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**Emotion lateralization in a graduated emotional chimeric face task –  
an online study**

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## **Abstract**

**Objective:** To resolve inconsistencies in the literature regarding the dominance of the right cerebral hemisphere (RH) in emotional face perception, specifically investigating the role of the intensity of emotional expressions, different emotions, and conscious perception.

**Method:** The study used an online version of the well-established Emotional Chimeric Face Task (ECFT) in which participants judged which side of a chimeric face stimulus was more emotional. We tested the laterality bias in the ECFT across six basic emotions and experimentally modified the intensity of the emotional facial expression from neutral to fully emotional expressions, in incremental steps of 20%.

**Results:** The results showed an overall left hemiface bias across all emotions, supporting the RH hypothesis of emotional lateralization. However, the left hemiface bias decreased with decreasing intensity of the emotional facial expression.

**Conclusions:** The results provide further support for the RH hypothesis and suggest that the RH dominance in emotional face perception may be affected by task difficulty and visual perception strategy.

**Keywords:** functional cerebral asymmetries; face recognition; visual perception strategies; facial expression; task difficulty

**Key Points**

**Question:** The present study aimed to investigate to what extent emotion perception lateralization depends on the emotion presented and the intensity of the emotional facial expression.

**Findings:** Participants identified ECFT stimuli as being more emotional when the emotion was displayed on the left side of the face, corresponding to the well-established right-hemisphere bias when processing emotional faces. However, this bias was diminished until eliminated as the task became more difficult and the emotional facial expressions became less salient.

**Importance:** We significantly expanded the investigation of the relationship between functional cerebral asymmetries and cognitive ability within emotional face perception, and also helped elucidate the ongoing debate on hemispheric lateralization of emotional face perception.

**Next steps:** Further research is required to determine what underlies the relationship between hemispheric laterality bias and task difficulty found in our experiment.

## **Introduction**

It is well established that the left and right cerebral hemispheres differ in the processing of emotions and, more specifically, in emotion perception (Borod, Bloom, Brickman, Nakhutina & Curko, 2002). However, the literature on the relative contribution of the left and right cerebral hemispheres in emotional processing in general, and in processing of emotional face expressions specifically, is inconsistent, and the underlying mechanisms are not fully understood. Two partially conflicting models of emotion lateralization are most frequently discussed and referenced, although modifications to these models have also been proposed. The right hemisphere hypothesis (RHH, Borod et al., 1998; Christman & Hackworth, 1993; Ley & Bryden, 1979) argues that all basic emotions are dominantly processed by the right hemisphere. The valence specific hypothesis (VSH, Ahern & Schwartz, 1985; Dimond & Farrington, 1977; Jansari, Rodway & Goncalves, 2011) suggests that negative emotions are dominantly lateralized to the right hemisphere and positive emotions are dominantly lateralized to the left hemisphere. Some research has suggested that emotion lateralization is not primarily based on emotional valence of stimuli but instead on the approach-withdrawal dimension, where approach motivation is preferentially processed by the left hemisphere and withdraw motivation is preferentially processed by the right hemisphere (Anderson, Spencer, Fulbright & Phelps, 2000; Davidson, Ekman, Saron, Senulis & Friesen, 1990; Harmon-Jones, 2004). The key empirical difference between these two versions of the dimensional hypothesis is with anger, which is negative in valence but an approach-motivated emotion. Other researchers have supported modified versions of the valence-hypothesis, with both Adolphs, Jansari and Tranel (2001) and Abbott, Cumming, Fidler and Lindell (2013) proposing that the right hemisphere processes negative emotions, as the VSH suggests, but that positive emotions are processed

bilaterally, whereas Najt, Bayer and Hausmann (2013) found support for a negative (only) valence model, where only negative emotions showed a hemispheric bias towards the right hemisphere. Alternatively, rather than valence, emotional perception asymmetries have been proposed to involve behavioral approach/inhibition system strength (Sutton & Davidson, 1997), emotion complexity (Ross, Homan & Buck, 1994; Shamay-Tsoory, Lavidor & Aharon-Peretz, 2008) and emotional dominance (Demaree, Everhart, Youngstrom & Harrison, 2005). Finally, there have also been proposals that the RHH and VSH are not mutually exclusive and are in fact both correct (Killgore & Yurgelun-Todd, 2007; Wyczesany, Capotosto, Zappasodi & Prete, 2018), with each model accounting for different methods for examining emotion perception such as with the VSH explaining tachistoscopic presentations of emotional faces and the RHH accounting for results with longer duration presentations of facial stimuli (Prete, Laeng, Fabri, Foschi & Tommasi, 2015).

