Brain areas for reversible symbolic reference, a potential singularity of the human brain

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Abstract

The emergence of symbolic thinking has been proposed as a dominant cognitive criterion to distinguish humans from other primates during hominization. Although the proper definition of a symbol has been the subject of much debate, one of its simplest features is bidirectional attachment: the content is accessible from the symbol, and vice versa. Behavioural observations scattered over the past four decades suggest that this criterion might not be met in non-human primates, as they fail to generalise an association learned in one temporal order (A to B) to the reverse order (B to A). Here, we designed an implicit fMRI test to investigate the neural mechanisms of arbitrary audio-visual and visual-visual pairing in monkeys and humans and probe their spontaneous reversibility. After learning a unidirectional association, humans showed surprise signals when this learned association was violated. Crucially, this effect occurred spontaneously in both learned and reversed directions, within an extended network of high-level brain areas, including, but also going beyond, the language network. In monkeys, by contrast, violations of association effects occurred solely in the learned direction and were largely confined to sensory areas. We propose that a human-specific brain network may have evolved the capacity for reversible symbolic reference.

Keywords

fMRI, primate, human, symbol, mathematic, language, learning

Introduction

It is a longstanding question whether there is something unique about the cognitive abilities of humans relative to other animals (Hauser et al., 2002; Fitch et al., 2005; Iriki, 2006; Hopkins et al., 2012; Kietzmann, 2019; Penn et al., 2008; Berwick and Chomsky, 2016). Symbols are ubiquitous in many domains of human cognition, underlying not only language but also mathematical, musical or social representations and many others domains (Deacon, 1998; Dehaene et al., 2022; Kabdebon and Dehaene-Lambertz, 2019; Nieder, 2009; Sablé-Meyer et al., 2021). The appearance of symbolic representations, which would develop in parallel with the expansion of prefrontal and parietal associative areas, has therefore been suggested as a potential marker signalling hominization (Deacon, 1998; Dehaene et al., 2022; Henshilwood et al., 2002; Neubauer et al., 2018).

This proposal, however, hinges on the definition of what a symbol is. The term symbol is often used as a synonym for a sign, which is classically defined by Ferdinand de Saussure as an arbitrary binding between a "signifier" (for instance a word, a digit, but also a traffic sign, logo, etc.) and a "signified" (the meaning or content to which the signifier refers) (Saussure et al., 1995). In that respect, however, many non-human animals, including chimpanzees, macaques, but also dogs, are able to learn hundreds of such indexical relationships, even with arbitrary signs (Kaminski et al., 2004; Livingstone et al., 2010; Matsuzawa, 1985; Premack, 1971). Even bees can learn to associate arbitrary visual shapes to abstract representations such as visual quantities (2 or 3 elements) independently of the density, size and colour of the elements in the visual display (Howard et al., 2019). More recently, it has been proposed to reserve the term "symbol" for a collection of such signs that can be syntactically manipulated according to precise compositional rules (Deacon, 1998; Dehaene et al., 2022; Nieder, 2009). The symbols then entertain relationships between each other that are parallel to the relationships between the objects, or concepts, they represent. For example, numerical symbols allow manipulations such as "2+3=5" irrespective of whether they apply to apples, oranges or money. Performing the "sum" operation internally allows expectations about a specific outcome in the external world. Non-human animals may be conditioned to acquire iconic or indexical associations (i.e. signs which bear, respectively, a non-arbitrary or arbitrary relationships between the signifier and the signified), and even perhaps perform operations on the learned signs, such as addition (Livingstone et al., 2014), but their capacities for novel symbolic composition, especially of a recursive syntactic nature, appear limited, or absent (Berwick and Chomsky, 2016; Dehaene et al., 2022, 2015; Penn et al., 2008; Sablé-Meyer et al., 2021; Yang, 2013; Zhang et al., 2022).

The characterization of the difference between humans and animals in terms of symbolic access remains controversial. Furthermore, comparing human and non-human primates is difficult in part because learning complex tasks require considerable training in animals, and a variety of factors such as motivation, learning rate or working memory capacity may therefore explain an animal's failure. Here, we propose to circumvent this difficulty by testing a basic element of symbolic representations, i.e., the temporal reversibility of a learned arbitrary association. While the associations between indices and objects (such as those acquired during classical conditioning) are unidirectional, as in the famous example of the bell indicating the food, symbolic associations are bidirectional or symmetric (Deacon, 1998; Nieder, 2009). When hearing the word 'dog' for example, you can think of a dog, but when seeing a dog, you can also come up with the word. Such reversibility is crucial for communication (the language learner must acquire both comprehension and production skills), but also for symbolic computations, which require bidirectional exchanges between the real world (e.g., seeing three sets of four objects), the internal symbols (e.g. 3x4, allowing the computation 12) and back (to expect a total quantity of twelve objects). In the current work, we test the "reversibility hypothesis", which proposes that because of a powerful symbolic system, humans are biassed to spontaneously form bidirectional associations between an object and an arbitrary sign. It implies that the referential function of the sign immediately operates in both directions (i.e., comprehension and production), allowing to retrieve the signified (meaning) from the signifier (symbol) and vice-versa. Such reversibility is a core and necessary property of symbols, although we readily acknowledge that it is not sufficient, since genuine symbols present additional referential and compositional properties that will not be tested in the present work.

A small number of behavioral studies, spread over four decades, report that non-human animals such as bees and pigeons, but also macaques, baboons and chimpanzees, struggle to reverse the associations that they learned in one direction (Imai et al., 2021; Kojima, 1984; Lipkens et al., 1988; Medam et al., 2016; Sidman et al., 1982; Howard et al., 2019; see Chartier and Fagot, 2022, for a review and discussion). In a recent experiment, Chartier and Fagot (2022) explored this question in 20 free-behaving baboons. After having learned to pair visual shapes (two pairs A-B) above 80% success, their performance dropped considerably when the order of presentation was subsequently reversed (B-A; 54% correct, chance = 50%), although their relearning performance was only slightly but significantly better when the reversed pairs were congruent (B1-A1; B2-A2) rather than incongruent (B1-A2; B2-A1). Even for the famous case of chimpanzee *AI*, who learned Arabic numerals and other arbitrary tokens for colours and objects (Matsuzawa, 2009, 1985), it turns out that her capacity to associate signs and their meanings was based on an explicit and sequential training in both directions, at least initially (Kojima, 1984). In sharp contrast, humans as young as 8 months, even when tested under the same conditions as monkeys or baboons (Sidman

et al., 1982), show behavioural evidence of immediate spontaneous reversal of learned associations (Imai et al., 2021; Ogawa et al., 2010; Sidman et al., 1982).

Still, behavioural tests depend on an explicit report which could hide an implicit understanding of symbolic representations. This confound can be alleviated by directly recording the brain responses, providing a more direct comparison between species. Here, we propose a simple brain-imaging test of reversible associations. First, the participant receives evidence of several stimulus pairings between an object (O) and an arbitrary sign or label (L) in a fixed 'canonical order', e.g., from O_1 to L_1 and from O_2 to L_2. Knowledge of these learned (i.e., congruent) associations is then tested using a classic violation-of-expectation paradigm, by evaluating the brain's surprise response or "prediction error" when, say, O_1 is followed by L_2. This response can then also be evaluated in the converse direction, by switching the order of presentation of the two items within a pair. The crucial question is whether the brain shows a surprise response to an incongruent pairing presented in reversed order (e.g., L_1 followed by O_2), relative to the corresponding congruent pairing (L_1 followed by O_1). The reversibility hypothesis predicts that if symbolic associations are formed, pairs presented in canonical and reversed order should be similarly processed, and so a similar surprise response to incongruent pairings should be found in both cases.

A recent study from our lab used EEG to apply this approach to 4-5 month-old human infants (Kabdebon and Dehaene-Lambertz, 2019). The infants were trained with pairs of stimuli in which a specific picture (a lion or a fish) was associated with tri-syllabic none words, depending on a rule concerning syllable-repetition in the word (e.g. xxY words such as *babagu*, *didito*, etc. were followed by the fish picture whereas xYx words such as *lotilo*, *fudafu*, etc. were followed by the lion picture). Violation-of-expectations responses were recorded in both canonical and reverse order, suggesting that preverbal human infants already have the ability to reversibly attach a symbol to an abstract rule. In human adults, an fMRI study with a more complex design using explicit reports on associations between abstract patterns also showed brain signatures suggestive of spontaneous reversal of learned associations (Ogawa et al., 2010). The network of brain areas overlapped with the multiple-demand system that is ubiquitously observed in high-level cognitive tasks (Duncan, 2010; Fedorenko et al., 2013), including bilateral inferior and middle frontal gyrus (IFG and MFG), anterior insula (AI), intraparietal sulcus (IPS), and dorsal anterior cingulate cortex (dACC). In contrast, a human fMRI study investigating association learning between two natural visual objects found that violation effects in the learned direction were restricted to low level visual areas (Richter et al., 2018). Similarly, in macaque monkeys violation effects in the learned direction have been found selectively in visual areas, using fMRI as well as single-neuron recordings (Kaposvari et al., 2018; Meyer et al., 2014; Meyer and Olson, 2011; Vergnieux and Vogels, 2020). One of these studies (Meyer and Olson,

2011) also tested, in a small subset of 17 neurons, whether the learned associations spontaneously reversed, and showed no such reversal. From these studies, it is difficult to draw a conclusion about a potential difference between species, due to important differences in recording techniques and task design.

Here, we directly compared the ability to spontaneously reverse learned associations in humans and macaque monkeys using identical training stimuli and whole-brain fMRI measures. Our goals were to (1) probe the reversibility hypothesis in an elementary passive paradigm in both species; (2) to shed light on the brain mechanisms of symbolic associations in humans. Indeed, two alternative hypotheses may be formulated. First, given that symbolic learning is a defining feature of language, reversible violation-of-expectation effects might be restricted to the left-hemispheric temporal and inferior frontal language areas. Alternatively, since symbolic learning is manifest in many domains outside of language, for instance in mathematics or music, each attached to a dissociable fronto-posterior brain network (Amalric and Dehaene, 2016; Chen et al., 2021; Dehaene et al., 2022; Fedorenko et al., 2011; Nieder, 2019; Norman-Haignere et al., 2015), reversibility could be expected to arise from a broad and bilateral network of human brain areas, including dorsal intraparietal and middle frontal nodes. We thus tested audio-visual and visual-visual symbolic pairing in two successive experiments.

Results

Summary of the experimental design. In the first experiment, we examined the learning and reversibility of auditory-visual pairs, i.e. between a visual object and an auditory label. Over the course of 3 days, we exposed humans (n=31) and macaque monkeys (n=2) to four pairs of visual objects and speech sounds (**Figure 1A;** see **Supplementary Figure 1** for the 5 series of 4 pairs of audio-visual stimuli). Two of the pairs were presented in the auditory-to-visual direction and two in the visual-to-auditory direction, ensuring that all subjects had experience with both orders and would not be surprised by their temporal reversal *per se* (see discussion of the utility of this point in Medam et al, 2016). After 3 consecutive days of exposure to 100% of congruent canonical trials (24 canonical trials in total per pair, presented outside the scanner), subjects were tested for learning using 3T fMRI, during which they were passively exposed to pairs that respected or violated the learned pairings (**Figure 1B**). To sustain the memory for learned pairs, the design still included 70% of congruent canonical trials (identical to the trials to which they have been exposed outside the scanner). In addition, there were 10% of incongruent canonical trials, in which the temporal order was maintained but the pairings between auditory and visual stimuli were violated. Enhanced brain responses to such incongruent pairs would indicate surprise and therefore prove that the associations had been learned. Note that all auditory and visual stimuli themselves were familiar: only their pairing was

unusual. The design also included 10% of reversed congruent and 10% of reversed incongruent trials, in which the habitual (i.e. canonical) order of presentation of the pairs was reversed (**Figure 1A**). Observing an incongruity effect on such reversed trials would indicate that subjects spontaneously reversed the pairings and were surprised when they were violated. Note that the frequency of the two types of reversed trials was equal, and thus did not afford any additional learning of the reversed pairs (unlike Chartier and Fagot, 2022).

Experiment 1| audio-visual stimulus pairs. We first mapped the cortical regions that were activated by visual and auditory stimuli, modelling the two stimuli within each pair with separate regressors (**Figure 1B, C**). Even though the onset of the two stimuli within a pair were just 800ms apart, the fast acquisition allowed us to separate the timing of the activation of the visual and auditory pathways in both humans and monkeys (**Figure 1 D, E**). In the visual cortex, the response evoked by the pair arose earlier when the first stimulus of the pair was visual compared to when it was auditory, and the other way around for the auditory cortex (**Figure 1 D, E**). In the auditory cortex of monkeys the response was relatively weak (**Figure 1 C, E**), in line with previous studies (Erb et al., 2019; Petkov et al., 2009; Uhrig et al., 2014). This might be related to the small size of auditory cortex relative to visual cortex in monkeys, (Felleman and Van Essen, 1991), as well as relative to the size of the human auditory cortex (Woods et al., 2010).

We next investigated whether the subjects had learned the associations, whether the brain responses showed signatures of generalisation to the reversed direction, and which brain areas were involved. If participants had learned the associations, incongruent trials should evoke a surprise response relative to congruent trials, when presented in the same order as the training pairs (canonical trials). Crucially, if they spontaneously reversed the associations, a similar incongruity effect should also be seen on reversed trials. According to the reversibility hypothesis, humans should show a spontaneous reversal while monkeys should not. Only for monkeys, we should therefore find a significant interaction effect between incongruity and canonicity, indicating a significant difference between the congruity effect in the learned direction compared to the congruity effect in the reversed direction.

