

Hemispheric asymmetries in categorical perception of orientation in infants and adults

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ARTICLE INFO

Article history:

Received 7 August 2009

Received in revised form 30 April 2010

Accepted 5 May 2010

Available online 16 May 2010

Keywords:

Spatial

Category

Lateralization

ABSTRACT

Orientation CP is the faster or more accurate discrimination of two orientations from different categories (e.g., oblique1 and vertical1) compared to two orientations from the same category (e.g., oblique1 and oblique2), even when the degree of difference is equated across conditions. Here, we assess whether there are hemispheric asymmetries in this effect for adults and 5-month-old infants. Experiment 1 identified the location of the vertical–oblique category boundary. Experiment 2, using a visual search task with oriented lines found that adult search was more accurate when the target and distractors were from different orientation categories, compared to targets and distractors of an equivalent physical difference taken from the same category. This effect was stronger for targets lateralized to the left visual field (LVF) than the right visual field (RVF), indicating a right hemisphere (RH) bias in adult orientation CP. Experiment 3, replicated the RH bias using different stimuli and also investigated the impact of visual and verbal interference on the category effect. Experiment 4, using the same visual search task, found that infant search was also faster when the target and distractors were from different orientation categories than the same, yet this category effect was stronger for RVF than LVF lateralized targets, indicating a LH bias in orientation CP at 5 months. These findings are contrasted to equivalent studies on the lateralization of color CP (e.g., Gilbert, Regier, Kay, & Ivry, 2005). The implications for theories on the contribution of the left and right hemispheres of the infant and adult brain to categorical computations are discussed.

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1. Introduction

There is converging evidence that the two hemispheres of the brain differ in the extent to which they process information categorically. For example, findings from studies using the visual half field technique, fMRI, rTMS and lesion studies suggest that categorical spatial relationships (e.g., on/off, left/right) are computed by the left hemisphere (LH), whilst co-ordinate spatial relationships (e.g., 4 cm, 2 cm) are computed by the right hemisphere (RH: e.g., Baci et al., 1999; Hellige & Michimata, 1989; Kosslyn et al., 1989; Laeng, 1994; Slotnick & Moo, 2006; Trojano, Conson, Maffei, & Grossi, 2006). A categorical bias for the LH is also found for other types of categorical processing. For example, research suggests that the LH is more efficient at forming category prototypes (e.g., Marsolek, 1995), that the LH encodes the basic-level category whereas the RH encodes the exemplars in object classification and recognition (e.g., Laeng, Zarrinpar, & Kosslyn, 2003; Marsolek, 1999; Marsolek & Burgund, 2008), and that LH activation, as measured by fMRI, increases as abstract categories are learnt (Seeger et al., 2000). This

body of research has led to a dominant view that the LH processes information in terms of categories, whereas the RH processes information metrically.

Further support for the pervasiveness of the categorical nature of the LH has been provided from evidence that categorical perception (CP) of color in adults is stronger in the left than the RH (e.g., Drivonikou et al., 2007; Gilbert, Regier, Kay, & Ivry, 2005). CP is found when stimuli along a physical continuum are parsed into separate categories, and the categorical relationship between stimuli affects the accuracy and/or speed of stimulus discriminations. For example, for color CP, two stimuli from different hue categories (e.g., B1 and G1) are discriminated faster or more accurately than stimuli from the same hue category (e.g., G1 and G2), even when same- and different-category stimulus hue separation sizes are equated. From a series of visual half field studies, it appears that color CP in adults is stronger for RVF-LH hue discriminations than for those in the LVF-RH. For example, adults are faster at searching for a colored target amongst colored distractors when the target and distractors are from different categories than from the same category, but this category effect is stronger when targets are presented to the RVF (Gilbert et al., 2005). The stronger category effect in the LH than the RH has since been replicated using different tasks and color category boundaries (e.g., Drivonikou et al., 2007;

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Roberson, Pak, & Hanley, 2008), and further evidence for LH color CP has been provided from Event-Related-Potential (ERP: Liu et al., 2009) and fMRI (Siok et al., 2009) studies.

However, research on the lateralization of color CP has also provided instances of categorical computations that are not LH lateralized. For example, blue-green color CP in 4–6-month-old infants appears to be lateralized to the RH. Infants are faster at initiating an eye-movement to a lateralized colored target presented on a colored background when the target and background are from different- than same categories, yet only when targets are lateralized to the LVF-RH (Franklin, Drivonikou, Bevis, et al., 2008). This evidence from infants challenges the view that there is always a LH bias in categorical processing. One theory that could account for RH infant color CP is that the pattern of color CP lateralization is dependent on whether linguistic processes contribute to the category effect. In support of this theory, color CP is also lateralized to the RH if toddlers have not reliably learnt the color terms for the relevant categories, but is lateralized to the LH for toddlers who have (Franklin, Drivonikou, Clifford, et al., 2008). One interpretation of this is that the onset of the LH bias in color CP is related to the lexicalization of the relevant categories. The LH bias could be due to a temporary on-line effect of the activation of verbal color codes on color judgments in the LH. Alternatively, color naming could lead to low-level perceptual change in the LH through a process of perceptual warping (see Özgen & Davies, 2002). In support of the former explanation, the category effect in the LH is reversed when verbal interference (remember a word) but not visual interference (remember a spatial grid) is added to the visual search task (Gilbert et al., 2005). However, the latter explanation is supported by evidence that the LH bias is accompanied with stronger activation for between- than within-category RVF discriminations in areas of visual cortex (Siok et al., 2009).

The research on the lateralization of color CP leads to the testable hypothesis that the lateralization of categorical processing in the brain depends on the underlying mechanisms of the categorical computation such as whether or not there is a contribution from language. If the findings for color CP extend to other types of categorical processing, then categorical processing should be lateralized to the LH when language contributes to the categorical computation, yet when there is no contribution of linguistic processes (as for pre-linguistic color CP) then categorical processing would actually be RH lateralized. To test these ideas we investigate the lateralization of orientation CP in both adults and infants. Although orientation is a physical continuum ranging from 0° to 360°, this continuum can be parsed into discrete categories (e.g., vertical, oblique, horizontal), and these categories affect discrimination in adults (e.g., Quinn, 2004; Rosielle & Cooper, 2001) and infants (e.g., Bomba, 1984; Quinn & Bomba, 1986; Quinn, Siqueland, & Bomba, 1985). In contrast to adult color CP, it has been argued that orientation CP is unlikely to be based on linguistic mechanisms, and is more likely to occur from low-level perceptual mechanisms ‘in the initial structure of the perceptual system’ (p. 904, Quinn, 2004). If orientation CP is purely perceptual, according to the theory of category lateralization outlined above, we could expect orientation CP to be RH lateralized in both adults and infants. Alternatively, the lateralization of orientation CP may be unrelated to whether or not language contributes to the category effect.

The current study investigated the lateralization of orientation CP in infants and adults, testing for CP around the vertical–oblique category boundary. Previous research has established that the orientation continuum is parsed into vertical and oblique categories at around 8.75° (perfect vertical = 0°)—participants classified any orientation between 0° and 8.75° as belonging to the vertical category (Quinn, 2004). Quinn (2004) found orientation CP across this category boundary using a recognition memory task where targets and foils were either both vertical (within-category ver-

tical: 5–7.5°), both oblique (within-category oblique: 10–12.5°) or straddled the vertical–oblique boundary (between-category: 7.5–10°). Adults’ recognition memory was at chance for within-category vertical and oblique, but was significantly better than chance for between-category discrimination, despite all target-foil pairs having an equal separation size of 2.5° across conditions. Similar categorical effects across the vertical–oblique category boundary are also found in infancy (e.g., Bomba, 1984). In Bomba’s study, a series of preliminary experiments established that the vertical–oblique category boundary for infants is in the same region as the adult boundary—at around 8–11° from the vertical. Orientation CP at 3 months was then tested for using the habituation technique (e.g., Bornstein, Kessen, & Weiskopf, 1976). Following habituation to one orientation, infants only dis-habituated to a novel stimulus when novel and habituated stimuli were from different categories (2.5–25°), and not when they were from the same category (22.5–45°), even though the degree of difference between habituated and novel orientations was equated (22.5°) in both conditions. The generalization of habituation to a same category but not a different-category stimulus indicates the greater perceived difference for between- than within-category stimuli (CP).