Work with patients with brain damage also provided mixed evidence supporting both models. Some patient studies showed that patients with unilateral right hemisphere damage exhibited poorer performance in discriminating emotional faces and recognizing emotions than those with unilateral left hemisphere damage (Adolphs, Damasio, Tranel & Damasio, 1996; Borod, 1992; Cicone, Wapner & Gardner, 1980; DeKosky, Heilman, Bowers & Valenstein, 1980; Gazzaniga & Smylie, 1983), supporting the RHH. However, later work suggested that this was only true for negative emotions (Adolphs, Jansari & Tranel, 2001; Mandal, Tandon & Asthana, 1991) and others noted the pathological laughing associated with right-sided damage and pathological crying associated with left-sided brain lesions (Sackeim, Greenberg, Weiman, Gur, Hungerbuhler & Geschwind, 1982), lending support to the VSH from other domains as well.

Further mixed evidence is provided by measures of neural activity. Wyczesany et al. (2018) recorded brain activation using EEG while showing participants happy and angry emotional faces and found a strong pattern of connectivity lateralized to the right hemisphere for both emotions. Ahern and Schwartz (1985) found greater left hemisphere EEG activation for positive emotion-eliciting questions and greater right hemisphere activation for negative emotion-eliciting questions and similar EEG results were found by Davidson et al. (1990). The Fox (1991) review of EEG studies concluded that the studies supported the approach-withdrawal model. Fusar-Poli et al. (2009) conducted a review of fMRI studies investigating the laterality of emotion perception and generally found a bilateral network of activation with limited support for the valence hypothesis, where negative emotions showed a processing bias to the left amygdala.

A popular behavioral paradigm used to investigate emotion lateralization in emotional face perception has been the visual half-field paradigm (VHF, Safer, 1981), which utilizes the fact that visual information presented to each visual half-field is finally projected to the primary visual cortex of the contralateral cerebral hemisphere. Ley and Bryden (1979) showed cartoon drawings displaying positive and negative expressions and found significant left visual-field (LVF) advantages for the emotional expression recognition. Suberi and McKeever (1977) found faster discrimination of emotional faces presented to the LVF compared to the RVF. Alves, Aznar-Casanova and Fukusima (2009) replicated these results with a larger number of emotional expressions. However, Reuter-Lorenz and Davidson (1981) found that happy expressions were responded to more quickly when presented to the right visual-field (RVF) compared to the LVF and the opposite was true for sad expressions, and Prete, Laeng and Tommasi (2014) found that expressions were rated as less friendly when

shown to the LVF/RH compared to the RVF/LH. Najt, Bayer and Hausmann (2013) found a significant LVF advantage, but only for angry, fearful and sad faces. Overall, clinical and experimental work has supported both models of emotion lateralization, although the results have been inconsistent across stimulus type and modality.

The emotional chimeric face task (ECFT, Sackeim & Gur, 1978) is a well-established visual paradigm that has revealed few contradictory results for emotion perception lateralization (Hausmann et al., 2019). The typical ECFT uses faces which are split down the middle vertically, with one side displaying an emotion and the other side being neutral. During the task, participants are presented with two mirror-versions of such a chimeric face, one above the other. The participants are asked to decide which of the chimeric faces appears more emotional. Similar to VHF tasks (Alves, Aznar-Casanova & Fukusima, 2009; Prete, Laeng & Tommasi, 2014), ECFT relies on the fact that the left and right hemispheres have visual attentional biases toward their contralateral hemispheres. Most ECFT studies have found that participants more frequently choose the face where the emotion is displayed in the left hemifield, corresponding to the right hemisphere, even though the two chimeric faces shown are identical, apart from being mirrored (Hausmann, Innes, Birch & Kentridge, 2021; Innes, Burt, Birch & Hausmann, 2016; Levy, Heller, Banich & Burton, 1983; Moreno, Borod, Welkowitz & Alpert, 1990). The preference bias measured in ECFT studies typically supports the RHH (Bourne, 2005, 2008, 2010, 2011; Christman & Hackworth, 1993; David, 1989; Levine & Levy, 1986; Rueckert, 2005; Watling & Bourne, 2013).