Indeed, in humans, a vast network was activated by incongruity on both canonical and reversed trials (voxel $p<0.001$, cluster $p<0.05$ corrected, n=31 participants) (**Figure 2A, Table 1**). This network included a set of high-level brain regions previously described as the multiple demand system (Duncan, 2010; Fedorenko et al., 2013), including bilateral IFG, MFG, anterior insula, IPS, and dACC. It also included the language network (Pallier et al., 2011), with the left superior temporal sulcus (STS), in addition to the left inferior frontal region already mentioned. However, in our case the activation was bilateral, thereby supporting the model that the language network is part of a larger symbolic network (Dehaene et al., 2022). Furthermore,

201 we also found activations in the precuneus, similar to the network that has been found for top-down attention
202 to memorised visual stimuli (Sestieri et al., 2010), which also included bilateral STS and IPS. Notably, we
203 did not find any congruity effects in visually activated regions (compare to **Figure 1B**), in contrast to a
204 previous human fMRI study (Richter et al., 2018). **Figure 2B** shows the hemodynamic response within the
205 different clusters and the different conditions. In all analyses, since there were a majority of canonical
206 congruent trials, sensitivity was higher in the canonical direction, and thus the size of the significant clusters
207 was larger on canonical than on reversed trials. However, no significant cluster exhibited any interaction
208 between congruity and canonicity, indicating that there was no statistical difference between the effect of
209 congruity for the trained and the reversed direction. Thus, the human brain fully and spontaneously reverses
210 the auditory-visual associations that it learns.

211 We next asked whether monkeys (n=2) learned the associations and did so in both directions. We used 5
212 stimulus sets comprising 4 pairs in each set to train and test monkeys (**Supplementary Figure 1**). The
213 canonical congruity effect, which indexes learning, was not significant when analysing the first imaging
214 sessions (n=5) after the first 3 days of exposure to the canonical pairs. Thus for 3 of the 5 stimulus sets,
215 monkeys were further exposed during two weeks (with in total ~960 canonical trials per pair) and tested
216 during 4 consecutive days. After this extended exposure, we found consistent effects in both monkeys
217 (averaged over the 12 scan sessions, 4 per stimulus set per monkey), with clusters in early visual areas (V1,
218 V2, V4), and auditory association areas in the left temporo-parieto-occipital cortex (TPO) (AV and VA
219 trials combined, $p<0.001$, cluster $p<0.05$, n=2) (**Figure 3, Table 2**). Crucially, however, this effect was
220 confined to the canonical direction, with no significant clusters in the reversed direction at the whole-brain
221 level, in accordance with the reversibility hypothesis. We specifically tested the difference between the
222 congruity effect in the learned and the reversed direction by calculating the interaction effect between
223 congruity and canonicity, which showed an activation pattern that was similar to the canonical congruity
224 effect, which reached significance in areas V2 and V4. **Figure 3C** shows the corresponding hemodynamic
225 signals, with an enhanced response to incongruent pairs in the canonical direction (continuous red curve)
226 but not in the reversed direction (dashed red curve). The results thus indicated that monkey cortex could
227 acquire audio-visual pairings, as also shown by prior visual-visual experiments (Meyer and Olson, 2011;
228 Vergnieux and Vogels, 2020), but with two major differences with humans: the congruity effects did not
229 involve a broad network of high-level cortical areas but remained restricted to early sensory areas, and the
230 learned associations did not reverse.

231 **Experiment 2 | visual-visual stimulus pairs.** The non-reversal in monkeys in the above audio-visual
232 experiment could be due to a number of methodological choices. First, although the visual stimuli were
233 optimised for monkeys, as 3 out of 5 sets of stimuli were pictures of familiar toys, the auditory stimuli

234 (pseudowords) might have been suboptimal for them (although note that monkeys in our lab have extensive
235 experience with human speech). It might be argued that this choice made their discrimination difficult
236 (although note that the canonical congruity effect is evidence of discrimination). Indeed, the auditory cortex
237 is relatively small in monkeys compared to humans (Woods et al., 2010), and there is evidence that auditory
238 memory capacity is reduced in monkeys compared to humans (Scott and Mishkin, 2016). Second, the
239 instructions differed: while we asked human subjects to fixate a dot at the centre of the screen and to pay
240 attention to the stimuli, monkeys were simply rewarded for fixation.

241 To address those concerns, we replicated the experiment with reward-dependent visual-visual associations
242 in three macaque monkeys, one of which participated in both experiments (**Figure 4; Supplementary**
243 **Figure 2A**). First, we replaced the spoken auditory stimuli with abstract black-and-white shapes similar to
244 the lexigrams used to train chimpanzees to communicate with humans (Matsuzawa, 1985) (**Supplementary**
245 **Figure 2B**). Second, to enhance attention for the monkeys, we introduced a reward association paradigm
246 that made the stimuli behaviorally relevant for them (Wikman et al., 2019). Within each presentation
247 direction, one of the two pictures of objects was associated with a high reward, and one with a low reward
248 (**Supplementary Figure 2A**). Monkeys were still rewarded for fixation, but object identity predicted the
249 size of the reward during the delay period following the presentation of the stimuli (two objects predicted
250 a high reward, and two predicted a low reward). To calculate congruity effects, the two pairs within each
251 direction were always averaged, making the reward association an orthogonal element in the design.

252 Using this design, we obtained significant canonical congruity effects in monkeys on the first imaging day
253 after the initial training (24 trials per pair), indicating that the animals had learned the associations (**Figure**
254 **4B, Table 3**). The effect was again found in visual areas (V1, V2 & V4), also spreading to the prefrontal
255 cortex (45B, 46v), very similar to the visually activated areas (compare to **Figure 1C**). In addition, small
256 clusters were also found in area 6 and in STS. Crucially, the congruity effect remained restricted to the
257 learned direction, as no area showed a significant reversed congruity effect, again in accordance with the
258 reversibility hypothesis. The interaction between congruity and canonicity indicated that there was a
259 significant difference between the canonical and the reversed direction in a similar set of regions (V1, V2,
260 area 45A, 46v and 6).

261 The greater involvement of the frontal cortex in the congruity effect in this paradigm fits with previous
262 reports on the impact of reward association on long-term memory for visual stimuli in macaque monkeys
263 (Ghazizadeh et al., 2018) . To further investigate this, we split high versus low rewarded pairs and found
264 that congruity effect was present only for high-reward conditions, with a significant interaction of congruity
265 and reward in area 45 and caudate nucleus (**Supplementary Figure 3**). Overall, these results indicate that,

266 even when stimuli were optimised and made relevant for monkeys, leading to enhanced activations and an
267 activation of prefrontal cortex to violations of expectations, the learned associations did not reverse in
268 monkeys.

269 We also ran this visual-visual paradigm in human participants (n=24) with the goal to clarify the role of
270 language in the reversibility process. Humans again gave evidence of reversed association, although weaker
271 than with spoken words (**Figure 4C, Table 4**). At the normal threshold (voxel $p<0.001$, cluster $p<0.05$
272 corrected), the main effect of congruity was significant in a network very similar to experiment 1, including
273 bilateral middle frontal gyrus (MFG), left intraparietal sulcus (IPS), bilateral anterior insula, dorsal anterior
274 cingulate cortex (dACC), with an additional focus in left inferior temporal gyrus (**Figure 4C, Table 4**). The
275 involvement of the language network was limited. In particular a main effect of congruity in the STS was
276 absent, in agreement with the shift to visual symbols. Still, bilateral middle frontal gyri, STS and the
277 precuneus were again activated by the incongruent minus congruent contrast on reversed trials (voxel
278 $p<0.001$, cluster $p<0.05$ corrected), thereby extending beyond the multiple-demand system (Duncan, 2010;
279 Fedorenko et al., 2013). While sensory activated regions were again absent, in contrast to a previous study
280 on congruity effects in humans when using associations between two visual objects (Richter et al., 2018).
281 And crucially, no interaction effect was again found between congruity and canonicity, neither at the
282 classical threshold ($p<0.001$) nor at a lower threshold ($p<0.01$). Those results indicate that humans can also
283 encode pairs of visual stimuli in a symmetrical, reversible fashion, involving a network of high-level
284 cortical areas, unlike monkeys.

285 Further evidence was obtained from a behavioural test, performed after imaging, where we collected
286 familiarity ratings for each stimulus pair (see Methods, **Figure 4**). Although participants reported a higher
287 familiarity with congruent canonical pairs (which were presented on 70% of trials) than with congruent
288 reversed pairs (which were presented on 10% of trials, $t(20)=2.8$, $p=0.01$), both pairs were rated as much
289 more familiar than their corresponding incongruent pairs (although they were also presented 10% of time),
290 and than never-seen pairs (all $t(20) >7$, $p<0.0001$, bilateral paired t-test). This familiarity task thus confirms
291 that humans spontaneously reverse associations and experience a memory illusion of seeing the reversed
292 pairs.

293 **Joint analysis of audio-visual and visual-visual stimulus pairs.** In order to better characterise the human
294 reversible symbol learning network and its dependence on modality, we reanalyzed both human
295 experiments together (n=55) (**Supplementary Figure 4**). There was, unsurprisingly, a main effect of
296 experiment with greater activation in a bilateral auditory and linguistic network in the AV experiment, and
297 in the occipital, occipito-temporal and occipito-parietal visual pathways in the VV experiment. A main

effect of congruity was observed and was again significant in both directions, canonical and reversed, in bilateral regions: insula, MFG, precentral, IPS, precuneus, ACC and STS. Crucially, there was still no region sensitive to the congruity X canonicity interaction, indicating that the learned associations were fully reversible. Finally, a single region, the left posterior STS, showed a significantly different congruity effect in the two experiments, as it was slightly larger in the AV relative to VV paradigm ([-60 -40 8], z=4.51; 183 vox, pcor=0.049), compatible with a specific role in learning of new spoken lexical items. The results therefore suggest that a broad and bilateral network, encompassing language areas but extending beyond them into dorsal parietal and prefrontal cortices, responded to violations of reversible symbolic association regardless of modality.

To interrogate more finely the role of language-related and non-related areas, we turned to a sensitive subject-specific region-of-interest (ROI) analysis. We used a separate set of data acquired during a "localizer" task during the same fMRI session (Pinel et al., 2007) to recover, in a subject-specific manner, the coordinates of the 10% best voxels within ROIs which are considered as the main hubs of language (Pallier et al., 2011), mathematics (Amalric & Dehaene, 2016) and reading networks. Specifically in the conditions of that localizer, we considered activations to amodal sentence processing for the language ROIs, to simple mental arithmetic for the mathematical ROIs, and in sentence reading relative to listening for the visual word form area (VWFA). We added this last region as it is activated by written words, visual symbols *par excellence*. We then performed ANOVAs on the betas of the main experiment averaged over these voxels, thus the analyses were performed on a different dataset than the localizer data used to select the voxels.

A main congruity effect was observed in all ROIs (**Table 5**). There was also a main effect of experiment in all language ROIs, VWFA and right Inferior Temporal (IT), due on the one hand to larger activations in the AV than VV experiment in frontal and superior temporal ROIs, and on the other hand to the converse trend in the VWFA and IT ROIs. A significant congruity x experiment interaction was seen only in the pSTS and IFG triangularis, because these ROIs showed a large congruity effect in the AV experiment, but no effect in the VV experiment – thus further confirming that these areas contribute specifically to the acquisition of linguistic symbols, while all other areas were engaged regardless of modality. Importantly, in all these analyses, no significant interaction canonicity X congruity nor experiment x canonicity X congruity were observed, confirming the whole brain analyses (**Supplementary Figure 4** and **Table 5**).

Finally, in experiment 2 in which participants rated the familiarity of the pairs, we computed a within-subject behavioural index of reversibility as the difference in familiarity rating between incongruent and congruent reversed pairs. Across subjects, this index was correlated with the fMRI congruity effect

330 (difference between incongruent and congruent trials in the ROI) on canonical trials (r=0.49, p=0.028) and
331 especially on reversed trials (r=0.64, p=0.002) in the left dorsal part of area 44. In the right cerebellum, a
332 similar correlation was observed but only for the reversed trials (r=0.57, p=0.008). No significant
333 correlation was observed in other ROIs.

334 Discussion

335 Using fMRI in human and non-human primates, we studied the learning of a sequential association between
336 either a spoken label and an object (Exp. 1), or a visual label and an object (Exp. 2). In humans, we observed
337 no difference in brain activation between the learned and the temporally reversed associations: in both
338 directions, violations of the learned association activated a large set of bilateral regions (insula, prefrontal,
339 intraparietal, cingulate cortex,) that extended beyond the language processing network. Thus, humans
340 generalised the learned pairings across a reversal of temporal order (**Figure 5**). In contrast, non-human
341 primates showed evidence of remembering the pairs only in the learned direction and did not show any
342 signature of spontaneous reversal. Crucially, we found a significant interaction between congruity and the
343 direction of the learned association, thereby going beyond a mere negative finding. Monkey responses to
344 incongruent pairings were entirely confined to the learned canonical order and occurred primarily within
345 sensory areas, with propagation to the frontal cortex only for rewarded stimuli, yet still only in the forward
346 direction (**Figure 5**).