Although general orientation discrimination is thought to be lateralized to the RH (e.g., Corballis, Funnell, & Gazzaniga, 2002), there has been no investigation of lateralization of categorical processing of orientation. Even if the RH has an advantage for general orientation discrimination, it does not necessarily follow that the RH will also be more sensitive to the categorical difference between different orientations, and that orientation categories will have a stronger effect on discrimination in the RH. The current investigation provides a direct test of this. Experiment 1 replicates Quinn’s classification experiment to confirm the location of the vertical–oblique boundary. Experiment 2 tests for lateralized CP using the visual search task that was originally used to find LH color CP in adults (Gilbert et al., 2005), with LVF or RVF targets that were the same- or different-category to the distractors, yet here stimuli were oriented lines rather than colored patches. Experiment 3, using a different set of orientations, investigates the underlying mechanisms of orientation CP found in Experiment 2, by assessing the effect of adding verbal and visual interference to the visual search task. To further investigate the lateralization of orientation CP in the absence of a contribution from language, Experiment 4 investigated the lateralization of orientation CP in 5-month-old infants. An identical visual search task to the adult studies was used, and as for the study of lateralized infant color CP (Franklin, Drivonikou, Clifford, et al., 2008), eye-movement latencies to lateralized targets were recorded.

2. Experiment 1: establishing the category boundary with a classification task

To confirm the location of the category boundary between vertical and oblique, Experiment 1 used an adapted version of the classification task used by Quinn (2004). Participants were shown oriented lines varying from 0° to 30° in steps of 1° and were asked to indicate which one of two reference orientations (0° or 30°) each stimulus looked more like. Quinn’s task used 45° as a reference stimulus, but here we use 30° to check that the location of the category boundary is unaffected by stimulus range (e.g., Parducci, 1965). Quinn also tested a range of stimuli in steps of 2.5°, yet here we have steps of 1° to provide a more precise estimation of the category boundary.

2.1. Method

2.1.1. Participants

There were 25 participants, 16 of whom were male, with a mean sample age of 29.8 years (SD = 8.6). Participants were recruited from the University of Surrey,

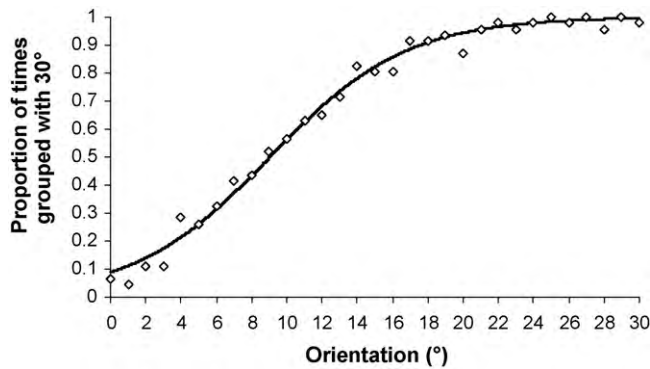


Fig. 1. Sigmoid classification curve fitted to the proportion of times that participants classified stimuli ranging from 0° to 30° as looking more like 30° than 0°.

gave informed consent before participating, and Ethics approval was granted by the University of Surrey Ethics Committee (as for all subsequent experiments).

2.1.2. Stimuli and task

Stimuli were black oriented lines (0.5 cm wide and 7.5 cm long) that were displayed on a grey background ($Y = 45.72 \text{ cd/m}^2$) on a Sony Trinitron CRT monitor, 57 cm from the participant with viewing distance maintained using a chin rest. There were 31 angles, varying in 1° steps from 0° (vertical) to 30°. Participants were presented with the two reference stimuli (0° and 30°) simultaneously, in left and right positions 110 mm from the central point of the monitor. Reference stimuli were shown for as long as participants needed, and then stimuli were presented centrally, one at a time in a random order, in the absence of the two reference stimuli. Participants were told to identify which one of the two reference stimuli each given stimulus most resembled by pressing left and right keys on a button box.

2.2. Results

Fig. 1 gives the percentage of times each stimulus was grouped with the 30° reference stimulus across the 25 participants. A sigmoid curve was fitted to the data: $y = a / (1 + \exp(-(x - b)/c))$; a = asymptote; b = point of inflection (9.05°); c = slope (3.88); $R^2 = 0.99$. Defining the category boundary using the sigmoid curve ($y = 0.5$), gave a vertical–oblique category boundary of 9.05°.

2.3. Discussion

The findings from the classification task indicate that the vertical–oblique boundary is around 9.05°—in the same region as the 8.75° boundary identified by Quinn, and in the same region as the 8–11° vertical–oblique boundary in infancy (Bomba, 1984). The boundary of 9.05° is used to classify stimulus pairs for all subsequent experiments.

3. Experiment 2: lateralized category effects on the visual search task

Gilbert et al. (2005) first established that color CP was lateralized to the LH using a visual search task where targets were lateralized to either the L- or RVF and were either the same or different category to distractors. Here, using their visual search task but with oriented line stimuli, we test the lateralization of orientation CP. Orientation category effects have previously been found on visual search tasks (e.g., for categories such as steep and shallow: Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992), yet not when using the classic CP design with within- and between-category stimulus pairs of equal physical difference. In Experiment 2, oriented lines were classified as vertical (less than 9.05°) or oblique (greater than 9.05°) on the basis of the classification curve in Experiment 1. Targets and distractors were either both vertical (within-category vertical), both oblique (within-category oblique) or straddled the vertical–oblique category boundary (between-category). As in Gilbert et al., targets

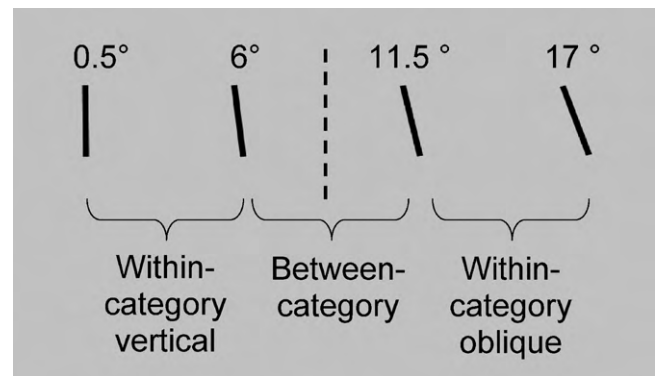


Fig. 2. The three stimulus pairs: within-category vertical; between-category; within-category oblique, with 5.5° difference in orientation for all three pairs. The stimuli shown here are anticlockwise from vertical, but a clockwise set was also used. The category boundary at 9.05° is indicated by a dashed line.

were presented only briefly to the LVF or RVF and participants had to decide the left/right location of the target. Stimulus separation sizes were increased from the 2.5° separation in Quinn's study to 5.5°, in order to make target detection achievable at short presentation times.

3.1. Method

3.1.1. Participants

There were 46 participants, 36 of whom were female, and the mean age of the sample was 19 years ($SD = 2.8$). Participants received course credits for their participation. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971) and only participants who were right handed were included in the study. All participants had normal or corrected-to-normal vision.

3.1.2. Apparatus and experimental setup

Stimuli were presented on a Sony Trinitron CRT monitor (model GDM-F520), with the centre of the monitor at the participants' eye-level and a viewing distance of 57 cm maintained using a chin rest. The experiment was conducted in a darkened room.

3.1.3. Stimuli and task

Stimuli were black lines that were 3 mm thick and 45 mm long. Stimuli were 0.5°, 6°, 11.5° or 17° from vertical (0°). There were two stimulus sets where stimuli were either oriented to the right of perfect vertical (clockwise set, $N = 23$) or to the left of perfect vertical (anticlockwise set, $N = 23$). Two sets were used (as a between-subjects factor) to check that any visual field differences in the category effect are unaffected by the left or right direction in which the stimuli are oriented. As the boundary between vertical and oblique was established to be around 9.05° in Experiment 1, two of the stimuli are classified as vertical and two of them as oblique. Three stimulus pairs were formed with a 5.5° difference in orientation between stimuli, giving a within-category vertical stimulus pair (0.5° and 6°), a between-category pair (6° and 11.5°) and a within-category oblique pair (11.5° and 17°) (see Fig. 2 for anticlockwise set).