The ECFT paradigm has undergone several improvements in recent years. Early ECFT studies utilized chimeric stimuli, where the midline separating the two halves of the face was clearly visible (Christman & Hackworth, 1993; David, 1989; Levine & Levy, 1986; Levy, Heller, Banich & Burton, 1983; Moreno, Borod, Welkowitz &

Alpert, 1990). Burt and Perrett (1997) argued that this may force participants to adopt a non-standard visual processing of the stimuli compared to a normal face. Consequently, more recent ECFT studies have used chimeric stimuli with a blended midline (e.g., Hausmann et al., 2019; Innes et al., 2016). Also, earlier ECFT studies used only a small subsection of emotions in their experiments (e.g., Bourne, 2005; Christman & Hackworth, 1993; David, 1989; Levy et al., 1983; Rueckert, 2005), rather than using all six basic emotions (anger, disgust, fear, happiness, sadness, and surprise) identified by Ekman and Friesen (1975). This issue may partly explain why previous studies could not contribute much to solving the conflict between the RHH and VSH models.

In two ECFT studies, Carbary, Almerigi & Harris (2001, 2002) investigated how emotion lateralization in this task was affected by task difficulty. The authors hypothesised that the right hemisphere bias increases as the difference between the two sides of the chimeric face decreases and thus the task became more difficult. Based on the known bias for the left visual half-field for observing faces (Kolb, Milner & Taylor, 1982) and past research showing that identification of difficult-to-read letters led to an LVF bias (Wagner & Harris, 1994), the authors hypothesised that the right hemisphere bias would increase as the task became more difficult with the difference between the two sides of the chimeric faces decreasing. Carbary et al. (2001) recorded subjective ratings of task difficulty by asking participants how difficult they found the choice of which of two chimeric faces was happier. Contrary to their hypothesis, the authors found that the right hemisphere bias decreased as perceived task difficulty increased. In a follow up study, Carbary et al. (2002) manipulated task difficulty directly by changing the intensity of emotion visible in their face stimuli consisting of both photographic chimeric faces with a visible midline and relatively simple cartoon drawings. The authors used three levels of stimuli: on easy trials, emotional facial expressions were

strong and evident (e.g., a beaming smile), the emotional facial expression was less clear on medium trials, and on difficult trials, the emotion was difficult to discern (e.g., a barely perceptible smile). In line with their first study, Carbary et al. (2002) revealed that the right hemisphere bias decreased with increased task difficulty, opposite to the proposed hypothesis.

The negative relationship between task difficulty (i.e., operationalized by the emotional intensity of the stimuli) and laterality can potentially explain some of the inconsistent findings in emotion lateralization studies and may also contribute to our understanding of the link between laterality degree and cognitive performance in general. The traditional view was that functional cerebral asymmetries can enhance cognitive performance (Corballis, 1991, 2009) – a view that received some empirical support. For example, Everts et al. (2009) found that greater language lateralization was related to increased language ability (see also O'Regan & Serrien, 2018; Qi, Schaadt & Friederici, 2019; Springer et al., 1999). However, other studies have shown that reduced lateralization was beneficial for cognitive processes, such as parallel processing (Hirnstein, Hausmann & Güntürkün, 2008), language processing (Hirnstein, Hugdahl & Hausmann, 2014), and face perception (Hirnstein, Leask, Rose & Hausmann, 2010). While the relationship between functional cerebral asymmetries and cognitive performance has been investigated in various domains (e.g., visual lexical decisions, spatial cognition: Boles, Barth & Merrill, 2008; auditory processing: Brechmann & Angenstein, 2019; language functions: Hirnstein et al., 2014), very little research has studied how emotion lateralization may be related to task difficulty.

