Neuroscience, **25**, 2471-2477.
- Ashby, F. G & Maddox, W. T. (2005). Human category learning. *Annual Review of Psychology*, **56**, 149-178.
- Ashby, F.G, & Valentin, V.V. (2005). Multiple systems of perceptual category learning: Theory and cognitive tests. In H. Cohen and C. Lefebvre (Eds.) *Categorization in cognitive science*. New York: Elsevier.
- Ashby, F. G., Queller, S., & Berretty, P. M. (1999). On the dominance of unidimensional rules in unsupervised categorization. *Perception & Psychophysics*, **61**, 1178-1199.
- Ashby, F.G., Alfonso-Reese, L. A., Turken, A. U., & Waldron, E. M. (1998). A Neuropsychological Theory of Multiple Systems in Category Learning. *Psychological Review*, **105**, 442-481.

- Barcelo, F., & Knight, R.T. (2002). Both random and perseverative errors underlie WCST deficits in frontal patients. *Neuropsychologia*, **40**, 349-356.
- Buchsbaum, B.R., Greer, S., Chang, W-L., & Berman, K.F. (2005). Meta-analysis of neuroimaging studies of the Wisconsin Card-Sorting Task and component processes. (2005). *Human Brain Mapping*, **25**, 35-45.
- Dosenbach, N.U.F., Visscher, K.M., Palmer, E.D., Miezin, F.M., Wenger, K.K., Kang, J.C., Burgund, E.D., Grimes, A.L., Schlaggar, B.L., & Petersen, S.E. (2006). A core system for the implementation of task sets. *Neuron*, **50**, 799-812.
- Duncan, J., & Owen, A.M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences*, **23**, 475-483.
- Eldridge, L.L., Knowlton, B.J., Furmanski, C.S., Bookheimer, S.Y., & Engel, S.A. (2000). Remembering episodes: A selective role for the hippocampus during retrieval. *Nature Neuroscience*, **3**, 1149-1152.
- Filoteo, J. V., Lauritzen, J.S., & Maddox, W.T. (2010). Removing the Frontal Lobes: The Effects of Engaging Executive Functions on Perceptual Category Learning. *Psychological Science*, **21**, 415-423.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., & Noll, D.C. (1995). Improved assessment of significant activation in functional magnetic-resonance imaging (fMRI) use of a cluster size threshold. *Magnetic Resonance in Medicine*, **33**, 636-647.
- Grossman, M., Smith, E.E., Koenig, P., Glosser, G., DeVita, C., Moore, P., & McMillan, C. (2002). The neural basis for categorization in semantic memory. *Neuroimage*, **17**, 1549-1561.

- Hayama, H.R., & Rugg, M.D. (2009). Right dorsolateral prefrontal cortex is engaged during postretrieval processing of both episodic and semantic information. *Neuropsychologia*, **47**, 2409-2416.
- Helie, S., Roeder, J.L., & Ashby, F.G. (2010). Evidence for cortical automaticity in rule-based categorization. *The Journal of Neuroscience*, **30**, 14225-14234.
- Helie, S., Waldschmidt, J.G. & Ashby, F.G. (2010). Automaticity in rule-based and informationintegration categorization. *Attention, Perception, & Psychophysics*, **72**, 1013-1031.
- Hodgson, T.L., Chamberlain, M., Parris, B.A., James, M., Gutowski, N., Husain, M. & Kennard, C. (2007). The role of the ventrolateral frontal cortex in inhibitory oculomotor control. *Brain*, **130**, 1525-1537.
- Johansen, M.K., & Palmeri, T.J. (2002). Are there representational shifts in category learning? *Cognitive Psychology*, **45**, 485-553.
- Kimberg, D.Y., D'Esposito, M., & Farah, M.J. (1997). In T.E. Feinberg & M.J. Farah (Eds.). Frontal
 lobes: Neuropsychological aspects. In *Behavioral Neurology and Neuropsychology*. (pp. 409-418)
 New York: McGraw-Hill.
- Koenig, P., Smith, E. E., Glosser, G., DeVita, C., Moore, P., McMillan, C., Gee, J., & Grossman, M. (2005). The neural basis for novel semantic categorization. *NeuroImage*, **24**, 369-383.
- Maddox, W.T., & Ashby, F.G. (1993). Comparing decision bound and exemplar models of categorization. *Perception & Psychophysics*, **53**, 49-70.
- Maddox, W.T., & Ashby, F.G. (2004). Dissociating explicit and procedural-learning based systems of perceptual category learning. *Behavioural Processes*, **66**, 309-332.