347 Several studies previously found behavioural evidence for a uniquely human ability to spontaneously
348 reverse a learned association (Imai et al., 2021; Kojima, 1984; Lipkens et al., 1988; Medam et al., 2016;
349 Sidman et al., 1982), and such reversibility was therefore proposed as a defining feature of symbol
350 representation reference (Deacon, 1998; Kabdebon and Dehaene-Lambertz, 2019; Nieder, 2009). Here, we
351 went one step further by testing this hypothesis at the brain level. Indeed, a limit of previous behavioural
352 studies is that animals could have understood the reversibility of a symbolic relationship, but failed to
353 express it behaviorally because of extraneous procedural or attentional factors, or because of a conflict
354 between different brain processes (e.g., for maintaining the specific and rewarded learned pairing vs.
355 generalising to the reverse order). Here, we used fMRI and a passive paradigm to directly probe whether
356 any area of the monkey brain would exhibit surprise at a violation of the reversal of a learned association.
357 Our results show that this is not the case.

358 Interpretation must remain cautious, as there are also some occasional behavioural reports of spontaneous
359 reversal of learned associations, for instance in one well-trained California sea lion and a Beluga whale

(Kastak et al., 2001; Murayama et al., 2017; Schusterman and Kastak, 1998) and possibly in 1 out of 20 baboons in Medam et al. (2016). These studies may indicate that, with sufficient training, symbolic representation might eventually emerge in some animals, as also suggested by the small reversal trend in a recent behavior study in baboons (Chartier and Fagot, 2022). However, they may also merely show that animals may begin to spontaneously reverse new associations once they have received extensive training with bidirectional ones (Kojima, 1984). The bulk of the literature strongly suggests that while animals easily learn indexical associations, especially monkeys and chimpanzees (Diester and Nieder, 2007; Livingstone et al., 2010; Matsuzawa, 1985; Premack, 1971), but also dogs (Fugazza et al., 2021; Kaminski et al., 2004), vocal birds (e.g. Pepperberg, 2009) and even bees (Howard et al, 2019), they exhibit little or no evidence for genuine symbolic processing. Discriminating symbolic from indexical representations can be achieved by testing for spontaneous reversibility between the labels and the objects, as in the current study, or by testing for the presence of systematic compositional relationships among the labels (Nieder, 2009).

One previous study showed preliminary evidence for a lack of reversibility in macaque monkey inferotemporal cortex (Meyer & Olson, 2011), but only recorded on a subset of neurons, and after extensive training on pairs of visual images (816 exposures per pair). Interestingly, a similar set of arbitrary stimuli and extensive training protocol (258 trials per pair) was used in an fMRI study of stimulus association in humans, where congruity effects were also found to be restricted to early visual areas (Richter et al., 2018). Such extensive training might have led to low-level and rigid encoding in the trained direction. It is therefore instructive that, here, in monkeys, we found irreversibility after a very short training period. Indeed, in experiment 2, just 24 exposures per pair were sufficient to observe a surprise effect in the canonical direction, yet without generalisation in the reverse direction, even after longer exposures. In addition, we strived to make the objects concrete and recognizable to the monkeys (by using pictures of toys that were familiar to them, taken from various angles), while the labels were as abstract as possible to promote a symbol-referent asymmetry in the pairs. We considered using macaque vocalisations for the sounds, but these already have a defined meaning, often emotional, that could have disrupted the experiments. Furthermore, the present animals had extensive experience with human speech. Finally, while the present lab setting could be judged artificial and not easily conducive to language acquisition, previous evidence indicates that human preverbal infants easily learn labels in such a setting (Mersad et al., 2021) and spontaneously reverse associations after only a short training period (Ekramnia and Dehaene-Lambertz, 2019; Kabdebon and Dehaene-Lambertz, 2019).

Non-human primates are often considered the animal model of choice to understand the neural correlates of high-level cognitive functions in humans (Feng et al., 2020; Newsome and Stein-Aviles, 1999;

392 Roelfsema and Treue, 2014). Accordingly, many studies have emphasized the similarity between human
393 and non-human primates in terms of brain anatomy, physiology and behavior (Caspari et al., 2018; De
394 Valois et al., 1974; Erb et al., 2019; Hackett et al., 2001; Harwerth and Smith, 1985; Dante Mantini et al.,
395 2012; D. Mantini et al., 2012; Mantini et al., 2011; Margulies et al., 2016; Petrides et al., 2012; Uhrig et al.,
396 2014; Warren, 1974; Wilson et al., 2017; Wise, 2008). At the same time, important differences between
397 human and monkey brains have been reported as well (Passingham 2008). Using a direct comparison with
398 fMRI, some specific functional differences have been found (Denys et al., 2004a, 2004b; Mantini et al.,
399 2013; Vanduffel et al., 2002). Particularly relevant is that, in contrast to humans, monkeys show clear
400 feature tuning in the prefrontal cortex, which is in line with the sensory activation we found in monkey PFC
401 (**Figure 1C**) and the involvement of monkey PFC in the congruity effect in experiment 2 (**Figure 4B**).
402 Many anatomical differences have been reported between humans and monkeys using MRI as well as
403 histological methods. In particular, the human brain is exceptionally large (Herculano-Houzel, 2012), and
404 contains a number of structural differences compared to the brains of other primates (Chaplin et al., 2013;
405 Leroy et al., 2015; Neubert et al., 2014; Palomero-Gallagher and Zilles, 2019; Rilling, 2014; Schenker et
406 al., 2010; Takemura et al., 2017). Notably, while the human arcuate fasciculus provides a strong direct
407 connection between inferior prefrontal and temporal areas involved in language processing, this bundle is
408 reduced and does not extend as anteriorly and as ventrally in other primates, including chimpanzees
409 (Balezeau et al., 2020; Eichert et al., 2020; Rilling et al., 2012, 2008; Thiebaut de Schotten et al., 2012).
410 Also, the PFC is selectively increased in terms of tissue volume (Chaplin et al., 2013; Donahue et al., 2018;
411 Hill et al., 2010; Smaers et al., 2017). While this may not translate to a selective increase in terms of the
412 number of PFC neurons (Gabi et al., 2016), dendritic arborizations and synaptic density are larger in human
413 PFC (Elston, 2007; Hilgetag and Goulas, 2020; Shibata et al., 2021). These anatomical differences may
414 underlie the fundamental differences in language learning abilities between these species, but this is still
415 controversial (e.g. Hopkins et al., 2012; Iriki, 2006). Here, we show that reversibility of associations, a
416 crucial element in the ability to attach symbols to objects and concepts, sharply differs between human and
417 non-human primates and offers a more tractable way to investigate potential differences between species.

418 The striking inter-species difference in size and extent of the violation effect as measured with fMRI, even
419 for purely canonical stimuli, points to a more efficient species-specific learning system, that our experiment
420 tentatively relates to a symbolic competence. The areas that specifically activated in humans when the
421 reversed association was violated were not limited to the classical language network in the left hemisphere.
422 They extended bilaterally to homolog areas of the right hemisphere, which are involved for instance in the
423 acquisition of musical languages (Patel, 2010). They also extend dorsally to the middle frontal gyrus and
424 intraparietal sulcus which are involved in the acquisition of the language of numbers, geometry and higher

425 mathematics (Amalric and Dehaene, 2016; Piazza, 2010; Wang et al., 2019). Finally, an ROI analysis shows
426 that they also include the VWFA and vicinity. The VWFA is known to be sensitive to letters, but also to
427 other visual symbols such as a new learned face-like script (Moore et al., 2014) or emblematic pictures of
428 famous cities (e.g. the Eiffel tower for Paris; Song et al., 2012), and the nearby lateral inferotemporal cortex
429 responds to Arabic numerals and other mathematical symbols (Amalric and Dehaene, 2016; Shum et al.,
430 2013). Strikingly, these extended areas, shown in **Figure 2**, correspond to regions whose cortical expansion
431 and connectivity patterns are maximally different in humans compared to other primates (Chaplin et al.,
432 2013; Donahue et al., 2018; Hill et al., 2010; Smaers et al., 2017). They also fit with a previous fMRI
433 comparison of humans and macaque monkeys, where humans were shown to exhibit uniquely abstract and
434 integrative representations of numerical and sequence patterns in these regions (Wang et al., 2015).

435 In all of these studies, the observed changes are bilateral, extended, and go beyond the language network
436 per se. Such an extended network does not fit with the hypothesis that a single localised system, such as
437 natural language or a universal generative faculty, is the primary engine of all human-specific abstract
438 symbolic abilities (Hauser and Watumull, 2017; Spelke, 2003). Rather, our results suggest that multiple
439 parallel and partially dissociable human brain networks possess symbolic abilities and deploy them in
440 different domains such as natural language, music and mathematics (Amalric and Dehaene, 2017; Chen et
441 al., 2021; Dehaene et al., 2022; Fedorenko et al., 2011; Fedorenko and Varley, 2016).

442 The neurobiological mechanisms that enable reversible symbol learning in humans remain to be discovered.
443 Interestingly, most learning rules, such as spike-time-dependent plasticity, are sensitive to temporal order
444 and timing, a feature of fundamental importance for predictive coding. In contrast, as indicated by the
445 behavioural results of experiment 2, humans seem to forget the temporal order in which pairs of stimuli are
446 presented when they store them at a symbolic level. This has been interpreted as improper causal reasoning
447 (Ogawa et al., 2010). Indeed, if A repeatedly precedes B, then perceiving A predicts the appearance of B;
448 but if B is observed, concluding to the likely presence of A is a logical fallacy. Still, brain mechanisms for
449 temporal reversal do exist in the literature. The most prominent candidate, in both humans and non-human
450 animals, is hippocampal-dependent neuronal replay of sequences of events, which can occur in forward and
451 reverse temporal order (Foster, 2017; Liu et al., 2019). Sequence reversal may be important during learning,
452 in order to trace back to a memorised event that led to a reward. In line with this, a retroactive gradient has
453 been shown in memory storage in humans, where memory is strongest for stimuli that were presented close
454 to the reward but preceding it (Braun et al., 2018). This memory trace may explain the slight facilitation
455 observed in baboons when they learn reversed congruent pairs relative to reversed incongruent pairs
456 (Chartier et al, 2022). Although neuronal replay in both forward and reverse directions exists in non-human

457 animals, it might be that this mechanism has selectively expanded to symbol-related areas of the human
458 brain – a clear hypothesis for future work.

459 Obviously, even humans do not always disregard temporal order for all associations between stimulus pairs
460 – for instance, they remember letters of the alphabet in a fixed temporal order (Klahr et al., 1983). Thus,
461 future work should also clarify which conditions promote reversible symbolic learning. Here, the pairs
462 comprised one fixed and abstract element (either linguistic or graphical), which served as a label, paired
463 with several different views of a concrete object. In human infants, the association of a label with the
464 presentation of objects helps them construct the object category, as revealed by several experiments in
465 which infants discriminate between categories (Ferry et al., 2013), or correctly process the number of
466 objects (Xu et al., 2005) when the categories and objects are named, but not in the absence of a label.
467 Interestingly, preverbal infants are flexible and accept pictures as labels for a rule (Kabdebon et al, 2019),
468 as well as monkey vocalisations and tones as labels for an animal category (Ferguson and Waxman, 2016;
469 Ferry et al., 2013), whereas older infants who have been exposed to many social situations in which
470 language is the primary symbolic medium to transfer information, expect symbolic labels to be in the native
471 language (Perszyk and Waxman, 2019). Later, they recover flexibility, suggesting that this transient
472 limitation might be a contextual strategy due to the pivotal role of language in naming at this time of life.

473 While our results suggest a dramatic difference in the way human and non-human primates encode
474 associations between sensory stimuli, several limitations of the present work should be kept in mind. First,
475 due to ethical and financial reasons we only tested 4 monkeys, while we tested 55 humans in total. While
476 it is common in primate physiological studies to report the results for 2 animals, this makes it challenging
477 to extrapolate the results to the whole species (Fries and Maris, 2022). To address this point, we combined
478 the results from two different labs, collecting data from 2 animals in each lab. A second limitation is that
479 the interspecies differences that we observed could be due to a number of hard-to-control factors. While we
480 ensured greater attention and motivation in experiment 2, other obvious differences include a lifetime of
481 open-field experiences and education in our human adults, which was not available to monkeys and includes
482 a strong bias towards explicit learning of symbolic systems (e.g. words, letters, digits, etc). As noted above,
483 however, the fact that 5-month-old infants, who lack such extensive experience, also show a similar
484 symbolic reversibility effect (Kabdebon et al, 2019) suggest that these factors may not fully explain our
485 findings.

486 A third limitation is that we only compared humans to a single species, macaque monkeys. Testing non-
487 human primates closer to humans, such as chimpanzees, might yield different conclusions, and chimpanzee
488 Ai's failure of reversibility (Kojima, 1984), although striking, may not be representative. Reversible

489 symbolic learning should also be evaluated in vocal learners such as songbirds and parrots, as some of them
490 demonstrate sophisticated and flexible label learning (see e.g. Pepperberg and Carey, 2012). Furthermore,
491 in dogs, social interactions between the dog and the experimenter during learning facilitate associations
492 (Fugazza et al., 2021), as is also the case in infants. Social cues were absent in our design, and whether they
493 would favour a switch to a symbolic system might be interesting to explore. Finally, we only tested adult
494 monkeys, yet there might be a critical period during which reversible symbolic representation might be
495 possible with appropriate training procedures; indeed, juvenile macaques learn better and faster to associate
496 an arbitrary label with visual quantities than adults (Srihasam et al., 2012). The present work provides a
497 simple experimental paradigm that can easily be extended to all these cases, thus offering a unique
498 opportunity to test whether humans are unique in their ability to acquire symbols.