Oriented line stimuli were presented in a ring at 12 locations. The search array was constructed by having 14 notional circles equally spaced around a larger notional circle of 110 diameter. Stimuli appeared in all notional circles except the top and bottom circles on the vertical midline which were neither left nor right (12:00 and 6:00 in terms of a clock face). The 12 notional circles used for stimulus locations defined the ends of the line stimuli and the lines were rotated around the midpoint of the circles. This resulted in the vertical midpoint of each line being equally separated for left and right visual field stimuli (see Fig. 3).

On each trial, one of the stimuli (the target) was of a different orientation to the 11 distractors. Each stimulus in a pair appeared for an equal number of times as the target or the distractor. The location of the target was randomized, with the constraint that the target appeared to the left or the right of fixation an equal number of times. There were six repeated-measures conditions (within-category oblique LVF and RVF; between-category LVF and RVF; within-category oblique LVF and RVF) with 16 trials per condition, giving 96 trials in total which were presented in a randomized order.

On each trial, a white central fixation dot was shown on a grey background ($Y = 45.72 \text{ cd/m}^2$) for 1250 ms, followed by a stimulus display for 250 ms, followed by the grey background that was presented until a response was made. Participants were asked to indicate the left/right position of the 'odd-one out' using two horizontally aligned buttons on a joystick, with the left index finger on the left button for left targets and the right index finger on the right button for right targets (as

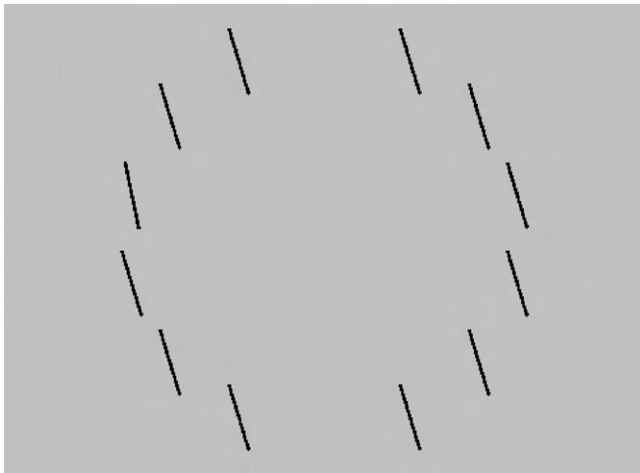


Fig. 3. Example of a stimulus display in Experiment 2, with one target which varies in orientation to the 11 distractors which are all of the same orientation.

in Gilbert et al., 2005). Participants completed 10 practice trials before starting the experimental trials.

3.2. Results

The mean percentage accuracy and the median RT on accurate trials were calculated for each of the six conditions for each participant. Analyses were conducted on accuracy and RT separately.

3.2.1. Accuracy

Three-way ANOVA with Stimulus Pair (within-category oblique/within-category vertical/between-category), Visual Field (LVF/RVF) and Set (clockwise/anticlockwise) as factors revealed a significant main effect of Stimulus Pair ($F(2, 88) = 14.43$, $p < .001$, $\eta_p^2 = 0.25$), and a significant interaction of Stimulus Pair and Visual Field ($F(2, 88) = 3.72$, $p < .05$, $\eta_p^2 = 0.08$; see Fig. 4). All other main effects and interactions were not significant (largest $F = 2.60$, smallest $p = .08$, $F = 0.42$, $p = .66$ for the three-way interaction).

To follow up the significant interaction of Stimulus Pair and Visual Field, one-way ANOVAs were conducted with Stimulus Pair as a factor, separately for both visual fields. There was a significant difference in accuracy across stimulus pairs for LVF ($F(2, 88) = 18.72$, $p < .001$, $\eta_p^2 = 0.30$), but not RVF targets ($F(2, 88) = 0.61$,

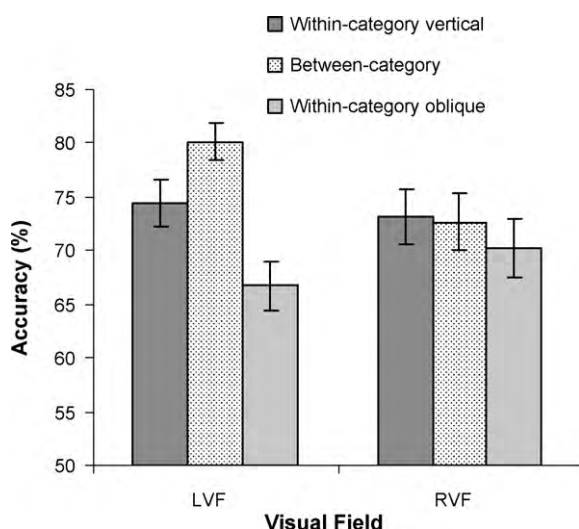


Fig. 4. Mean percentage accuracy ($\pm 1se$) for targets presented to the LVF and the RVF, for between-category trials and within-category oblique and vertical trials.

$p = .55$, $\eta_p^2 = 0.014$). In the LVF, accuracy was significantly greater for between-category than within-category vertical ($t(45) = 2.69$, $p < .05$) and within-category oblique ($t(45) = 6.51$, $p < .001$). In the LVF, accuracy was also greater for within-category vertical than within-category oblique ($t(45) = 3.08$, $p < .005$). Comparing across visual fields, between-category accuracy was greater for LVF than RVF targets ($t(45) = 2.29$, $p < .05$), yet there was no difference across visual field for either within-category vertical ($t(45) = 0.42$, $p = .67$), or within-category oblique trials ($t(45) = 0.99$, $p = .30$).

3.2.2. Reaction time

Three-way ANOVA with Stimulus Pair (within-category oblique/within-category vertical/between-category), Visual Field (LVF/RVF) and Set (clockwise/anticlockwise) as factors revealed no significant main effects or interactions for the analysis of median RT (largest $F = 1.16$, smallest $p = .32$). For the two-way interaction of Category and Visual Field and the three-way interaction: largest $F = 0.32$, smallest $p = .73$.

3.3. Discussion

Experiment 2 finds orientation CP on a visual search task, yet only for discriminations made in the LVF-RH. Whereas within- and between-category search was equally accurate for targets in the RVF, for the LVF, between-category search was significantly more accurate than either within-category vertical or within-category oblique search. It is unlikely that general hemispheric asymmetries in visuo-spatial attention (e.g., Kwon, Reiss, & Menon, 2002) could account for these results as a general bias in visuo-spatial attention should lead to visual field differences for both within- and between-category search, yet here it is only accuracy for the between-category condition that varies across visual field. Additionally, it appears that the enhanced accuracy for between-category search relative to within-category search is due to the categorical status of the target and the distractors rather than being due to other anisotropic effects. For example, the oblique effect (where there is greater sensitivity to cardinal vertical and horizontal orientations than oblique ones: e.g., Essock, 1980), would lead to greater accuracy for the within-category vertical pair which is closest to cardinal vertical than the between-category pair (although this effect could explain why within-category vertical is easier than within-category oblique). Orientation search asymmetries, such as the easier detection of oblique targets amongst vertical distractors than vertical targets amongst oblique distractors (e.g., Treisman & Souther, 1985), also cannot account for the pattern of findings in the current experiment. Therefore, we interpret the more accurate between- than within-category search in the LVF as evidence of RH lateralized orientation CP. The RH has an advantage over the LH for visual search when targets and distractors are from different orientation categories, but there is no difference between hemispheres when targets and distractors are from the same orientation category. RH lateralized orientation CP is the reverse pattern of lateralization to color CP which is LH lateralized (e.g., Gilbert et al., 2005).