- Maddox, W.T., Aparicio, P., Marchant, N.L., & Ivry, R.B. (2005). Rule-based category learning is impaired in patients with Parkinson's Disease but not in patients with cerebellar disorders. *Journal of Cognitive Neuroscience*, **17**, 707-723.
- Maddox, W. T., Filoteo, J. V., Hejl, K. D., Ing, A. D. (2004) Category Number Impacts Rule-Based but not Information-Integration Category Learning: Further Evidence for Dissociable Category Learning Systems. *Journal of Experimental Psychology: Learning, Memory, and Cognition,* 30, 227-235.
- Maldjian, J.A., Laurienti, P.J., Burdette, J.B., Kraft, R.A. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage*, 19, 1233-1239.
- Medin, D. L. & Schaffer, M. M. (1978). Context Theory of Classification Learning. Psychological *Review*, **85**, 207-238.
- Milner, B. (1964). Some effects of frontal lobectomy in man. In J.M. Warren & K. Akert (Eds.). *The frontal granular cortex and behavior.* (pp. 313-331) New York: McGraw-Hill.
- Milton, F. & Wills, A. J. (2004). The influence of stimulus properties on category construction. *Journal of Experimental Psychology: Learning, Memory, and Cognition,* **30**, 407-415.
- Milton, F. & Wills, A.J. (2009). Long-term persistence of sort strategy in free classification. *Acta Psychologica*, **130**, 161-167.
- Milton, F., Wills, A.J., & Hodgson, T.L. (2009). The neural basis of overall similarity and singledimension sorting. *Neuroimage*, **46**, 319-326.
- Milton, F., Muhlert, N., Butler, C.R., Benattayallah, A., Zeman, A.Z.J. (2011). The neural correlates of everyday recognition memory. *Brain and Cognition*, **76**, 369-381.

- Morgan, M. J. (2005). The visual computation of 2-D area by human observers. *Vision Research*, **45**, 2564-2570.
- Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J-B. (2005). Valid conjunction inference with the minimum statistic. *Neuroimage*, **25**, 653-660.
- Nomura, E.M., & Reber, P.J. (2008). A review of medial temporal lobe and caudate contributions to visual category learning. *Neuroscience and Biobehavioral Reviews*, **32**, 279-291.
- Nomura, E. M., Maddox, W. T., Filoteo, J. V., Ing, A. D., Gitelman, D. R., Parrish, T. B., Mesulam, M.
 M., & Reber, P. J. (2007). Neural correlates of rule-based and information-integration visual category learning. *Cerebral Cortex*, **17**, 37-43.
- Nosofsky, R.M. (1984). Choice, similarity, and the context theory of classification. *Journal of Experimental Psychology: Learning, Memory & Cognition,* **10**, 104-114.
- Nosofsky, R.M., Palmeri, T.J., & McKinley, S.C. (1994). Rule-Plus-Exception Model of Classification Learning. *Psychological Review*, **101**, 53-79.
- Nosofsky, R.M., Stanton, R.D., & Zaki, S.R. (2005). Procedural interference in perceptual classification: Implicit learning or cognitive complexity? *Memory & Cognition*, **33**, 1256-1271.
- Patalano, A.L., Smith, E.E., Jonides, J., & Koeppe, R.A. (2001). PET evidence for multiple strategies of categorization. *Cognitive Affective and Behavioral Neuroscience*, **1**, 360-370.
- Poldrack, R.A., Clark, J., Pare-Blagoev, E.J., Shohamy, D., Creso Moyano, Myers, & Gluck, M.A. (2001). Interactive memory systems in the human brain. *Nature*, **414**, 546-550.
- Pothos, E. M. & Bailey, T. M. (2009). Predicting category intuitiveness with the rational model, the simplicity model, and the Generalized Context Model. Journal of Experimental Psychology: Learning, *Memory, and Cognition*, **35**, 1062-1080.

- Pothos, E. M. & Chater, N. (2002). A Simplicity Principle in Unsupervised Human Categorization. *Cognitive Science*, **26**, 303-343.
- Pothos, E. M. & Close, J. (2008). One or two dimensions in spontaneous classification: A simplicity approach. *Cognition*, **107**, 581-602.
- Pothos, E. M. & Wood, R. L. (2009). Separate influences in learning: evidence from artificial grammar learning with traumatic brain injury patients. *Brain Research*, **1275**, 67-72.
- Pothos, E. M., Perlman, A., Bailey, T. M., Kurtz, K., Edwards, D. J., Hines, P., & McDonnell, J. V. (in press). Measuring category intuitiveness in unconstrained categorization tasks. *Cognition*.
- Rao, S.M., Bobholz, J.A., Hammeke, T.A., Rosen, A.C., Woodley, S.J., Cunningham, J.M., Cox, R.W.,
 Stein, E.A., Binder, J.R. (1997). Functional MRI evidence for subcortical participation in
 conceptual reasoning skills. *Neuroreport*, 27, 1987-1993.
- Reverberi, C., D'Agostini, S., Skrap, M., & Shalice, T. (2005). Generation and recognition of abstract rules in different frontal lobe subgroups. *Neuropsychologia*, **43**, 1924-1937.