499 # Methods

500 *Participants*

501 We tested four adult rhesus macaques (male, 6-8 kg, 5-19 years of age). YS and JD participated in
502 experiment 1 and JD, JC and DN in experiment 2. All procedures were conducted in accordance with the
503 European convention for animal care (86-406) and the NIH's guide for the care and use of laboratory
504 animals. They were approved by the Institutional Ethical Committee (CETEA protocol # 16-043) and by
505 the ethical committee for animal research of the KU Leuven. Animal housing and handling were according
506 to the recommendations of the Weatherall report, allowing extensive locomotor behaviour, social
507 interactions, and foraging. All animals were group-housed (cage size at least 16-32 m3) with diverse cage
508 enrichment (auditory and visual stimuli, toys, foraging devices etc.).

509 We also tested 55 healthy human subjects with no known neurological or psychiatric pathology (Exp. 1,
510 n=31; Exp2., n=24; in experiment 2, an additional 3 subjects were not included because they showed no
511 evidence of learning the canonical pairs). Human subjects gave written informed consent to participate in
512 this study, which was approved by the French national Ethics Committee.

513 *Stimuli*

514 Five sets of four images each were designed (**Supplementary Figure 1**). All five sets were used for each
515 macaque monkey, while 1 set was used per human subject, alternating between sets 2 and 3 for subsequent
516 subjects. The 2 first sets were 3D renderings of objects differing in their visual properties and semantic
517 categories. As they might be considered as more familiar to humans, the other 3 sets of objects were

photographs of monkey toys which the monkeys were exposed to in their home cages for at least 2 weeks prior to the training blocks. They were mostly geometrical 3D objects with no evident and consistent name for naive human participants. The rendering and photos were taken from 8 different viewpoints. These stimuli were used in both experiments and are called "object" thereafter.

A label was associated with each object in each set. For experiment 1, the labels were auditory French pseudo-words with large differences in the number and identity of their syllables within each set (e.g. "tøjɑ̃", "gliʃu","byŋyŋy", "kʁɛfila"). Note that monkeys were daily exposed to French radio and television as well as to French-speaking animal caretakers. In experiment 2, the labels were abstract black-and-white visual shapes, difficult to name and similar to the lexigrams used to train chimpanzees to communicate with humans (Matsuzawa, 1985).

Experimental paradigm

Stimulus presentation. Each set to be learned comprised 4 pairs. Two pairs were presented in the label-object direction (L1-O1 & L3-O3), and 2 in the object-label direction (O2-L2 & O4-L4). Labels were speech sounds in experiment 1, and black-and-white shapes in experiment 2. In each trial, the first stimulus (label or object) was presented during 700ms, followed by an inter-stimulus-interval of 100ms then the second stimulus during 700ms (trial total duration: 1500 ms). The pairs were separated by a variable inter-trial-interval randomly chosen among eight different durations between 3 and 4.75 seconds (step=250 ms). The series of eight intervals was randomised again each time it was completed. The visual stimuli were ~8 degrees in diameter, centred on the screen, with an average luminance set equal to the background. At each trial, the orientation of the object was randomly chosen among the 8 possibilities. A cross was present at the centre of the screen when no visual stimulus was present. Auditory stimuli were presented to both ears at 80dB.

Training. The experiment was designed to be also tested in 3-month-old human infants (Ekramnia and Dehaene-Lambertz, 2019), which explains our choice of short training sessions over 3 consecutive days because of the short attention span in infants and the reported benefit of sleep for encoding word meaning after a learning session (Friedrich et al., 2017). Therefore, training consisted of observing 24 trials as described above (1 block of 24 trials for each of the 3 training days). Two pairs (1 in each direction) were introduced on the first day of training (e.g., L1-O1 and O2-L2). First, 1 pair was shown for 6 trials, then the other pair for 6 trials, then the 2 pairs were randomly presented for 6 trials each. On the second day of training, the 2 other pairs (L3-O3 and O4-L4) were presented using the same procedure as on day 1. On the 3 day, all pairs were randomly presented (6 presentations each). The object-label pairing was constant but

549 the direction of presentation (O-L or L-O) and the introduction of the pair on the first or second day was
550 counterbalanced across participants. In experiment 1, the only sounds presented were the speech labels,
551 while no sound was present in experiment 2, the objects and labels being visual stimuli.

552 **Human protocol.** In experiment 1, the participants came to the lab to watch a first video presenting the
553 first block of trials, and on the next 2 consecutive days they received a web link on which a video was
554 uploaded that contained the block of training for that day (24 trials, ~3 min long). For experiment 2, all 3
555 videos were sent via a web link and participants were instructed to attentively watch the video
556 corresponding to the given day. The participants came for the fMRI session on the fourth day. Each
557 participant saw only 1 set of objects-labels, either stimulus set 2 or stimulus set 3, distributed equally across
558 participants.

559 In experiment 2, we added a behavioural test at the end of the MRI session to check their learning. They
560 were shown all 16 possible trial pairs (incongruent and congruent in canonical and non-canonical order),
561 plus 16 never seen, one by one. For each of them, they were asked to rate how frequently they had seen
562 them (on a 5-level scale ranging from never to rarely, sometimes, often and always). The results were
563 analysed using a 5-level ANOVA which included the canonicity X congruity 2x2 design. A computer crash
564 erased responses from 2 participants and 1 subject did not participate leaving 21 subjects for this analysis.

565 **Monkey protocol.** Monkeys were implanted with an MR-compatible headpost under general anaesthesia.
566 The animals were first habituated to remain calm in a chair inside a mock MRI setup, and trained to fixate
567 a small dot (0.25 degrees) within a virtual window of 1.25-2 degrees diameter (Uhrig et al., 2014). Then
568 similar to the human participants, they received 1 training block per day for 3 consecutive days (24 trials
569 per block) for each stimulus set. Rewards were given at regular intervals, asynchronous with the visual and
570 auditory stimulus presentation. On the fourth day, they were scanned while being presented with the test
571 blocks for the corresponding stimulus set. All monkeys were trained and tested with all of the stimulus sets.

572 For experiment 1, there was no congruity effect for the first imaging sessions at day 4 (i.e. no difference
573 between congruent and incongruent pairs in the canonical direction), which consisted in total of 62 valid
574 runs for monkey YS and 79 for monkey JD, for the 5 stimulus sets. After the first week with initial training
575 and the first imaging session at day 4, monkeys were further trained for an additional 2 weeks (~80 blocks,
576 with 12 trials per pair per block, so amounting to about 960 trials per pair) and then scanned during 4 days,
577 for the last 3 of the 5 stimulus sets. This additional training was planned in advance, as we expected that
578 pair learning in passively fixating macaque monkeys would require extensive training, based on previous
579 literature. In particular, pair learning was observed in the temporal cortex in macaque monkeys after about

580 1000 exposures per pair (Meyer & Olson, 2011). So, for each of the last 3 sets of stimuli, training and
581 testing took four consecutive weeks.

582 In experiment 2, a reward was introduced to promote monkeys' engagement in the task. The amount of
583 reward that the monkeys received after successfully fixating throughout the pair presentation was either
584 increased or decreased for a duration of 1450ms (starting 100ms after the offset of the second stimulus),
585 depending on the identity of the visual object. The amount of reward remained the same, but the time in
586 between consecutive rewards was set either twice as short (for high rewards) or twice as long (for low
587 rewards). For each direction, 1 visual object was associated with a high reward while the other one was
588 associated with a low reward (see **Supplementary Figure 2**). By design, the 2 pairs that were averaged for
589 each of the critical tested dimensions (direction, congruity and canonicity of the pair) had opposite reward
590 size, making reward size an orthogonal design element. The first stimulus set was used for procedural
591 training on this reward association paradigm for 2 weeks. Stimulus sets 2-5 were used for training as in
592 experiment 1 (with 1 block per day for 3 consecutive days) and an fMRI test session on the fourth day.

593 **Test in MRI.** The MRI session comprised 4 test blocks in a single fMRI session in humans and between
594 12 and 32 blocks per day per monkey (see below for the total number of valid runs). In both humans and
595 monkeys, each block started with 4 trials in the learned direction (congruent canonical trials), 1 trial for
596 each of the 4 pairs (2 O-L and 2 L-O pairs). The rest of the block consisted of 40 trials in which 70% of
597 trials were identical to the training (28 trials); 10% were incongruent pairs but the direction (O-L or L-O)
598 was correct (4 incongruent canonical trials), thus testing whether the association was learned; 10% were
599 congruent pairs but the direction within the pairs was reversed relative to the learned pairs (4 congruent
600 reversed trials) and 10% were incongruent pairs in reverse (4 incongruent reversed trials). As the percentage
601 of congruent and incongruent pairs was the same in the reversed direction, a difference can only be due to
602 a generalisation from the canonical direction. For incongruent trials, the incongruent stimulus always came
603 from the pair presented in the same direction (see figure 1), in order to avoid that a change of position
604 within the pair itself (1st or 2nd stimulus) induced the perception of an incongruity.

605 Human participants were only instructed to keep their eyes fixed on the fixation point and pay attention to
606 the stimuli. The monkeys were rewarded for keeping their eyes fixed on the fixation point, as in the training.
607 In Experiment 1, the reward was constant, whereas in Experiment 2, they received the differential reward
608 that was implemented during training.

609 *Data acquisition*

610 For experiment 1, both humans and monkeys were scanned with the 3T Siemens Prisma at NeuroSpin using
611 a T2*-weighted gradient echo-planar imaging (EPI) sequence, using a 64-channel head coil for humans and
612 a customised eight-channel phased-array surface coil (KU Leuven, Belgium) for monkeys. The imaging
613 parameters were the following: in humans, resolution: 1.75mm isotropic, TR: 1.81s, TE: 30.4ms, PF: 7/8,
614 MB3, slices: 69; in monkeys, resolution: 1.5mm isotropic, TR: 1.08s, TE: 13.8ms, PF: 6/8, iPAT2, slices:
615 34.

616 Monkeys were trained to sit in a sphinx position in a primate chair with their head fixed. MION
617 (monocrystalline iron oxide nanoparticle, Molday Ion, BioPAL, Worchester MA) contrast agent (10 mg/kg,
618 i.v.) was injected to monkeys before scanning (Vanduffel et al., 2001). Eye movements were monitored
619 and recorded by an eye tracking system (EyeLink 1000, SR Research, Ottawa, Canada). In total, we
620 recorded 583 valid runs, 278 for YS and 305 for JD.

621 For Experiment 2, the settings remained the same for the humans and for one of the monkeys (JD). Two
622 new monkeys (JC and DN) were included at the Laboratory of Neuro- and Psychophysiology of KU Leuven
623 and scanned with a 3T Siemens Prisma using a T2*-weighted gradient echo-planar imaging (EPI) sequence.
624 For JC, an external 8-channel coil was used and the imaging parameters were the following: resolution:
625 1.25mm isotropic, TR: 0.9s, T7: 15ms, PF: 6/8, iPAT3, multi-band 2, slices: 52. For DN, an implanted 8-
626 channel coil was used and the imaging parameters were the following: resolution: 1.25mm isotropic, TR:
627 0.9s, TE: 15ms, PF: 6/8, iPAT3, multi-band 2, slices: 40. Monkeys were trained to sit in a sphinx position
628 in a primate chair with their head fixed, and MION was again injected before scanning (11 mg/kg, i.v.).
629 Eye movements were monitored and recorded by an eye tracking system (ETL200, ISCAN inc., Woburn,
630 MA, USA). The animals were also required to keep their hands in a box in front of the chair (as verified
631 with optical sensors), which limited body motion. In total, we recorded 279 valid runs, 81 for JD, 106 for
632 JC and 92 for DN.

633 *Preprocessing of monkey fMRI data*

634 Functional images were reoriented, realigned, resampled (1.00 mm isotropic) and coregistered to the
635 anatomical template of the monkey Montreal Neurologic Institute (Montreal, Canada) space using
636 Pypreclin, a custom-made scripts of Python programming language (Tasserie et al., 2020).

637 Eye-data was inspected for each run for quality. Only runs with more than 85% fixation (virtual window of
638 2-2.5 degrees diameter) were included for further analyses (n=16 excluded in experiment 1 and n=14
639 excluded in experiment 2). Moreover, a trial was excluded if the eyes were closed for more than 650ms
640 (out of 700) while an image was present on the screen. In experiment 1, the top 5% of runs where motion

641 was strongest across monkeys were excluded (n=30) because there remained significant residual motion.
642 In total, for experiment 1, 395 runs remained to be analysed, 184 for YS and 211 for JD. For experiment 2,
643 268 runs remained, 77 for JD, 107 for JC and 84 for DN.

644 *Preprocessing of human fMRI data*

645 SPM12 (http://www.fil.ion.ucl.ac.uk/spm) was used for preprocessing of human data as well as first and
646 second level models. Preprocessing consisted of standard preprocessing pipeline, including slice-time
647 correction, realign, top-up correction, segmentation, normalisation to standard MNI space and smoothing
648 with a 4-mm isotropic Gaussian.

649 *First and second-level analyses*

650 After imaging preprocessing, active brain regions were identified by performing voxel-wise GLM analyses
651 implemented in SPM12 in both monkeys and humans. For the first experiment, in a first-level SPM model,
652 the twelve predictors included: (1-4) the onsets of the first stimulus of the pair (4 regressors consisting in
653 the combinations of audio/visual and canonical/non-canonical factors), and (5-12) the onsets of the second
654 stimulus (8 regressors consisting in the combinations of audio/visual, canonical/non-canonical and
655 congruent/incongruent factors). These twelve events were modelled as delta functions convolved with the
656 canonical hemodynamic response function (for MION in case of monkeys). Parameters of head motion
657 derived from realignment were also included in the model as covariates of no interest. Contrast images for
658 the effect of congruity (incongruent-congruent canonical and incongruent - congruent non-canonical) as
659 well as the interaction (congruity x canonicity) were computed. For the second experiment, the analysis
660 was the same, except that given the two elements of the pair were in the same visual modality, only a single
661 predictor was used for each stimulus pair, giving 4 predictors: the onsets of the second stimulus of the pair,
662 with congruent/incongruent and canonical/non-canonical as the two factors. For the monkeys, an additional
663 factor was whether the pair was associated with a high or a low reward, giving 8 predictors. In this case,
664 the temporal derivative of the hemodynamic response function was added to the model as well. Before
665 entering the second-level analysis, the data was smoothed again, using a 5mm smoothing kernel in humans
666 and 2 mm in monkeys.