In the current study, we adapted the ECFT used in two previous studies (Hausmann et al., 2019; Innes et al., 2016) and developed a novel set of chimeric faces which varied in six different intensities of the emotional facial expression in

incremental steps of 20%, ranging from 0% to 100%, instead of only three gradations (easy, medium, difficult) used by Carbary et al. (2002). To identify the thresholds for participants' ability to perceive the emotional facial expressions, a control task was administered, which required participants to indicate which hemiface of the chimeric stimulus contained the emotion.

Our study expands on previous research, particularly by Carbary et al. (2002), in multiple ways. In contrast to Carbary et al. (2002), we used (1) highly ecologically valid stimuli of real human faces, rather than cartoon renditions, (2) significantly more trials per participant, and crucially (3) more steps in the emotional intensity gradation, which is a prerequisite for being able to determine if there is truly a linear relationship between task difficulty and the laterality bias. (4) The inclusion of the control task ensured that the emotions were being perceived in the stimuli, ensuring that the chimeric face task really assessed emotion perception. (5) The current study also used the full set of six basic emotions (i.e., anger, disgust, fear, happiness, sadness, surprise), whereas Carbary et al. (2002) only used two (i.e., positive and negative). Finally, (6) this was one of the first online studies on emotion lateralization, suggesting that useful neuropsychological data can be collected through online tasks with rigorous experimental procedures.

We hypothesised an overall LVF/RH bias for easily recognized chimeric faces (emotional intensity of 100%) across all six basic emotions, regardless of emotional valence, which is in line with the overall RH bias reported previously (Bourne, 2010; Hausmann et al., 2019; Sackeim & Gur, 1978; for a review see Gainotti, 2019). In line with Carbary et al. (2001, 2002), we also predicted that the ECFT bias decreases as the emotional facial expressions become less emotionally distinct. Finally, it was predicted that the well-established RH bias in ECFT disappears, if participants do not perceive, and are unaware of the facial expression.

## Materials and methods

### *Participants*

We collected data from 100 participants through opportunity sampling and from the university participant pool. Participants received credits for completion of the study. Participants' age had to be over 18 years and they had to report normal or corrected-to-normal vision. During preprocessing of the data, four participants had to be excluded from the statistical analysis: one participant only responded to 41% of the ECFT trials, two participants had technical issues with the recording of their instruction times, and one participant misunderstood the instructions for the second task. This left 96 participants (77 females, 18 males, 1 other) for the final analysis with a mean age of  $25.95 \pm 9.92$  years, ranging from 18 to 69 years. 77 participants reported their ethnicity as "White", 11 as "Asian/Asian British", 5 as "Mixed/Multiple Ethnic Groups" and 3 as "Other Ethnic Group". Sample size was estimated using a priori power analysis (G\*Power, Faul, Erdfelder, Lang & Buchner, 2007) based on two previous ECFT studies (Hausmann et al., 2019; Innes et al., 2016). The power analysis recommended a sample size of 42 participants to achieve an effect size Cohen's  $d$  of 0.25 with an alpha value of 0.05. Due to the COVID-19 pandemic, the experiment was moved online, and sample size was doubled to account for potential noise due to the online data collection. This study received ethical clearance by the local ethics committee at Durham University.

Hand preference was measured using the Edinburgh Handedness Inventory (Oldfield, 1971). A Laterality Index (LI) was calculated for each participant, expressed as  $([\text{Right} - \text{Left}]/[\text{Right} + \text{Left}]) * 100$ . The LIs thus potentially ranged from -100 (strongly left-handed) to 100 (strongly right-handed). The mean handedness LI for all participants was 72.60 (SD = 61.885, range: -100 – 100).