4. Experiment 3: the effect of visual and verbal interference

There is converging evidence that the LH bias in color CP is due to the contribution of linguistic processes to color CP in adults (e.g., Siok et al., 2009). In Experiment 2, we find a RH bias in orientation CP. This RH bias may indicate that, unlike other forms of CP, orientation CP is dependent on perceptual rather than linguistic mechanisms (as asserted by Quinn, 2004). Experiment 3 investigated the contribution of linguistic and perceptual processes to orientation CP by assessing the impact of adding visual and verbal

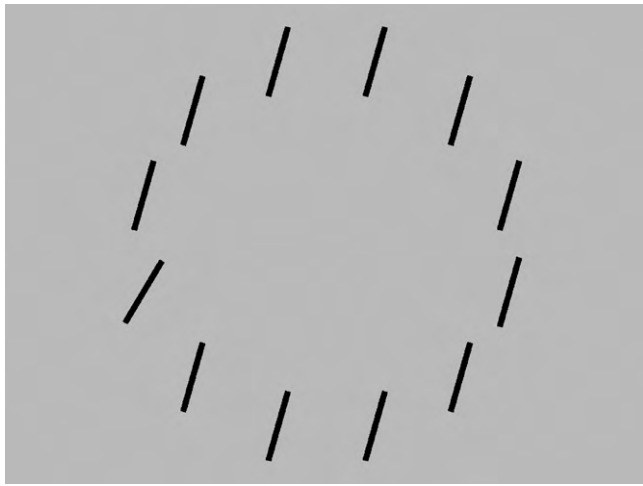


Fig. 5. Example of a stimulus display in Experiment 3, with one target which varies in orientation to the 11 distractors which are all of the same orientation.

interference to the visual search task. As in Gilbert et al., participants were required, whilst also completing the visual search task, to complete secondary visual or verbal interference tasks or no secondary task at all. The secondary tasks (based on those in Gilbert et al.) involved detecting the change in a nonsense word (verbal) or a spatial black and white grid (visual) when presented before and after the visual search trial. The stimulus separation size was increased from 5.5° (in Experiment 2) to 15° , both to compensate for increased task demands that could result from adding secondary tasks, and to verify that the effects of Experiment 2 generalize to other stimulus sets. This separation size is larger than the size of the vertical category, so a within-category vertical pair was not tested. As in Experiment 2, there were two stimulus sets with stimuli either oriented anticlockwise or clockwise from the vertical.

4.1. Method

4.1.1. Participants

There were 29 participants, 19 of whom were female, and the mean age of the sample was 24.8 years ($SD=2.5$). All other participant details were identical to Experiment 2.

4.1.2. Apparatus and experimental setup

Apparatus and experimental setup was identical to Experiment 2.

4.1.3. Stimuli and task

Oriented line stimuli were presented in a ring at 12 locations that were equally separated from the vertical midpoint of each line, on a notional circle of 110 mm diameter from a white central fixation dot. In terms of a clock face, one location was at 12:30 and the remaining locations were at hourly intervals thereafter (see Fig. 5). Stimuli were generated offline using the Microsoft .NET GDI+ software with high quality antialiasing to ensure smoothness of lines. There were two stimulus sets (sets 1 and 2), each with three stimuli that were 1° , 16° or 31° either anticlockwise ($N=14$) or clockwise from vertical ($N=15$). On the basis of the classification curve in Experiment 1, the three stimuli in a set formed within-category oblique (16° and 31°) and between-category (1° and 16°) pairs,¹ with a 15° difference for both pairs. All other stimulus details were identical to Experiment 2. There were 24 trials per condition (within-category LVF, within-category RVF, between-category LVF, between-category RVF) for each of the secondary task conditions, giving 96 trials

per secondary task, and 288 trials in total. Stimuli were presented in randomized order. Stimulus set (anticlockwise/clockwise) was a between-subjects factor.

At the start of a trial the central fixation dot was shown for 1250 ms and was followed by a blank grey screen (no interference); a nonsense word (verbal interference) or a black and white grid (visual interference) for 1250 ms. The fixation dot was then shown again for 1250 ms and the visual search display followed for 200 ms. There were 11 nonsense words: 'falc', 'lonn', 'basc', 'dasy', 'jafe', 'bris', 'eang', 'nist', 'efol', 'pake' and 'bawn'. The black and white grids were 5 cm squared, with 12 black and 13 white squares and a set of 11 different patterns. Participants were asked to indicate the left/right position of the 'odd-one out' on the visual search display using two horizontally aligned buttons on a joypad, with the left index finger on the left button for left targets and the right index finger on the right button for right targets (as in Gilbert et al., 2005). For the verbal and visual interference conditions participants were required to press a central key with both index fingers when the secondary task stimulus was identical to the one on the previous trial (stimulus was the same as previous one on 10% of trials). Secondary task conditions were blocked in a randomized order and within these blocks, the order of trials was randomized. Participants completed 8 practice trials of each secondary task condition before starting the experimental trials.

4.2. Results

Trials were excluded where a response on the secondary task was made, to prevent secondary task responses from slowing down the visual search task response (13.1% of trials). The mean percentage accuracy and the median RT on accurate trials were calculated for each of the four conditions, for each participant.

4.2.1. Accuracy

A four-way ANOVA with Category (within-category/between-category), Visual Field (LVF/RVF), Set (clockwise/anticlockwise) and Task (none/verbal/visual) was conducted on accuracy. There was significantly greater accuracy for between-category (mean = 91.92%, $SD=5.98$) than within-category (mean = 89.73%, $SD=5.74$) trials, $F(1, 28)=12.85$, $p<.005$, $\eta_p^2=0.32$. There was also significantly greater accuracy for RVF (mean = 92.66%, $SD=6.76$) than LVF (mean = 88.52%, $SD=7.02$) targets, $F(1, 28)=7.30$, $p<.05$, $\eta_p^2=0.21$. There were no other significant main effects or interactions (largest $F=2.98$, smallest $p=.06$), including no significant interaction of Category and Visual Field or three-way or four-way interactions of Category and Visual Field with Set or Task (largest $F=0.41$, smallest $p=.53$).

4.2.2. Reaction time

A three-way ANOVA with Category (within-category/between-category), Visual Field (LVF/RVF) and Task (none/verbal/visual) as factors was conducted on median RTs. Between-category trials (mean = 575 ms, $SD=80$) were significantly faster than within-category (mean = 595 ms, $SD=97$), $F(1, 28)=10.05$, $p<.005$, $\eta_p^2=0.27$. There was also a significant three-way Category, Visual Field and Task interaction, $F(2, 56)=4.80$, $p<.05$, $\eta_p^2=0.15$ (see Fig. 6). There were no other significant main effects or interactions (largest $F=2.32$, smallest $p=.14$).

To follow up the significant three-way interaction, two-way ANOVAs with Category and Visual Field as factors were conducted for each secondary task separately.

4.2.3. No interference

For the no interference condition, there was a significantly faster accurate response for between-category (mean = 570 ms, $SD=92$) than within-category (mean = 591 ms, $SD=109$), trials, $F(1, 28)=5.57$, $p<.05$, $\eta_p^2=0.17$. The speed of accurate response was not significantly different for RVF and LVF targets ($F(1, 28)=0.46$, $p=.51$, $\eta_p^2=0.02$), yet there was a significant interaction of Category and Visual Field, $F(1, 28)=4.91$, $p<.05$, $\eta_p^2=0.15$. Paired samples t -tests revealed a significant category effect for the LVF ($t(28)=3.46$, $p<.005$), but not the RVF ($t(28)=0.39$, $p=.70$). Paired samples t -tests also revealed a difference in reaction time for LVF

¹ As Experiment 3 is concerned with the contribution of language to orientation CP, a preliminary naming experiment was also conducted to check that stimuli were named in line with category membership. A separate group of participants (11 females, 2 males, mean age = 19 years, $SD\ age=1.19$) named each stimulus for clockwise and anticlockwise sets twice (as vertical or oblique) on a grey background (display same as in Experiment 1). Eighty-one percent of responses named 1° as vertical and 100% of responses named 16° and 30° as oblique. Therefore, the majority response indicates that stimuli are given different names for between-category pairs and the same name for within-category pairs, in line with category membership.