667 For the second-level group analysis, subjects were taken as the statistical unit for the humans and runs were
668 taken as statistical units for the monkeys. One-sample t-tests were performed on the contrast images to test
669 for the effect of the condition. Results are reported at an uncorrected voxelwise threshold of $p<0.001$ and a
670 cluster $p<0.05$ corrected for multiple comparisons (FDR).

ROI analyses

In a separate localizer, human participants listened and read short sentences. In some of the sentences, the participants were asked to compute easy mathematical operations (math sentences). Subtracting activations to math and non-math sentences allowed to separate the regions more involved in mathematical cognition than in general sentence comprehension. We selected seven left-hemispheric regions previously reported as showing a language-related activation (Pallier et al., 2011), 6 bilateral ROIs showing mathematically-related activations (Amalric & Dehaene, 2016) and finally a 10-radius sphere around the VWFA [-45 -57 -12]. In these ROIs, we recovered the subject-specific coordinates of each participant's 10% best voxels in the following comparisons: sentences vs rest for the 6 language Rois ; reading vs listening for the VWFA ; and numerical vs non-numerical sentences for the 8 mathematical ROIs. We extracted the beta of these voxels and performed ANOVAs with Congruity and Canonicity as within-subject factors and experiment as between-subjects factor. Two participants in experiment 1 and 1 participant in experiment 2 had no localizer, leaving 52 participants (n=29 and n= 23) for these analyses. P-values were FDR corrected considering all 15 ROIs in each comparison.

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Author contributions

Conceptualization : T.v.K., M.E., S.D. and G.D.L. Data acquisition : T.v.K., L.P., J.T., M.D., X.L., X.F., M.E., W.D. and B.J. Data analysis : L.P., G.D.L., T.v.K., and X.F. Writing: T.v.K., S.D. and G.D.L.

Table 1: Congruity effect in Experiment 1 in 31 human subjects, with 1 imaging session per subject after 3 days of exposure to congruent canonical pairs. MNI coordinates and t-values of the different contrasts at the peak voxel of each significant cluster (main effect of congruity, congruity effect for canonical trials, and congruity effect for reversed trials).

Region	MNI coordinates	Congruity Main	Congruity Canonical	Conguity Reversed
L sup frontal	-26 56 24	4.40	4.41	2.10
L precentral	-36 6 32	5.75	3.57	7.50
L triangularis	-48 16 2	7.65	5.45	6.08
L insula	-40 22 0	7.76	5.84	6.27
L temporal pole	-60 2 -10	6.56	3.95	5.71
L ant STS	-62 -24 0	5.71	4.28	4.09
L post STS	-54 -34 4	4.82	2.78	5.09
L precuneus	-6 -68 40	4.68	4.72	3.39
L inf parietal	-28 -58 42	5.85	3.97	4.56
L caudate	-10 2 14	5.22	5.15	3.03
L cerebellum	-6 -82 -34	5.59	3.98	3.27
R mid frontal	54 26 32	7.79	5.34	5.86
R opercularis	50 20 32	7.32	5.44	6.74
R insula	40 22 0	5.83	4.93	5.11
R temporal pole	60 4 -14	6.89	5.52	4.49
R post STS	48 -32 0	7.48	5.96	5.47
R precuneus	4 -62 40	6.36	5.16	2.88
R inf parietal	34 -64 44	5.14	3.57	4.49
R caudate	10 2 14	4.21	4.35	2.67
R cerebellum	10 -76 -24	5.06	5.06	2.02

R:Right; L: Left; STS: Superior temporal Sulcus

Table 2: Congruity effect in Experiment 1 in two monkeys after two additional weeks of exposure to congruent canonical pairs. Per subject, 3 stimulus sets were used, with 4 imaging sessions per stimulus set. MNI coordinates and t-values of the different contrasts at the peak voxel of each significant cluster (congruity effect for canonical trials, congruity effect for reversed trials, and interaction effect of congruity and canonicity).

region	MNI coordinates	Congruity Canonical	Congruity Reversed	Congruity X Canonicity
R V2, V4	17 -29 4	5.04*	-2.24	4.56*
L V2	-18 -30 2	4.6*	-0.09	3.08
R V4	21 -22 0	4.23*	-0.74	2.95
L TPO	-20 -21 11	4.13*	0.45	2.26
L LGN	-8 -8 -5	0.46	-4.27	3.98*

R = Right; L = Left; TPO = temporo-parieto-occipital cortex; LGN = lateral geniculate nucleus; *=p<0.05

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Table 3: Congruity effect in Experiment 2 in 3 monkeys after 3 days of exposure to congruent canonical pairs. Per subject, 5 stimulus sets were used, with 1 imaging session per stimulus set. MNI coordinates and t-values of the different contrasts at the peak voxel of each significant cluster (congruity effect for canonical trials, congruity effect for reversed trials, and interaction effect of congruity and canonicity).

region	MNI coordinates	Congruity Canonical	Congruity Reversed	Congruity X Canonicity
L V1, V2	-17 -36 1	5.18*	-2.64	4.82*
R V1, V2	15 -35 7	4.76*	0.98	1.31
L V4	-23 -23 8	3.92*	0.94	1.61
L area 45A, 46v	-17 14 6	3.89*	-2.20	4.00*
R Area 6 / STS 6	22 6 -3	3.65*	-1.26	3.37*
L TPO	-8 -17 13	3.45*	0.03	2.04

MNI coordinates and t-values of each significant cluster at the peak voxel. R = Right; L = Left; STS = superior temporal sulcus; TPO = temporo-parieto-occipital cortex; * = $p<0.05$

705 **Table 4:** Congruity effect in Experiment 2 in 23 human subjects, with one imaging session per subject
706 after 3 days of exposure to congruent canonical pairs. MNI coordinates and t-values of the different
707 contrasts at the peak voxel of each significant cluster (main effect of congruity, congruity effect for
708 canonical trials, and congruity effect for reversed trials).

Region	MNI coordinates	Congruity Main	Congruity Canonical	Congruity Reversed
L triangularis	-44 30 24	5.34	3.64	3.91
	-34 26 0	4.43	4.36	1.91
L ant cingulaire	-8 18 42	4.52	3.25	3.13
L suppl motor area	2 20 52	3.79	3.95	1.40
L precentral	-48 4 40	4.82	2.56	4.26
L inf parietal	-30 -50 44	5.09	3.90	3.30
L mid occipital	-28 -70 32	5.05	2.89	2.79
L visual word form area	-50 -60 -12	4.43	2.62	3.64
R sup frontal	56 24 36	4.93	3.41	3.57
R orbito frontal	26 26 -16	5.05	1.92	5.22
R operculum	50 16 -2	3.58	2.96	2.11
	48 10 28	4.74	2.20	4.39

R: Right; L: Left;

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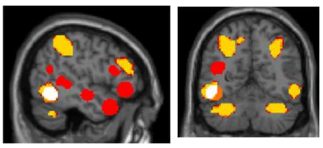
Table 5: ROIs analyses of the language and mathematics localizer : F-values of ANOVAs performed on the averaged betas of the main task across different ROIs (main effect of congruity, canonicity, experiment (1 or 2), and interaction effect of congruity and canonicity, and congruity and experiment). These ROIs correspond to the 10% best voxels selected in each participant thanks to an independent and short localizer, in regions commonly reported in the literature as activated in language and mathematical tasks. In this localizer, participants listened to and read short sentences of general content or requiring easy mental calculations. On the sagittal (x=-50mm) and coronal (y=-58mm) brain slices, the language and mathematical ROIs are presented as red and yellow areas respectively. The left-lateralized white area corresponds to the Visual Word Form Area (VWFA); n=52; df=50; p_{FDRcor}: *** <0.001, ** < 0.01, *< 0.05, ° < 0.1.



		Congruity	Canonicity	Experiment	Congruity X Canonicity	Congruity X Experiment
ROIs Language	Temporal pole	11.44 **	<1	6.02 *	<1	<1
	Anterior STS	5.41 *	<1	42.31 ***	<1	<1
	Posterior STS	18.70 ***	1.31	50.75 ***	<1	17.01 **
	Temporo Parietal junction	20.81 ***	1.85	9.39 **	<1	<1
	IFG orbitalis	22.47 ***	<1	11.40 **	<1	1.64
	IFG triangularis	16.98 ***	<1	22.42 ***	<1	10.45 *
	VWFA	22.29 ***	<1	11.77 **	<1	<1
ROIs Math	Left precentral BA44d	29.71 ***	<1	4.1°	<1	<1
	Right precentral BA44d	10.44 **	1.23	<1	1.49	<1
	Left IPS	27.4 ***	<1	1.81	1.77	<1
	Right IPS	18.19 ***	6.77	1.70	2.37	5.29
	Left IT	33.43 ***	<1	4.43°	<1	<1
	Right IT	5.41 *	<1	7.76 *	<1	<1
	Left Cerebellum	5.51 *	<1	<1	<1	2.87
	Right Cerebellum	19.20 ***	<1	<1	<1	<1

STS: superior temporal sulcus, IFG inferior frontal gyrus, IPS: intra-parietal sulcus, IT:inferior temporal

Figure legends

Figure 1. Experimental paradigm for auditory-visual label learning. A) Subjects were exposed to 4 different visual-auditory pairs during 3 days (6 repetitions of each pair, 3 minute video). Two pairs were always presented in the 'visual-then-auditory' order (object to label), and 2 in the 'auditory-then-visual' (label to object) order. During the test phase, this canonical order was kept on 80% of trials, including 10% of incongruent pairs to test memory of the learned pairs, and was reversed on 20% of the trials. On reversed trials, half the pairs were congruent and half were incongruent (each 10% of total trials), thus testing reversibility of the pairings without affording additional learning. **B**,**C**) Activation in sensory cortices. Although each trial comprises auditory and visual stimuli, these could be separated by the temporal offsets. Images show significantly activated regions in the contrasts image > sound (red-yellow) and sound > image (blue-light blue), averaged across all subjects and runs for humans (B) and monkeys (C). **D**,**E**) Average finite-impulse-response (FIR) estimate of the deconvolved hemodynamic responses for humans (D) and monkeys (E) within clusters shown in B and C respectively, separately for visual-audio (VA) and audio-visual (AV) trials. Sign flipped on y-axis for monkey responses.

Figure 2. Congruity effects in the auditory-visual task in humans (experiment 1). A) areas activated by incongruent trials more than by congruent trials in canonical trials (red), reverse trials (blue), and their overlap (green). Brain maps are thresholded at $p_{voxel} < 0.001$ & $p_{cluster} < 0.05$ corrected for multiple comparisons across the brain volume. No interaction effect was observed between congruity and canonicity. **B**) Average FIR estimate of the deconvolved hemodynamic responses within significant clusters in the left hemisphere, separately for VA and AV trials. 31 human subjects were tested, on a single imaging session per subject after 3 days of exposure to canonical trials.

Figure 3. Congruity effects in the auditory-visual task in monkeys (experiment 1). A) significant clusters from the incongruent-congruent canonical contrast. No significant clusters were found for the reversed direction. **B**) significant clusters from the interaction between congruity and canonicity. ($p_{voxel}<0.001$ & $p_{cluster}<0.05$ for both maps) **C**,**D**) Average FIR estimate of the deconvolved MION responses within the clusters from the incongruent-congruent canonical contrast, averaged over VA and AV trials. All clusters in early visual areas were taken together to create figure C. The two monkeys were scanned after two additional weeks of exposure (4 imaging sessions per subject per stimulus set, 3 stimulus sets were used).

Figure 4. Visual-visual label learning in humans and monkeys (experiment 2). A, Experiment paradigm. Subjects were habituated to 4 different visual-visual pairs during 3 days. Two pairs were in the 'object-then-label' order and two pairs in the 'label-then-object' order. For the monkeys, 1 object in each direction was associated with a high reward while the other 1 was associated with a low reward, making reward size orthogonal to congruity and canonicity (See Supplementary Figure 2 for details). **B, monkey fMRI results.** Significant clusters (p_{voxel}<0.001 & cluster volume >50) from the incongruent-congruent canonical contrast (left) and the interaction between congruity and canonicity (right). One imaging session per subject per stimulus set was performed after 3 days of exposure to canonical trials in each of the 3 monkeys, with 5 stimulus sets per subject. **C, human fMRI results.** Areas more activated by incongruent trials than by congruent trials in the canonical (red), and the reversed direction (blue), and their overlap (green) (right) (p_{voxel}<0.005 & cluster volume >50). No red voxels are visible because all of them figure in the overlap (green). One imaging session was performed per subject in 23 participants after 3 days of exposure to a short block of 24 canonical trials. **D, Human behavioural results**. After learning, human adults rated the familiarity of different types of pairs (including a fifth category of novel, never seen pairings). Each dot represents the mean response of a subject in each condition. Although the reversed congruent trials constituted only 10% of the trials, they were considered almost as familiar as the canonical congruent pairs.

Figure 5. Summary of the two experiments in humans and monkeys. (In experiment 1, p_{voxel} < 0.001 & $p_{cluster}$ < 0.05 for humans and monkeys. In experiment 2, p_{voxel}<0.005 & cluster volume >50 in humans and p_{voxel}<0.001 & cluster volume >50 in monkeys.)