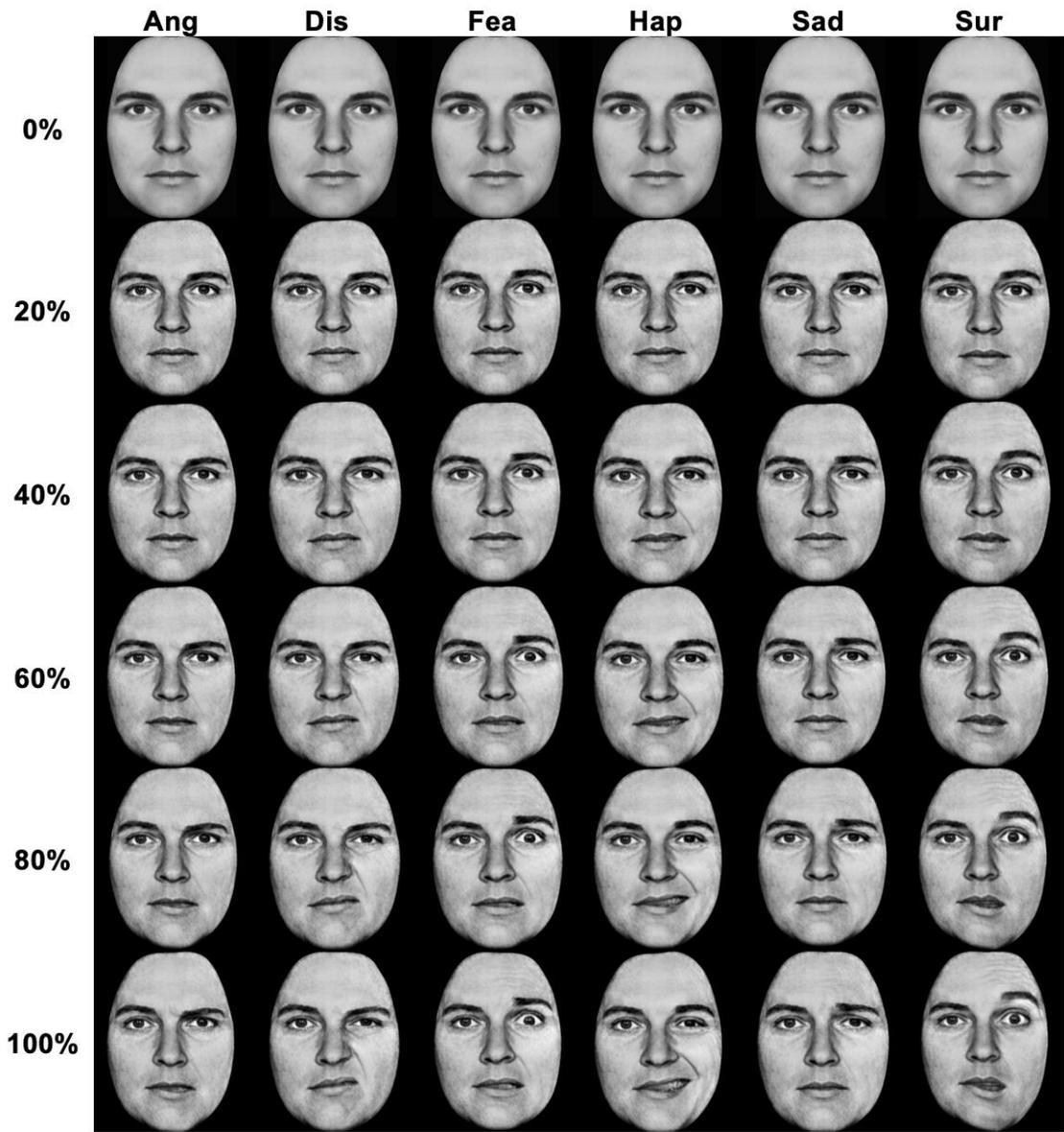
### *Apparatus*

Two experiments were designed using the Gorilla Experiment Builder ([www.gorilla.sc](http://www.gorilla.sc), Anwyl-Irvine, Massonnié, Flitton, Kirkham & Evershed, 2018). Data were collected between June and July 2020. All participants completed the tasks on a personal computer (no smartphones or tablets) with monitor sizes ranging from 834x1048 to 1920x961 pixels, as reported by Gorilla.