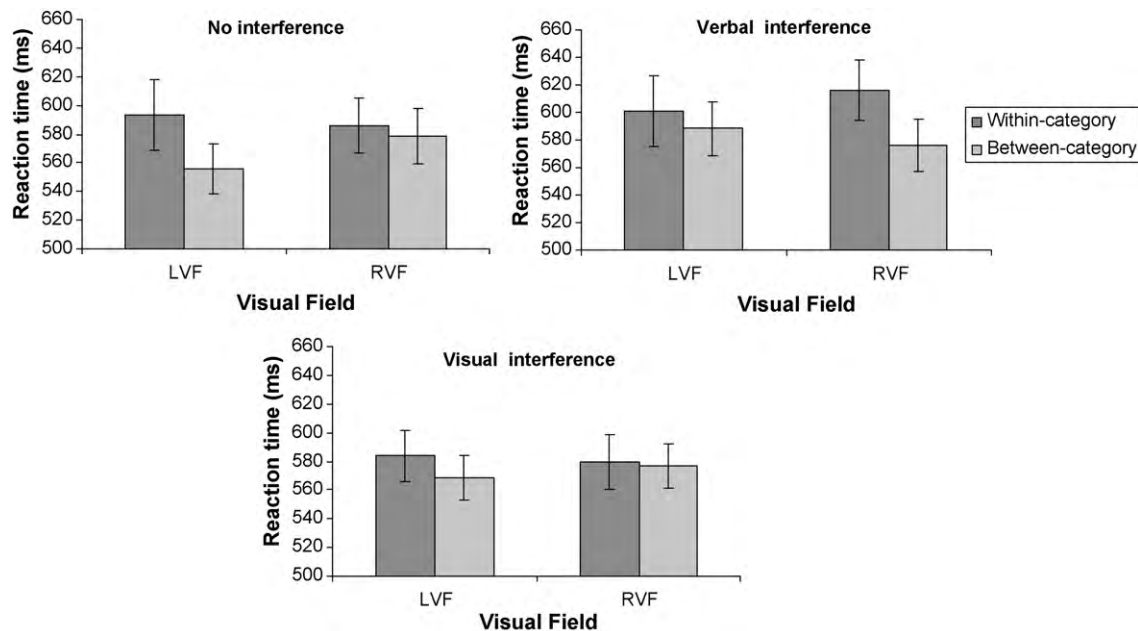


Fig. 6. Mean median reaction time (± 1 se) for targets presented to the LVF and the RVF, for within- and between-category trials, for the three secondary task conditions (none; verbal; visual).

and RVF targets that was approaching significance for between-category trials, $t(28)=1.85$, $p=.07$, but not for within-category trials, $t(28)=0.42$, $p=.68$.

4.2.4. Verbal interference

For the verbal interference condition, there was a significantly faster accurate response for between-category (mean = 583 ms, SD = 98) than within-category (mean = 611 ms, SD = 122), trials, $F(1, 28)=8.28$, $p<.01$, $\eta_p^2=0.23$. There was no significant main effect of Visual Field or interaction of Category and Visual Field (largest $F=2.76$, smallest $p=.11$: for the interaction).

4.2.5. Visual interference

Unlike the other secondary task conditions, there was no significant difference for between-category (mean = 573 ms, SD = 78) and within-category (mean = 583 ms, SD = 96), trials, $F(1, 28)=1.60$, $p=.22$, $\eta_p^2=0.05$. There was also no significant main effect of Visual Field or interaction of Category and Visual Field (largest $F=1.19$, smallest $p=.29$).

4.3. Discussion

In Experiment 3, for the no interference condition, there was a category effect in reaction time that varied with visual field. Between-category search was significantly faster than within-category for targets in the LVF, and there was no significant categorical effect for RVF targets. In addition to this lateralized category effect in reaction time, there was also a small but significant category effect in accuracy (around 3%) in both visual fields. These findings contrast to Experiment 2 (where smaller stimulus separations were used) in the way in which the category effect appeared in accuracy and reaction time measures. In Experiment 2, there was a substantial category effect for accuracy in the LVF, but no category effect in either visual field for reaction time. The presence of the minor category effect in accuracy for both visual fields in the no interference condition of the current experiment indicates some influence of orientation categories on visual search in the RVF. However, when the RT measure is considered as well, it is clear that the category effect is overall stronger in the LVF. Therefore, the no

interference condition of Experiment 3 suggests a less absolute lateralization of orientation CP than suggested by Experiment 2, but importantly the RH bias is replicated nevertheless.

Differences in orientation CP and its lateralization across the secondary task conditions were also found. These differences cannot be attributed to level of task demand as there were no significant differences in overall accuracy or speed across the different versions of secondary task. When verbal interference was added to the task, there was a category effect for both reaction time and accuracy. Therefore, with the addition of verbal interference to the visual search task, orientation CP remained. When visual interference was added to the task, there was a minor category effect in accuracy for both visual fields, although in contrast to the no interference and verbal interference conditions, there was no category effect in either visual field for reaction time. Therefore, the category effect in reaction time that was significant in the no interference and verbal interference conditions were no longer significant with visual interference.

The weakening of the category effect with visual interference and the survival of the category effect with verbal interference, could suggest that visual rather than verbal mechanisms underlie the effect. These effects of interference are in contrast to color CP which is eliminated by verbal but not visual interference, and could support Quinn's (2004) claim that orientation CP, unlike color CP, results from low-level perceptual processes rather than linguistic ones. If orientation CP is 'language independent' and RH lateralized, yet adult color CP is 'language dependent' and LH lateralized, we could infer that the lateralization of categorical computations in the brain is dependent on the underlying mechanisms of the categorical computation. More specifically, we could infer that categorical processing is lateralized to the LH when language contributes to the categorical computation (as for adult color CP), yet when there is no contribution from linguistic processes (e.g., for infant color CP and adult orientation CP), then categorical processing is RH lateralized.

However, there are further effects in Experiment 2 that hint that such a 'language theory' of category lateralization is inadequate. Although the addition of verbal interference did not eliminate orientation CP, it did appear to disrupt how the category effect was distributed across the two hemispheres. When there was no inter-

ference or when visual interference was added to the search task, there was no RVF category effect for reaction time. However, when verbal interference was added to the task, there was an overall category effect for reaction time that did not significantly vary across visual field. It is unclear why the addition of verbal interference appears to strengthen the LH category effect relative to the no interference and visual interference conditions. The addition of verbal interference should minimize linguistic processes such as the activation of stimulus verbal codes in the LH, yet the category effect in the LH actually appears to strengthen rather than reduce under these conditions. Therefore, if we assume verbal interference is minimizing linguistic processes, the findings do not fit with the theory that LH category effects are linguistic. However, although the interference tasks are clearly likely to elicit different levels of linguistic processing, and the level of task demand was equated across verbal and visual interference condition, it should also be recognized that the two tasks varied on other dimensions (e.g., spatial scale) which potentially could contribute to the pattern of effects. A purer method, that avoids these issues and ensures there is no linguistic processing at all, is to test pre-verbal infants who cannot name the stimuli. Therefore, we do this in Experiment 4. This will provide a further test of the theory that category lateralization depends on the contribution from language, and the findings could help to clarify the effects of verbal interference outlined above.

5. Experiment 4: lateralized category effects on a visual search task in infants

As outlined in Section 1, infants also respond categorically around the vertical–oblique category boundary (e.g., Bomba, 1984). Experiment 4 assesses whether orientation CP is lateralized in the infant brain. The visual search task from Experiment 3 was used but with a few modifications. As infants are unable to indicate manually whether the target appeared on the left or right of central fixation, we record eye-movements with an eye-tracker and use an eye-movement latency measure instead. Before each trial, infants were centrally fixated with a looming and contracting visual ‘attention-getter’ and on central fixation the search display was shown for 1500 ms. The time to target fixation would not be an appropriate measure to investigate hemispheric asymmetries, as once an eye-movement has been made away from central fixation the target would no longer be lateralized to right or left visual fields. Therefore, as in previous research (e.g., Franklin, Drivonikou, Bevis, et al., 2008; Franklin, Drivonikou, Clifford, et al., 2008), the time that elapsed before the initiation of an eye-movement from central fixation directly to the target was recorded. Infants were centrally fixated and targets appropriately lateralized for the duration of the initiation time measure. Eye-movement initiation time and reaction time measures reveal an equivalent pattern of hemispheric asymmetry in adults (Franklin, Drivonikou, Bevis, et al., 2008). The accuracy of infants in making a direct eye-movement to the target was also assessed to check that accuracy was above chance.

On the basis of previous research (e.g., Bomba, 1984) it is expected that infants will be faster at initiating an eye-movement to the target when the target and distractors are between- rather than within-category. There are several predictions that can be made about the lateralization of this category effect in pre-verbal infants. If categorical processing is only lateralized to the LH when language contributes to the categorical computation, then we would predict that there will be no LH lateralization for orientation CP in infants. If the findings for infant color CP extend to other domains, then we would predict that there will actually be RH lateralized orientation CP in infants. However, on the basis of the finding from Experiment 3 that the LH category effect appears to strengthen with verbal interference, we could also predict that orientation CP in infants

will be LH lateralized. A LH lateralization of categorical processing in infancy would provide evidence against the theory that the lateralization of categorical computations depends on the direct contribution from language.