Supplementary figure 1: Stimulus sets for experiment 1.

Supplementary Figure 2. A) Complete description of the task paradigm for visual-visual label learning. Subjects were habituated to 4 different visual-visual pairs during 3 days. Two pairs were in the 'object-label' order and two pairs in the 'label-object' order. During the test phase, the same canonical order was kept in 80% of the trials, including 10% of incongruent pairs. In reversed trials (20% of trials), the pairs were either congruent (10%) or incongruent (10%) with the learning. For the monkeys, 1 pair in each direction was associated with a high reward while the other one was associated with a low reward, making the reward size orthogonal to congruity and canonicity. **B)** Stimulus sets for experiment 2 in monkeys. Humans were tested with stimulus set 2.

Supplementary Figure 3 Effect of reward for the visual-visual task in non-human primates. A) Significant clusters from the incongruent-congruent canonical contrast in low reward trials. **B**) Significant from the incongruent-congruent canonical contrast in high reward trials. **C**) Significant clusters from the interaction between congruity and reward. $p_{voxel}<0.001$ & $p_{cluster}<0.05$ in all panels.

Supplementary Figure 4. Analyses of all human participants in experiments 1 and 2 merged. A) Main effect of experiment. **B)** Main effect of congruity, **C)** Effect of congruity in the canonical trials and D) in the reversed trials. **E)** No significant cluster was observed for the interaction canonicity X congruity. **F)** slices in the 3 planes showing the only significant cluster in the Experiment X Congruity interaction. $p_{voxel}<0.001$ & $p_{cluster}<0.05$ in all panels.

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Figure 1

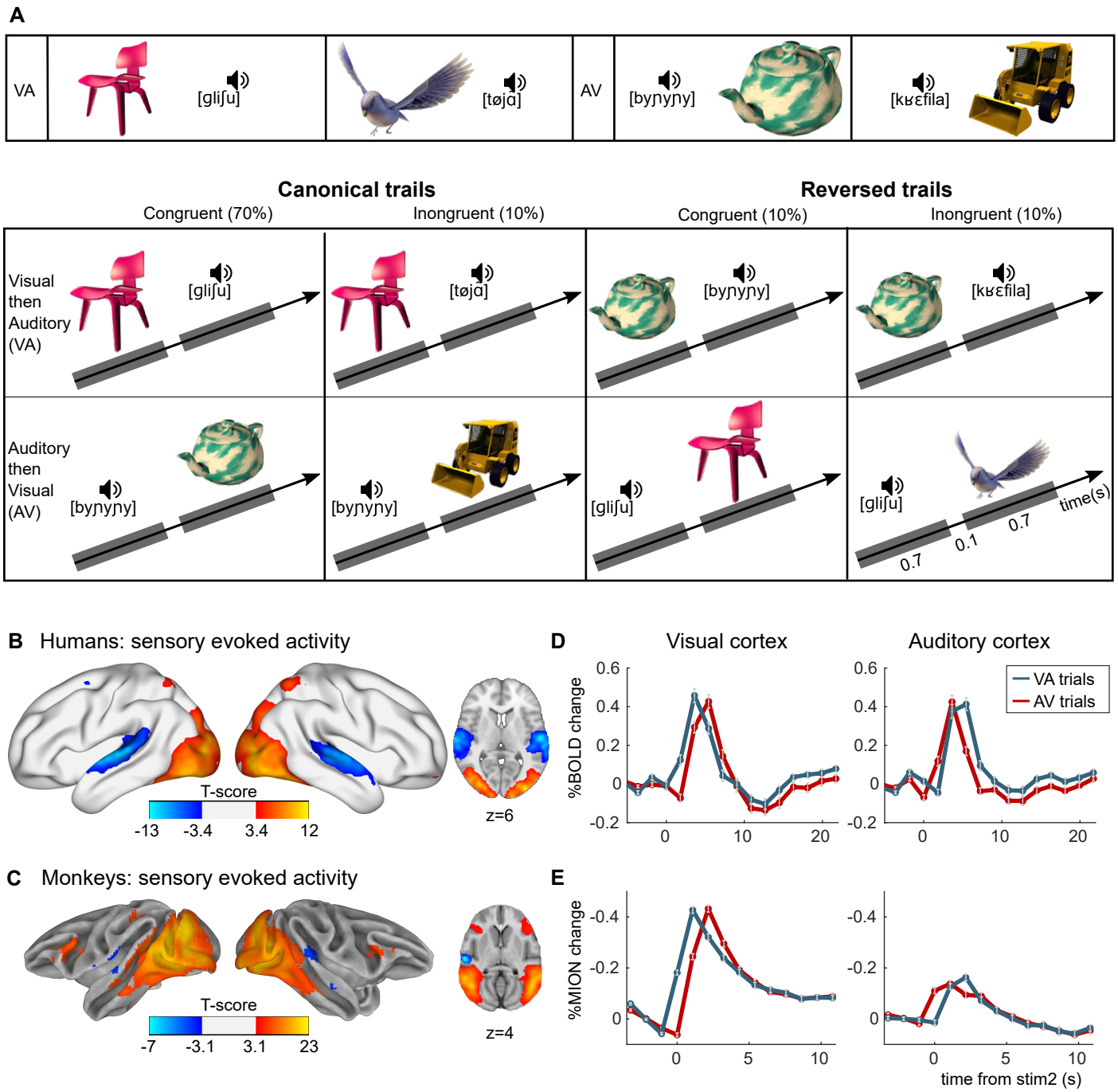

A
VA
[gliʃu]
[tøjɑ]
AV
[byɲyɲy]
[kʁɛfila]
Canonical trails
Congruent (70%)
Inongruent (10%)
Reversed trails
Congruent (10%)
Inongruent (10%)
Visual then Auditory (VA)
Auditory then Visual (AV)
0.7
0.1
0.7
0.7
time(s)
B Humans: sensory evoked activity
T-score
-13
-3.4
3.4
12
z=6
C Monkeys: sensory evoked activity
T-score
-7
-3.1
3.1
23
z=4
D
Visual cortex
Auditory cortex
%BOLD change
VA trials
AV trials
E
%MION change
time from stim2 (s)

Figure 2

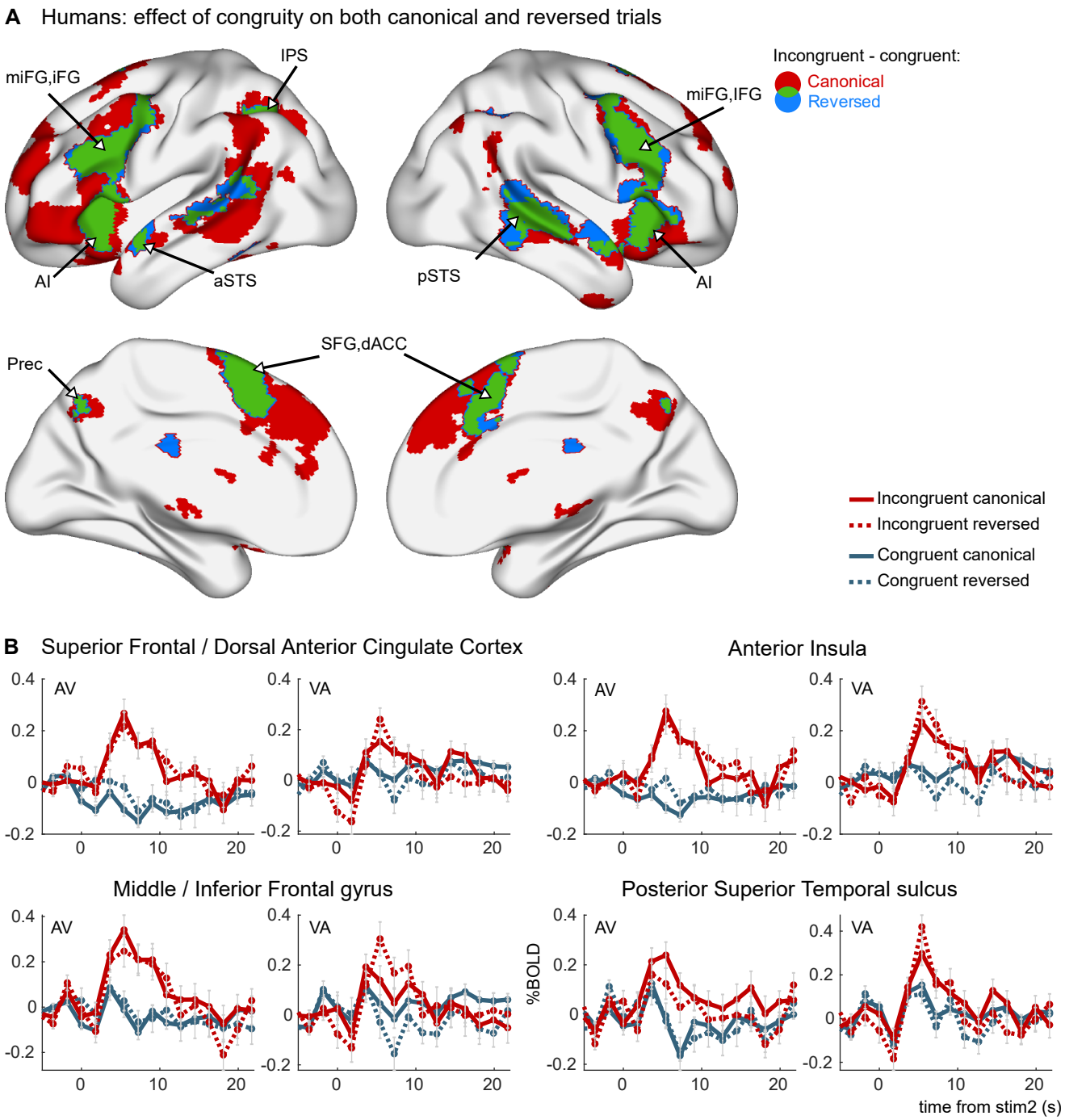

A Humans: effect of congruity on both canonical and reversed trials
miFG,iFG
IPS
AI
aSTS
miFG,IFG
pSTS
AI
Incongruent - congruent:
Canonical
Reversed
Prec
SFG,dACC
Incongruent canonical
Incongruent reversed
Congruent canonical
Congruent reversed
B Superior Frontal / Dorsal Anterior Cingulate Cortex
Anterior Insula
Middle / Inferior Frontal gyrus
Posterior Superior Temporal sulcus
AV
VA
%BOLD
time from stim2 (s)

Figure 3

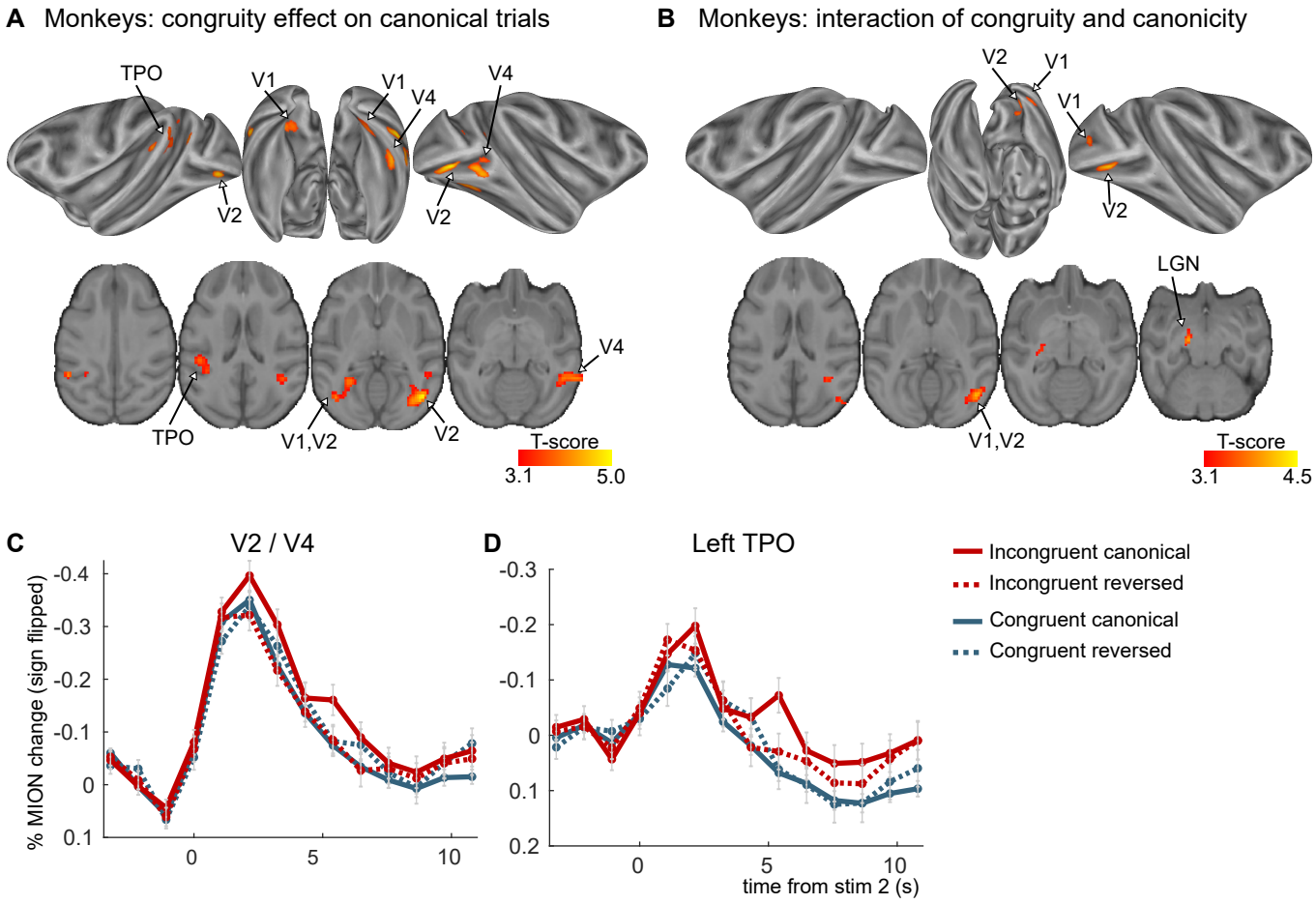
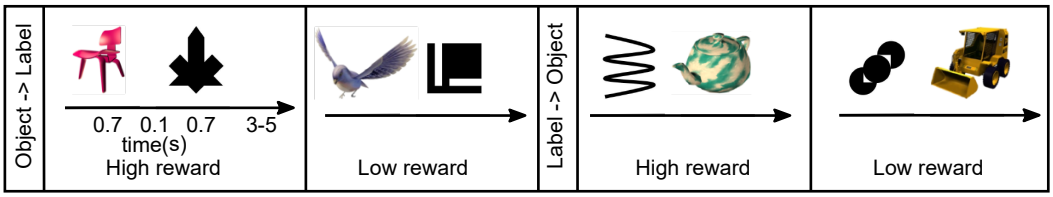
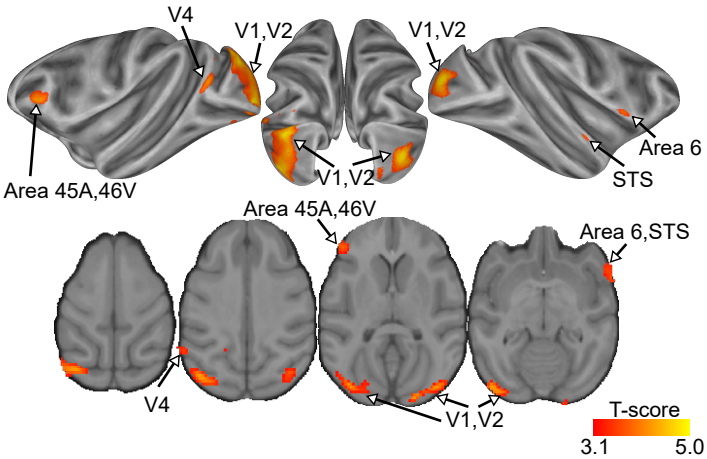