Rissanen, J. (1978). Modeling by shortest data description. Automatica, 14, 465-471.

- Robinson, A.L., Heaton, R.K., Lehaman, R.A.W., & Stilson, D.W. (1980). The utility of the Wisconsin Card Sorting Test in detecting and localizing frontal lobe lesions. *Journal of Consulting and Clinical Psychology*, **48**, 605-664.
- Rosch, E. & Mervis, B. C. (1975). Family Resemblances: Studies in the Internal Structure of Categories. *Cognitive Psychology*, 7, 573-605.
- Seger, C.A., & Cincotta, C.M. (2002). Striatal activity in concept learning. *Cognitive, Affective, & Behavioral Neuroscience*, **2**, 149-161.

- Seger, C.A., & Cincotta, C.M. (2005). The roles of the caudate nucleus in human classification learning. *The Journal of Neuroscience*, **25**, 2941-2951.
- Shepard, R. N., Hovland, C. L., & Jenkins, H. M. (1961). *Learning and memorization of classifications*. *Psychological Monographs*, **75**, whole no 517.
- Smith, E. E., Patalano, A. L., & Jonides, J. (1998). Alternative strategies of categorization. *Cognition*, **65**, 167-196.
- Squire, L.R. (1982). The neuropsychology of human memory. *Annual Review of Neuroscience*, **5**, 241-273.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotactic atlas of the human brain: 3-dimensional proportional system: An approach to cerebral imaging*. Stuttgart: Thieme.
- Tracy, J.I., Mohamed, F., Faro, S., Pinus, A., Tiver, R., Harvan, J., Bloomer, C., Pyrros, A., & Madi, S. (2003). Differential brain responses when applying criterion attribute versus family resemblance rule learning. *Brain and Cognition*, **51**, 276-286.
- Waldron. E.M., & Ashby, F.G. (2001). The effects of concurrent task interference on category
 learning: Evidence for multiple category learning systems. *Psychonomic Bulletin & Review*, 8, 168-176.
- Zeithamova, D. & Maddox, W. T. (2006). Dual-task interference in perceptual category learning. *Memory & Cognition*, **34**, 387-398.

Footnote

¹ Both this analysis and the analysis of activation in the Simple condition were, as noted in the Imaging Analysis section, contrasted against incorrect trials. In session 2, where accuracy was significantly higher than in Session 1, there were an average of 21.2 incorrect trials in the Simple condition and 26.6 incorrect trials in the Complex condition. One participant in each condition had less than 10 incorrect trials in Session 2. We ran the analyses without these participants but this did not change any of our conclusions. For completeness, we report the results with all the participants included in the analyses.

Figure captions

Figure 1. An example of the stimuli employed in the current study.

Figure 2. The left panel shows the Simple categorization and the right panel shows the Complex categorization (the curves/ rectangles show the clusters in each category structure). Note that figure shows all the actual stimuli used, reduced in size.

Figure 3. Mean performance across blocks for the Simple and Complex categorizations.

Figure 4. a) Regions associated with successful Simple categorization; b) Regions associated with successful Complex categorization; c) Common areas of activation for the Complex and Simple conditions; d) Regions where activation was significantly greater for the Complex condition than the Simple condition.

Figure 5. Regions showing significant activation for: a) Session 1 compared to Session 2 across the Simple and Complex conditions; b) Session 1 compared to Session 2 for the Simple condition; c) Session 1 compared to Session 2 for the Complex condition.

Figure 6. Regions showing significant activation for: a) Session 2 compared to Session 1 for the Simple condition; b) Session 2 compared to Session 1 for the Complex condition.

Supplementary Figures

Supplementary Figure 1: a) Regions activated when contrasting Correct Simple categorization – the interval between trials (p<.001, cluster threshold = 10); b) Regions activated when contrasting Correct Complex categorization – the interval between trials (p<.001, cluster threshold = 10); c) Common activation for the Complex and Simple categorizations when contrasted against the interval between trials (individual contrasts thresholded at p<.005 to give a conjoint probability of p<.001, cluster threshold = 10).