5.1. Method

5.1.1. Participants

Thirty-nine 5-month-old infants took part in the study. Eight infants were excluded from the study for general fussiness/excessive movement that meant the infant could not be eye-tracked or the infant could not sustain their attention to the computer monitor. A further 10 infants were excluded for a strong side bias in looking at the left (6) or right (4) of the monitor which meant that targets on the contralateral side to the bias were never fixated. The remaining 21 infants had a mean age of 24.46 weeks (1.04), with 10 males. All infants were born full term and the mean birth weight of the final sample was 3.51 kilograms (SD = 0.38). All infants were Caucasian and lived in mainly middle-class households.

5.1.2. Apparatus and experimental setup

The apparatus and experimental setup was identical to Experiments 2 and 3 with the exception that infants were strapped into an infant car-seat that was mounted at eye-level to the centre of the monitor at a distance of 57 cm. Eye-movements were recorded with an ASL 504 pan/tilt eye-tracking camera placed under the monitor, recording at 50 Hz. The eye-movement output gave a video of what the participant was shown with ‘cross-hairs’ superimposed. Cross-hairs are two crossing lines (one vertical and one horizontal), and where they cross indicates point of gaze. The output was digitized by using an analogue-to-digital video converter (Canopus ADVC-300), and the digital video was analyzed with i-Movie 2.1.2 software.

5.1.3. Stimuli and task

The stimuli and stimulus display for the visual search task were identical to Experiment 3 except that the search display was shown for 1500 ms and stimuli were 0°, 30° or 60°. As for Experiments 2 and 3, there were two stimulus sets (between-subjects factor), with the three stimuli varying either anticlockwise ($N = 11$) or clockwise from vertical ($N = 10$). The three stimuli in a set formed within-category oblique (30° and 60°) and between-category (0° and 30°) pairs, with a 30° difference for both pairs as in Experiment 3. There was a maximum of 24 trials per condition (within-category LVF, within-category RVF, between-category LVF, between-category RVF), giving a maximum of 96 trials in total, with trial order randomized. The session was ended when infant looking appeared to wane, or when the infant had completed all 96 trials.

5.2. Results

Infants completed on average 74.9 (SD = 16.6) trials. Trials were excluded from the analysis if fixation was not central at the start of the trial or if the eye-movement signal was lost before the initiation of an eye-movement to the target. This left on average 59.6 (SD = 16.6) valid trials per infant, and all infants had at least 6 included trials per condition. The accuracy of direct target detection was calculated by calculating the percentage of valid trials where a direct eye-movement to the target from central fixation was made. The latency of direct eye-movements to the target (‘initiation time’) was calculated by calculating the time that elapsed between stimulus onset and the initiation of the direct eye-movement to the target.

5.2.1. Accuracy

The percentage of trials for which infants went straight from central fixation to the target was calculated for all four conditions to check that infants were significantly above chance at making a direct eye-movement to the target (within-category LVF: mean = 23.53%, SD = 15.15; within-category RVF: mean = 26.13%, SD = 16.77; between-category LVF: mean = 23.57%, SD = 11.09; between-category RVF: mean = 31.56%, SD = 13.22). If the first eye-movement from central fixation was always made to a stimulus, then as there were twelve stimuli, there would be an 8.33% (1/12) probability that a target would be fixated by chance. One-sample *t*-tests against a test value of 8.33 revealed that infants were significantly above chance at making a direct eye-movement to the target in all four conditions (smallest $t = 4.47$, largest $p = .001$).

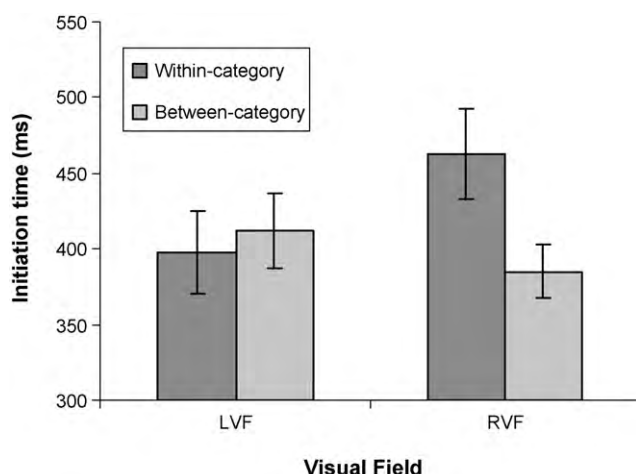


Fig. 7. Mean median initiation time (± 1 se) for direct eye-movements to the target, for within- and between-category conditions, for LVF and RVF targets.

5.2.2. Initiation time

Fig. 7 gives the initiation time for direct eye-movements to the target, on trials where the target and distractors were within-category or between-category, for LVF and RVF targets.

Three-way ANOVA with Category (within-category/between-category), Visual Field (LVF/RVF) and Set (clockwise/anticlockwise) as factors revealed a significant interaction of Category and Visual Field, $F(1, 19)=8.59$, $p<.01$, $\eta_p^2=0.31$. All other main effects and interactions were not significant (largest $F=2.57$, smallest $p=.13$ was for the main effect of Category: within-category mean=430 ms, $SD=116$; between-category mean=399 ms, $SD=78.10$), including a non-significant three-way interaction ($F=0.40$, $p=.54$). Paired samples t -tests revealed a significant category effect for the LVF, $t(20)=3.70$, $p<.005$, but not the RVF, $t(20)=0.5$, $p=.62$. There was also a significant difference in reaction time for LVF and RVF targets for within-category trials, $t(20)=2.31$, $p<.05$, but not for between-category trials, $t(20)=0.99$, $p=.33$.

5.3. Discussion

Experiment 4 finds LH lateralized orientation CP in 5-month-old infants. Infants were above chance at making a direct eye-movement to the target for all conditions. When infants did make a direct eye-movement to the target, the latency of this eye-movement was shorter when the target and distractors were between-category than within-category, but only when the target was presented to the RVF. The difference in this category effect across visual fields was actually due to within-category search being significantly slower for RVF than LVF targets—between-category search did not vary with visual field. These findings therefore indicate that the infant LH is relatively slow at discriminating two angles if they are from the same category.

The findings for infant orientation CP help to clarify the apparent strengthening of the LH category effect when verbal interference was added to the visual search task in Experiment 3. Comparison of the infant data (see Fig. 7) with the adult data when verbal interference is added to the task (see Fig. 6) reveals the striking similarity in how the category effect is distributed across the two hemispheres under these conditions. One interpretation of the effect of verbal interference is that reducing the activation of verbal codes for the stimuli during the search task strengthened the LH category effect. The infant data is consistent with this interpretation, as for infants who have no access to the verbal codes for the stimuli at all, the category effect is strongly LH lateralized. We discuss this further in Section 6.

The finding of LH orientation CP in pre-verbal infants provides strong evidence against claims that categorical processing is only lateralized to the LH when language contributes to the categorical computation. Whilst some LH biases in categorical processing, such as the LH bias in adult color CP, may well be due to linguistic processes such as the activation of verbal codes for stimuli (e.g., Gilbert et al., 2005), or language induced perceptual change (e.g., Siok et al., 2009), it does appear that not all LH biases in categorical processing are directly linguistic. The findings also do not support the hypothesis that there is a general RH bias for non-linguistic categorical computations. Whilst infant blue-green color CP is RH lateralized (e.g., Franklin, Drivonikou, Bevis, et al., 2008), infant orientation CP appears lateralized to the opposite hemisphere. It therefore appears that neither hemisphere of the infant brain is generally dominant for categorical processing—rather the lateralization of categorical processing in infancy varies across domains.

Interestingly, for both orientation and color CP, the category effect is lateralized to the opposite hemisphere in infants and adults. Further research is needed to establish whether this is the case for other types of categories also. Opposite lateralization of categories for infants and adults may reflect different underlying mechanisms of infant and adult categorization. One theory of CP is that it results from two categorical processes—the expansion of perceptual space across the category boundary (between-category expansion) and the compression of perceptual space within a category (within-category compression: Harnad, 1987). The findings of the current investigation suggest that LH infant orientation CP is due to within-category compression, as within-category search in the RVF is slower relative to the other search conditions. In contrast, RH adult orientation CP appears to be due to between-category expansion, as between-category search in the LVF is faster/more accurate relative to the other search conditions. These different underlying mechanisms in the category effect could explain the opposite pattern of category lateralization for infants and adults.