A Monkeys: congruity effect on canonical trials
TPO
V1
V1
V4
V4
V2
V2
TPO
V1,V2
V2
V4
T-score
3.1
5.0
B Monkeys: interaction of congruity and canonicity
V2
V1
V1
V2
LGN
V1,V2
T-score
3.1
4.5
C
V2 / V4
% MION change (sign flipped)
-0.4
-0.3
-0.2
-0.1
0
0.1
0
5
10
D
Left TPO
-0.3
-0.2
-0.1
0
0.1
0.2
0
5
10
time from stim 2 (s)
Incongruent canonical
Incongruent reversed
Congruent canonical
Congruent reversed

Figure 4

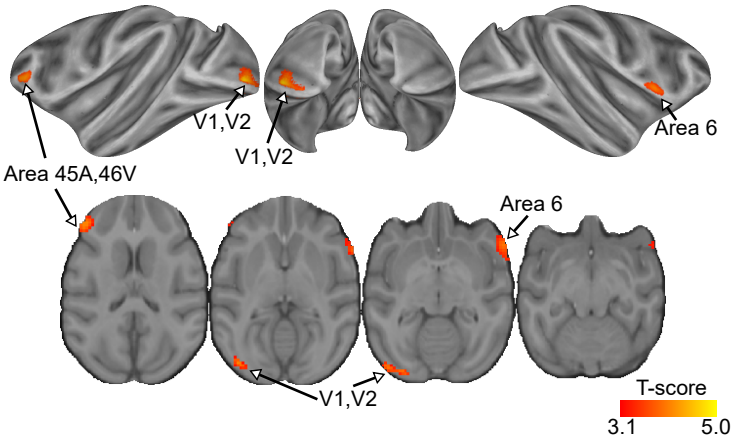
A Visual-visual experimental design



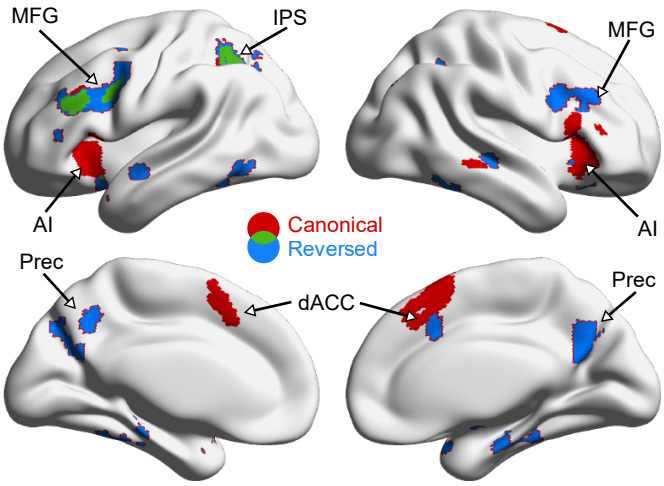
B Monkeys: congruity effect on canonical trials



Monkeys: interaction of congruity and canonicity



C Humans: effect of congruity on both canonical and reversed trials



D Humans: behavioral familiarity ratings

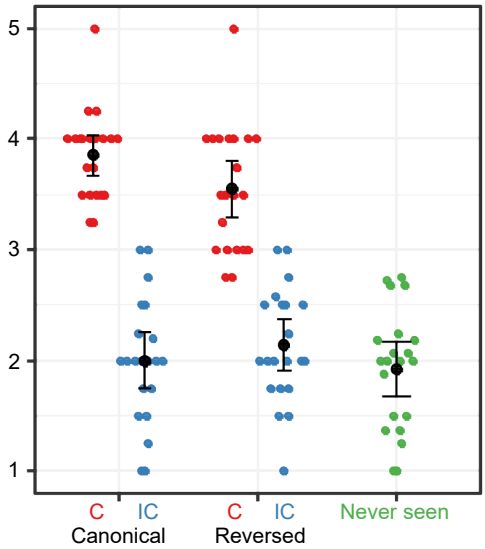
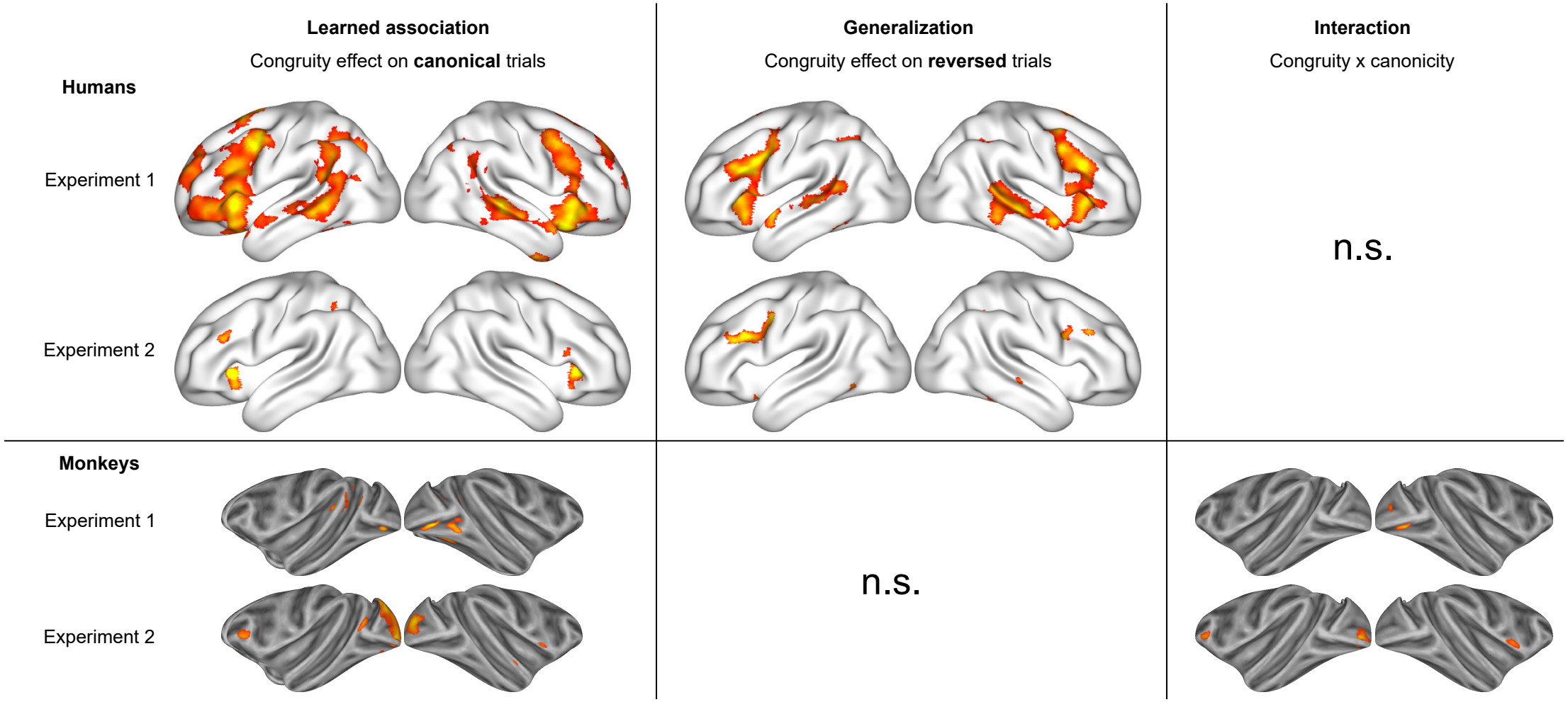
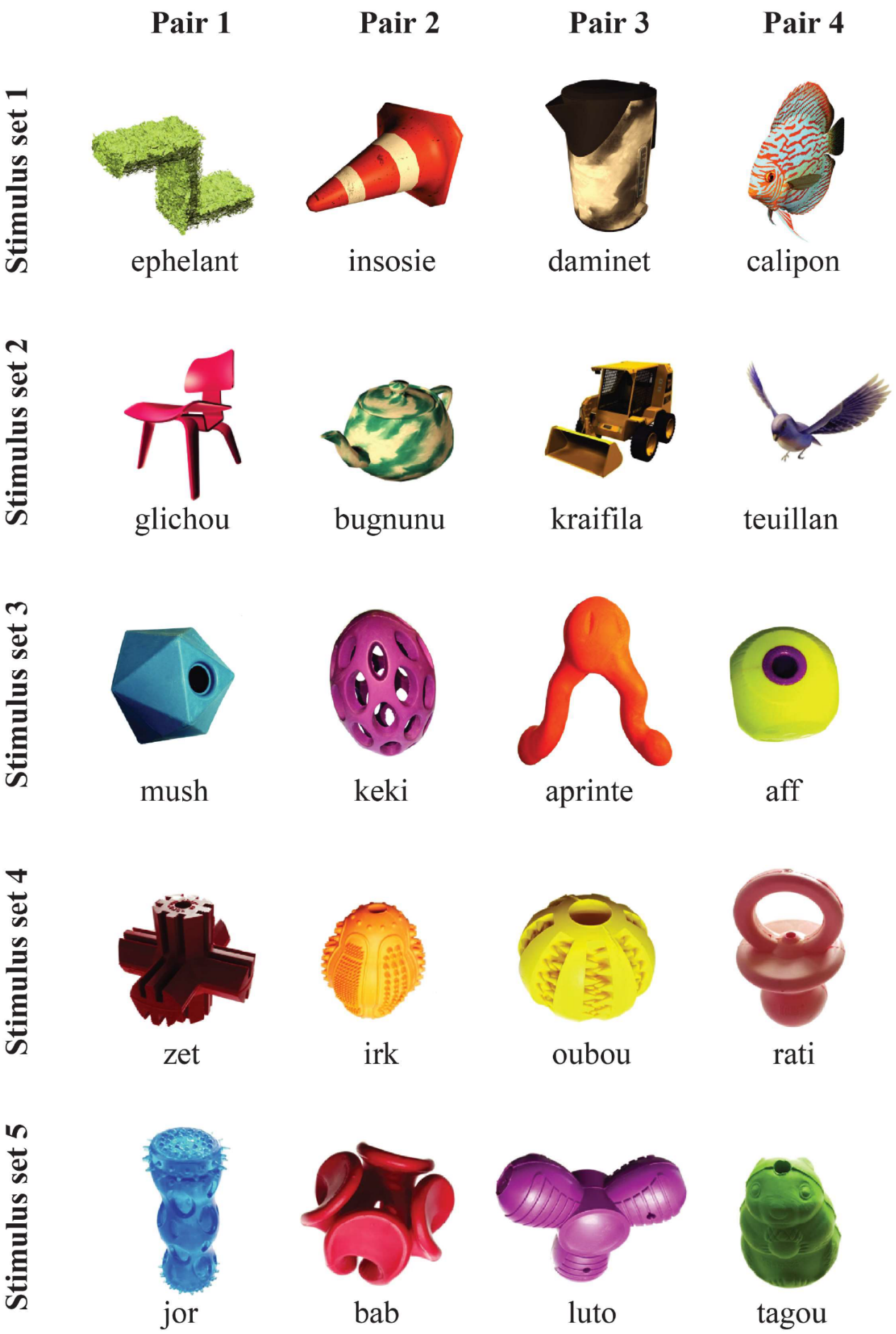


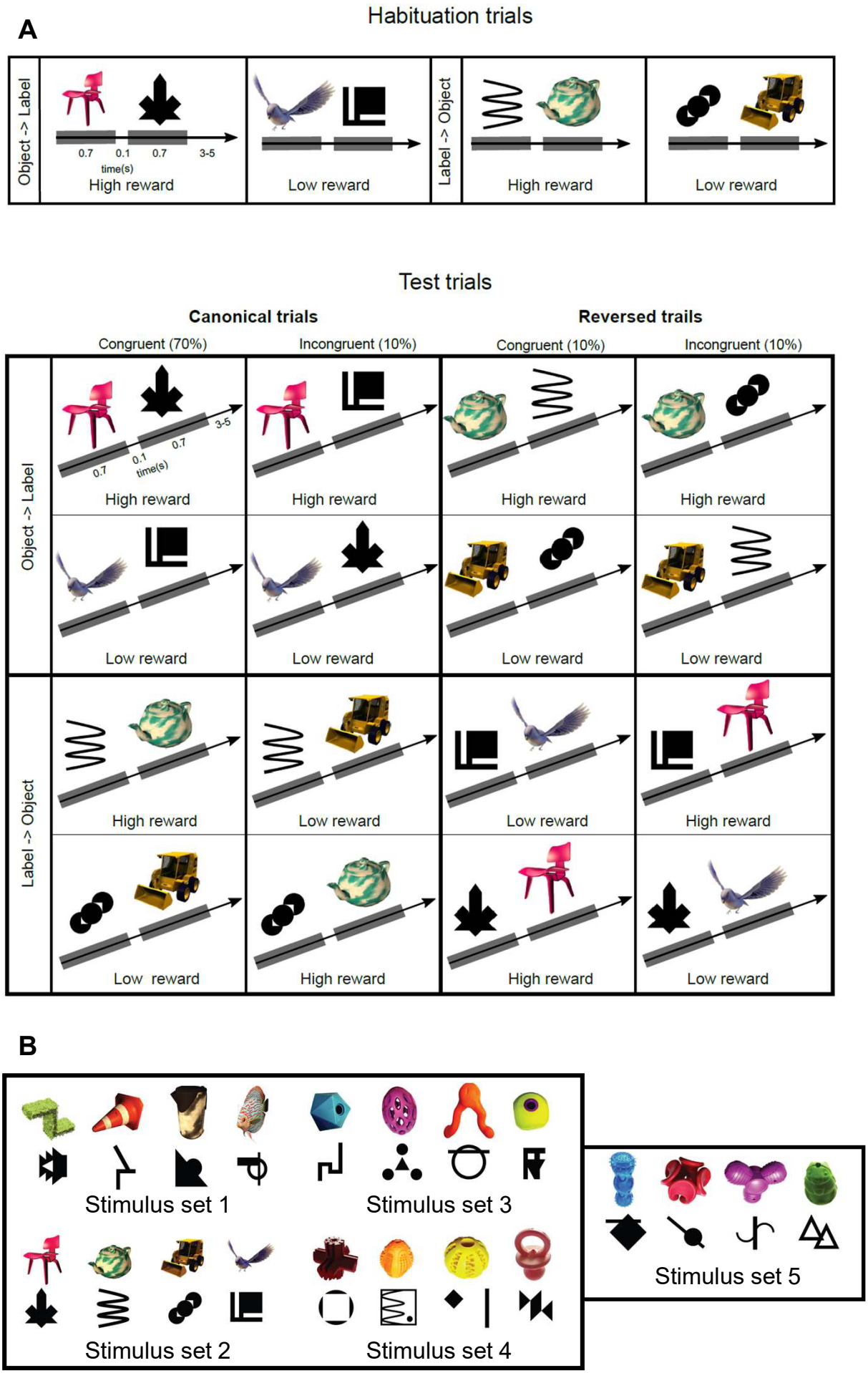
Figure 5


Learned association
Congruity effect on **canonical** trials
Generalization
Congruity effect on **reversed** trials
Interaction
Congruity x canonicity
Humans
Experiment 1
Experiment 2
n.s.
Monkeys
Experiment 1
Experiment 2
n.s.

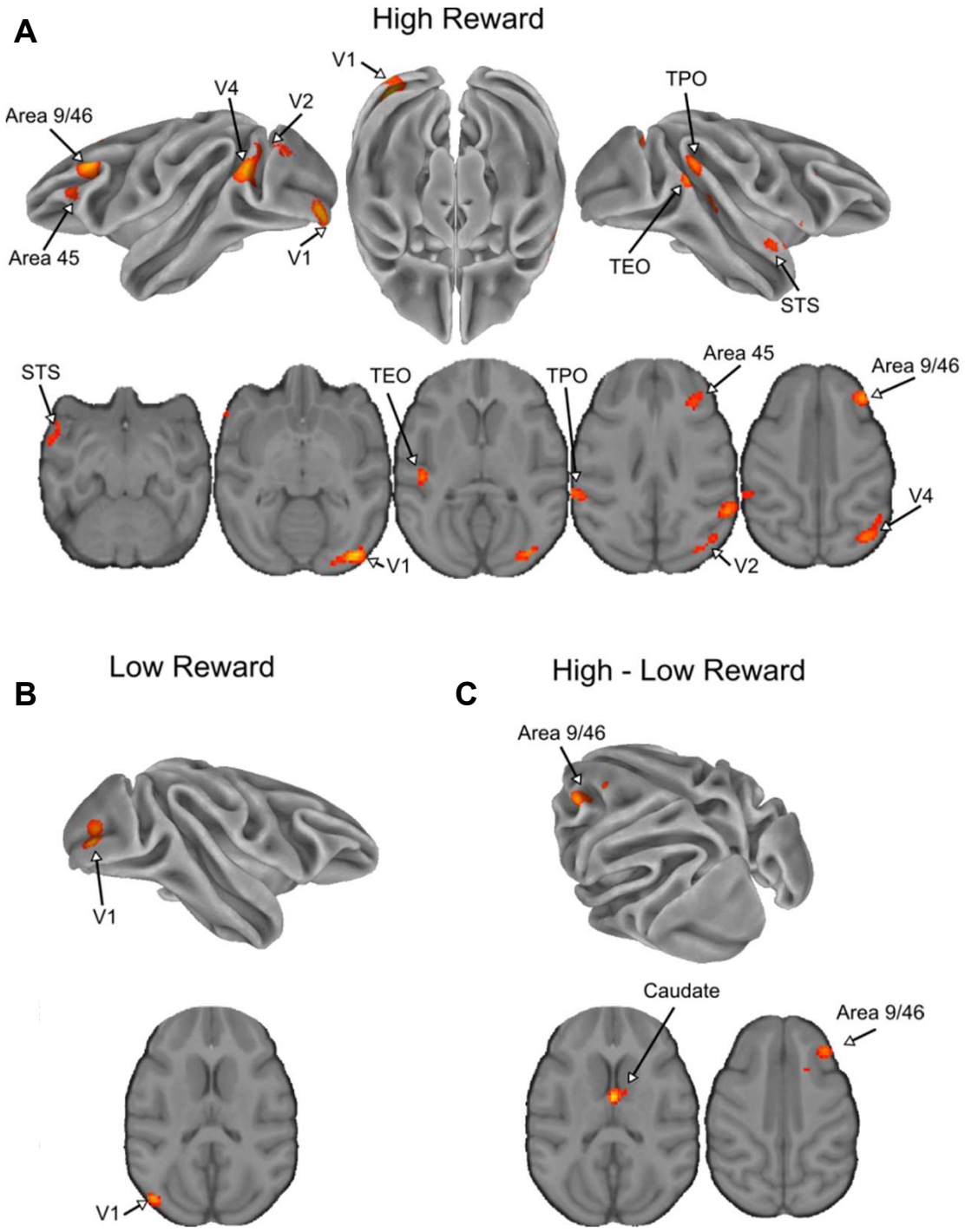
Supplementary Figure 1



Supplementary Figure 2

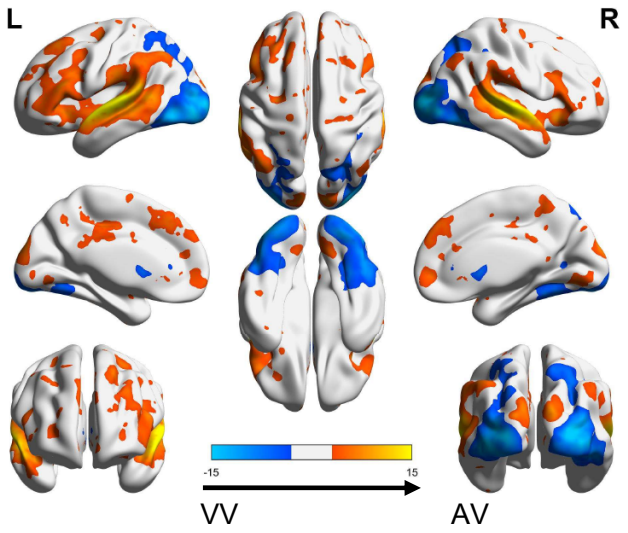


Supplementary Figure 3

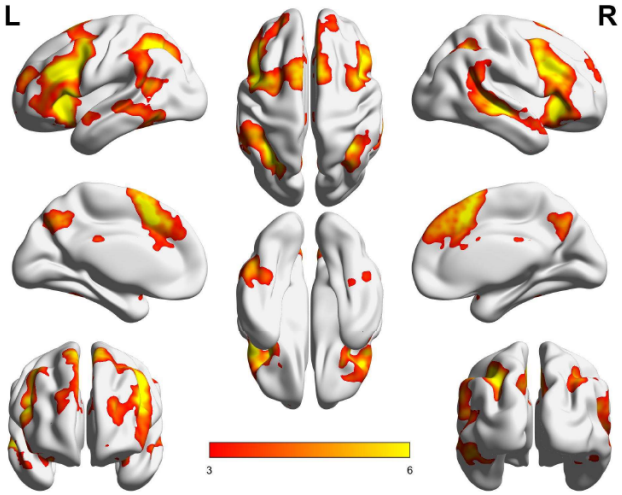


Supplementary Figure 4

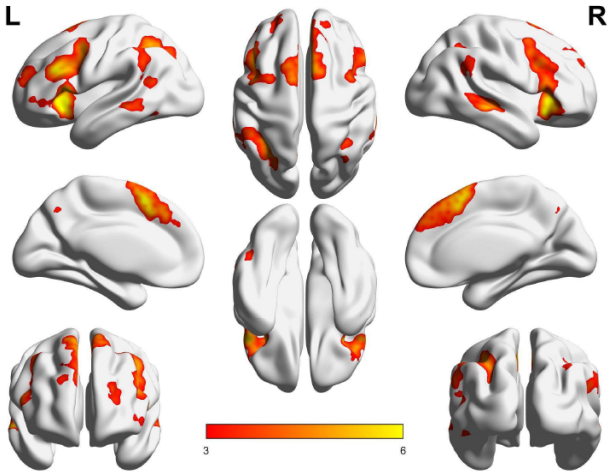
A Main effect: Exp1 vs. Exp2



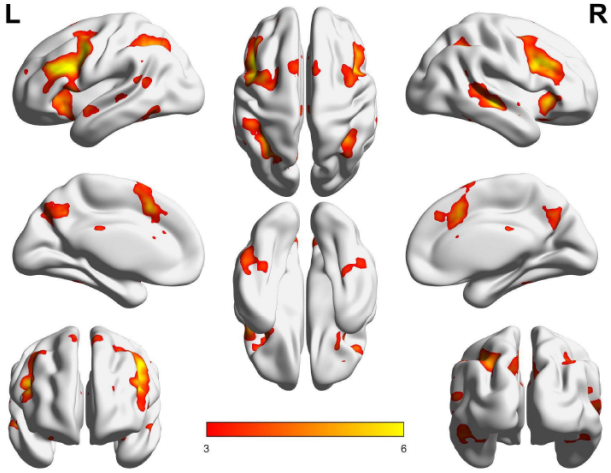
B Main congruity effect
Incongruent –Congruent trials



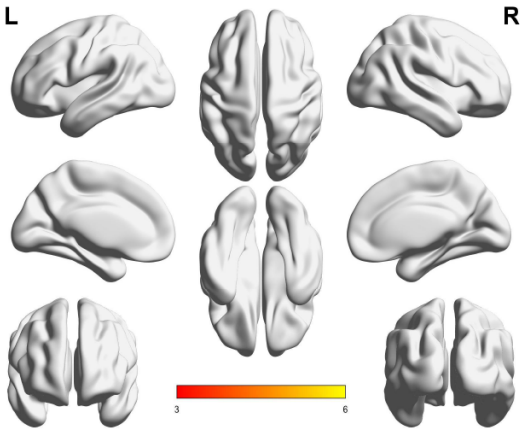
C Congruity effect in canonical trials
Incongruent –Congruent trials

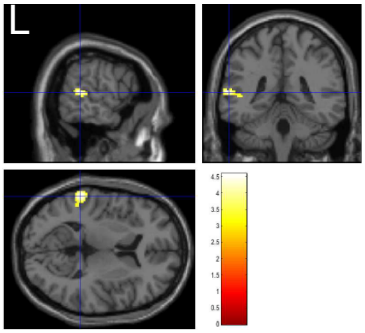


D Congruity effect in Reverse trials
Incongruent –Congruent trials



E Interaction Canonicity X congruity



F Larger congruity effect
in Exp1 than in Exp2

[-60 -40 8]