Other than the previous investigation of infant color CP and the current investigation of infant orientation CP, there have been no other published studies of how categorical processing of visual continua is lateralized in the infant brain. This is surprising given that categorization is a pervasive aspect of infant cognition (e.g., Mareschal & Quinn, 2001). Further developmental research on the lateralization of different types of categorical computations (e.g., categorization, prototype formation, category learning) for a range of different domains (e.g., shape, spatial relations, size), is needed to further understand the contribution of the left and right hemispheres to categorical processing in infancy. This research could help to clarify the factors that contribute to the functional organization of categorical processing in the infant brain, and could also contribute to a greater understanding of how the infant brain categorizes the visual world in the absence of language.

6. General discussion

The set of experiments presented here aimed to investigate the contribution of the left and right hemispheres of the human brain to categorical processing by investigating the lateralization of orientation CP in infants and adults. In two experiments using different stimulus sets (Experiments 2 and 3), adults were faster or more accurate at detecting targets amongst different- than same-category distractors even though the difference in orientation between targets and distractors was equated across conditions. In both of these experiments (when there was no secondary task), the effect of orientation categories on discrimination was stronger for discriminations made in the LVF than those in the RVF. This evidence suggests that orientation CP is lateralized to the RH in adults. In Experiment 3, the category effect appeared to weaken with the

addition of visual interference but not verbal interference to the search task. However, verbal interference did appear to affect how the category effect was distributed across the two hemispheres, with a suggestion that there was a strengthening of the category effect in the LH when verbal processes were interfered with. Consistent with this finding, in Experiment 4, orientation CP was strongly LH lateralized for pre-verbal 5-month-old infants. Infants were faster at initiating an eye-movement to targets amongst different-than same-category distractors, but only for targets presented to the RVF. This evidence suggests that orientation CP is lateralized to the LH in infants.

Collectively, these findings have several implications for theories of the contribution of the left and right hemispheres of the brain to categorical processing. First, the finding of RH lateralized orientation CP in adults challenges the dominant view that the LH has a general bias for categorical processing in adulthood (e.g., Kosslyn et al., 1989). It appears that the RH of the adult brain can also be dominant for some types of categorical computations. Second, the finding of LH lateralized orientation CP in infants challenges the theory that a LH category bias is due to the contribution of linguistic processes to the categorical computation (e.g., Gilbert et al., 2005). We provide clear evidence of a non-linguistic LH category effect. Therefore, although some LH biases in categorical processing could be due to language (such as LH adult color CP), the findings from the infant experiment here indicate that the LH can also be categorical in the absence of language. Third, LH infant and RH adult orientation CP challenges the theory that there is a general RH to LH developmental trajectory for category lateralization (e.g., Franklin, Drivonikou, Bevis, et al., 2008). For blue-green color CP, there is a RH to LH change in lateralization from infancy to adulthood, yet an opposite developmental trajectory is found for the lateralization of orientation CP.

Overall, the findings suggest that a language theory of category lateralization, where categorical processing is lateralized to the LH when there is a contribution from language but to the RH in the absence of language, is inadequate. Strangely however, language does seem to be somehow related to how orientation CP is lateralized, as when adults' verbal processes are interfered with, there are signs that the LH bias re-emerges. A strengthening of a LH category effect with a reduced contribution from language is of course counterintuitive to what one would expect based on the evidence that it is the LH which is language dominant. However, there are other ways in which language could affect category lateralization other than having a direct influence on strengthening categorical distinctions in the LH. For example, the presence of language could change categorization strategies such that the temporal dynamics of categorical processing or the contribution from low-level perceptual processes is affected and this could in turn affect the pattern of asymmetry. Although the role of language in the LH bias for categorical judgments of spatial relations has been considered (e.g., Kosslyn et al., 1989; Parrot, Doyon, Démonet, & Cardebat, 1999; Vauclair, Yamazaki, & Güntürkün, 2006), the role of other factors such as the effect of the temporal dynamics of categorical processing (e.g., van der Ham, van Wezel, Oleksiak, & Postma, 2007) and hemispheric differences in receptive field size, input from magnocellular and parvocellular pathways and the processing of high and low spatial frequency (e.g., Kosslyn, Chabris, Marsolek, & Koenig, 1992; Okubo & Michimata, 2004) have also been proposed. In addition, some investigations of hemispheric asymmetries in object categorization suggest that different strategies for categorization that vary with different stimulus features or task demands can affect the lateralization of categorical processing (e.g., Studer & Hübner, 2008). Language may interact with factors and effects such as these and the resulting interaction could explain both why the lateralization of categorical processing varies for infants and adults and also why it varies across different perceptual domains.

We propose that language does not directly determine category lateralization, but tentatively speculate that language affects the underlying mechanisms and strategies of categorical processing, and that it is these different mechanisms and strategies that vary in their lateralization. The current investigation provides evidence to suggest that the degree of linguistic processing affects the underlying mechanisms of CP. For example, pre-verbal orientation CP in infants is characterized by within-category compression, yet the adult CP is due to between-category expansion, with hints that within-category compression becomes stronger with verbal interference. If the computation of within-category compression or between-category expansion differ in their temporal characteristics or draw on different resources, and if these characteristics or resources vary across hemisphere, this could explain the varying patterns of CP lateralization for infants and adults. At this stage we cannot provide a more comprehensive explanation for why infant and adult CP varies in lateralization or why orientation and color CP follow opposite patterns of lateralization across development. The main contribution of the current investigation is to establish that language alone cannot explain how categorical processing is lateralized in the human brain, and to identify that a more comprehensive account of category lateralization needs to be developed with further research.

Consideration of the network of brain areas involved in categorical computations, as well as the time course and contribution from low-level and higher-order processes, should provide greater insight into how and why categorical processing is lateralized. For color, these issues have started to be investigated using ERP and fMRI techniques (e.g., Clifford, Franklin, Davies, & Holmes, 2009; Fonteneau & Davidoff, 2007; Holmes, Franklin, Clifford, & Davies, 2009; Liu et al., 2009; Siok et al., 2009). Equivalent studies are needed for orientation CP. For example, although it is known that areas of visual cortex (V1, V2, V3, VP) segregate neurons tuned to specific orientations (e.g., Vanduffel, Tootell, Schoups, & Orban, 2002), it is unknown whether orientation is coded categorically in these regions (Wakita, 2004). Studies that investigate orientation and color CP using ERP and fMRI techniques could provide answers for why orientation and color CP are lateralized to opposite hemispheres for both infants and adults.

7. Conclusions

The contribution of the left and right hemispheres of the adult human brain to categorical processing has been extensively investigated for a wide range of categorical processes and domains. Although there is converging evidence that categorical computations are lateralized to the LH (e.g., Gilbert et al., 2005; Kosslyn et al., 1989; Marsolek & Burgund, 2008), the investigation of infant color CP (Franklin, Drivonikou, Bevis, et al., 2008) and adult orientation CP in the current investigation has revealed two instances where categorical computations are actually RH lateralized. In addition, although there is evidence that some LH biases in categorical processing are due to the linguistic nature of the LH (e.g., Franklin, Drivonikou, Clifford, et al., 2008; Gilbert et al., 2005), the current investigation, by finding LH orientation CP in pre-verbal infants, provides evidence of a LH categorical bias that cannot be attributed to language. Orientation and color appear to follow an opposite developmental trajectory for category lateralization, although categorical processing in infants is lateralized to the opposite hemisphere than in adults for both domains. A simple language theory of category lateralization cannot account for the findings. Instead, it is suggested that we need to look beyond language to fully explain how and why categorical processing is lateralized in the human brain.

Acknowledgements

We thank Katie Chittenden, Sarah Finnegan, Emily Gibbons and Sarah Harris for assistance with data collection and Paul Sowden and Ian Davies for discussion of the findings. We thank two anonymous reviewers for their constructive comments. This research was supported by ESRC grant RES-000-22-2861 to AF and DC.

References

- Baciu, M., Koenig, O., Vernier, M.-P., Bedoin, N., Rubin, C., & Segebarth, C. (1999). Categorical and coordinate spatial relations: fMRI evidence for hemispheric specialization. *Cognitive Neuroscience*, 10, 1373–1378.
- Bornstein, M., Kessen, W., & Weiskopf, S. (1976). Color vision and hue categorisation in young human infants. *Journal of Experimental Psychology: Human Perception and Performance*, 2, 115–129.
- Bomba, P. C. (1984). The development of orientation categories between 2 and 4 months of age. *Journal of Experimental Child Psychology*, 37, 609–636.
- Clifford, A., Franklin, A., Davies, I. R. L., & Holmes, A. (2009). Electrophysiological markers of color categories in the infant brain. *Brain and Cognition*, 71, 165–172.
- Corballis, P. M., Funnell, M. C., & Gazzaniga, M. S. (2002). Hemispheric asymmetries for simple visual judgements in the split brain. *Neuropsychologia*, 41, 401–410.
- Drivonikou, V. G., Kay, P., Regier, T., Ivry, R., Gilbert, A., Franklin, A., et al. (2007). Further evidence of Whorfan effects to the right visual field. *Proceedings of the National Academy of Sciences*, 104(3), 1097–1102.
- Essock, E. A. (1980). The oblique effect of stimulus identification considered with respect to two classes of oblique effects. *Perception*, 9, 37–46.
- Franklin, A., Drivonikou, G. V., Bevis, L., Davies, I. R. L., Kay, P., & Regier, T. (2008). Categorical perception of color is lateralized to the right hemisphere in infants, but to the left hemisphere in adults. *Proceedings of the National Academy of Sciences, USA*, 105, 3221–3225.
- Franklin, A., Drivonikou, G. V., Clifford, A., Kay, P., Regier, T., & Davies, I. R. L. (2008). Lateralization of categorical perception of color changes with color term acquisition. *Proceedings of the National Academy of Sciences, USA*, 47, 18221–18225.
- Fonteneau, E., & Davidoff, J. (2007). Neural correlates of colour categories. *Neuroreport*, 18, 1323–1327.
- Gilbert, A. L., Regier, T., Kay, P., & Ivry, R. B. (2005). Whorf hypothesis is supported in the right visual field but not the left. *Proceedings of the National Academy of Sciences, USA*, 103, 489–494.
- Harnad, S. (1987). Psychophysical and cognitive aspects of categorical perception: A critical overview. In S. Harnad (Ed.), *Categorical perception: The groundwork of cognition* (pp. 287–301). New York: Cambridge University Press.
- Hellige, J. B., & Michimata, C. (1989). Categorization versus distance: Hemispheric differences for processing of spatial information. *Memory and Cognition*, 17, 770–776.
- Holmes, A., Franklin, A., Clifford, A., & Davies, I. R. L. (2009). Neuro-physiological evidence for categorical perception of colour: Evidence from Event-Related Potentials on a visual oddball task. *Brain and Cognition*, 69, 426–434.
- Kosslyn, S. M., Chabris, C. F., Marsolek, C. J., & Koenig, O. (1992). Categorical versus coordinate spatial relations: Computational analyses and computer simulations. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 562–577.
- Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. E. (1989). Evidence for two types of spatial representations: Hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 723–725.
- Kwon, H., Reiss, L., & Menon, V. (2002). Neural basis of protracted developmental changes in visuo-spatial working memory. *Proceedings of the National Academy of Sciences*, 99, 13336–13341.
- Laeng, B. (1994). Lateralization of categorical and coordinate spatial functions: A study of unilateral stroke patients. *Journal of Cognitive Neuroscience*, 6, 189–203.
- Laeng, B., Zarrinpar, A., & Kosslyn, S. M. (2003). Do separate processes identify objects as exemplars versus members of basic-level categories? Evidence from hemispheric specialization. *Brain and Cognition*, 53, 15–27.
- Liu, Q., Li, H., Campos, J. L., Wang, Q., Zhang, Y., Qiu, J., et al. (2009). The N2pc component in ERP and the lateralization effect of language on color perception. *Neuroscience Letters*, 454, 58–61.
- Mareschal, D., & Quinn, P. C. (2001). Categorization in infancy. *Trends in Cognitive Sciences*, 5, 443–450.
- Marsolek, C. J. (1995). Abstract visual-form representations in the left cerebral hemisphere. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 375–386.
- Marsolek, C. J. (1999). Dissociable neural subsystems underlie abstract and specific object recognition. *Psychological Science*, 10, 111–118.
- Marsolek, C. J., & Burgund, E. D. (2008). Dissociable neural subsystems underlie visual working memory for abstract categories and specific exemplars. *Cognitive, Affective & Behavioral Neuroscience*, 8, 17–24.
- Okubo, M., & Michimata, C. (2004). The role of high spatial frequencies in hemispheric processing of categorical and coordinate spatial relations. *Journal of Cognitive Neuroscience*, 16, 1576–1582.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: Edinburgh inventory. *Neuropsychologia*, 9, 97–113.
- Özgen, E., & Davies, I. R. L. (2002). Acquisition of categorical color perception: A perceptual learning approach to the linguistic relativity hypothesis. *Journal of Experimental Psychology: General*, 131(4), 477–493.
- Parducci, A. L. (1965). Category judgment: A range frequency model. *Psychological Review*, 72, 407–418.
- Parrot, M., Doyon, B., Démonet, J.-F., & Cardebat, D. (1999). Hemispheric preponderance in categorical and coordinate visual processes. *Neuropsychologia*, 37, 1215–1225.
- Quinn, P. C. (2004). Visual perception of orientation is categorical near vertical and continuous near horizontal. *Perception*, 33, 897–906.
- Quinn, P. C., & Bomba, P. C. (1986). Evidence for a general category of oblique orientations in 4-month-old infants. *Journal of Experimental Child Psychology*, 42, 345–354.
- Quinn, P. C., Siqueland, E. R., & Bomba, P. C. (1985). Delayed recognition memory for orientation by human infants. *Journal of Experimental Child Psychology*, 42, 345–354.
- Roberson, D., Pak, H. S., & Hanley, J. R. (2008). Categorical perception of colour in the left and right visual field is verbally mediated: Evidence from Korean. *Cognition*, 107, 752–762.
- Rosielle, L. J., & Cooper, E. E. (2001). Categorical perception of relative orientation in visual object recognition. *Memory and Cognition*, 29, 68–82.
- Seeger, C. A., Poldrack, R. A., Prabhakarn, V., Zhao, M., Glover, G. H., & Gabrieli, J. D. R. (2000). Hemispheric asymmetries and individual differences in visual concept learning as measured by functional MRI. *Neuropsychologia*, 38, 1316–1324.
- Siok, W. T., Kay, P., Wang, W. S. Y., Chan, A. H. D., Chen, L., Luke, K.-K., et al. (2009). Language regions of brain are operative in color perception. *Proceedings of the National Academy of Sciences*, 106, 8140–8145.
- Slotnick, S. D., & Moo, L. R. (2006). Prefrontal cortex hemispheric specialization for categorical and coordinate visual spatial memory. *Neuropsychologia*, 44, 1560–1568.
- Studer, T., & Hübner, R. (2008). The direction of hemispheric asymmetries for object categorization at different levels of abstraction depends on the task. *Brain and Cognition*, 67, 197–211.
- Treisman, A., & Souther, J. (1985). Search asymmetry: A diagnostic for preattentive processing of separable features. *Journal of Experimental Psychology: General*, 114, 285–310.
- Trojano, L., Conson, M., Maffei, R., & Grossi, D. (2006). Categorical and coordinate spatial processing in the imagery domain investigated by rTMS. *Neuropsychologia*, 44, 1569–1574.
- van der Ham, I. J. M., van Wezel, R. J. A., Oleksiak, A., & Postma, A. (2007). The time course of hemispheric differences in categorical and coordinate spatial processing. *Neuropsychologia*, 45, 2492–2498.
- Vanduffel, W., Tootell, R. B. H., Schoups, A. A., & Orban, G. (2002). The organization of orientation selectivity throughout macaque visual cortex. *Cerebral Cortex*, 12, 647–662.
- Vauclair, J., Yamazaki, Y., & Güntürkün, O. (2006). The study of hemispheric specialization for categorical and coordinate spatial relations in animals. *Neuropsychologia*, 44, 1524–1534.
- Wakita, M. (2004). Categorical perception of orientation in monkeys. *Behavioural Processes*, 67, 263–272.
- Wolfe, J. M., Friedman-Hill, S. R., Stewart, M. I., & O'Connell, K. M. (1992). The role of categorization in visual search for orientation. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 34–39.