### *Emotional face stimuli*

The emotional chimeric face stimuli were produced from stimuli taken from the Ekman and Friesen (1976) Pictures of Facial Affect series. The stimuli were created by warping the individual expressions of 8 posers (4 females and 4 males) to the average face image which was then made symmetrical for each basic emotion and neutral (for more precise details, see Tiddeman, Burt & Perrett, 2001; Hausmann et al., 2019). This produced a series of emotional chimeric face stimuli displaying anger, disgust, fear, happiness, sadness and surprise. The degrees of emotionality present in the faces were then varied systematically to produce 20%, 40%, 60%, 80% and 100% emotional intensity versions, ranging between a neutral face and the full emotion by morphing with the neutral face. The left hemiface of one stimulus was then combined with the right hemiface of another to create the chimeric faces. The vertical midline was blended to more resemble a typical face (for full details on chimeric stimuli production see Burt & Perrett, 1997). Thirty-one chimeric face stimuli were thus created, including five degrees of emotionality for each of the six basic emotion and one neutral stimulus (for an example of the varying degrees of emotionality see Figure 1). A recent study by Parker, Woodhead, Thompson and Bishop (in press), using stimuli identical to the

100%-degree stimuli used in our study, investigated the test-retest reliability of the stimuli and showed evidence of strong test-retest reliability ( $r = .88$ ).

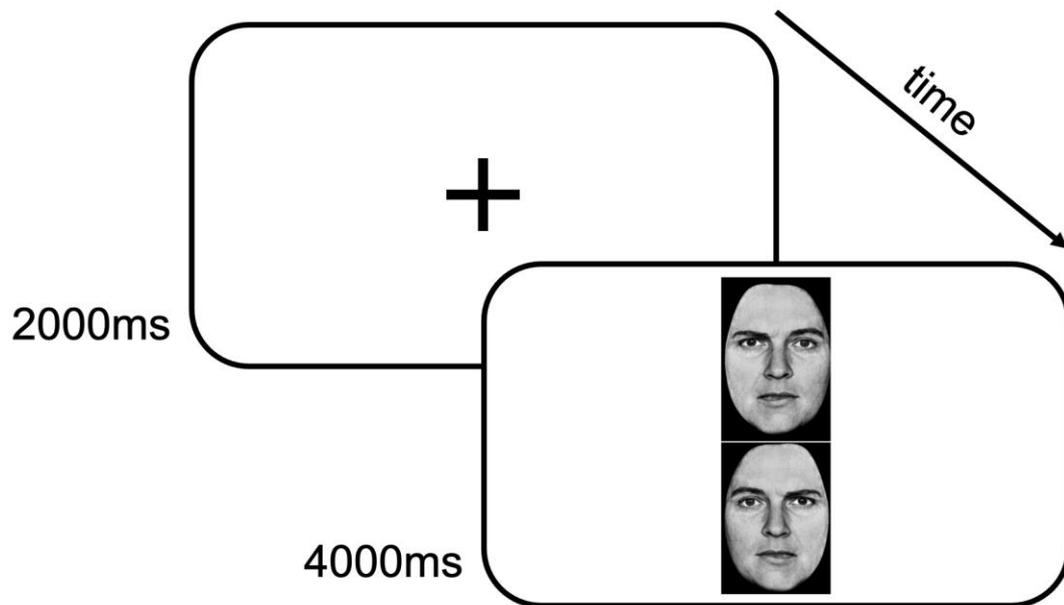


*Figure 1.* The emotional chimeric face stimuli showing the emotionality manipulation for each emotion (anger, disgust, fear, happiness, sadness, surprise). The degree of emotion increases by 20% from top to bottom, with 0% (a neutral face) at the top and 100% (a very emotional face) on the bottom. Emotions are in the right half of each face.

### ***Emotional chimeric face task (Experiment 1)***

Similar to previous ECFT studies (Hausmann et al., 2019; Innes et al., 2016), participants saw two mirror-reversed faces, one above the other. One chimeric face had the emotional facial expression on the left side of the face and the other chimeric face had the emotional facial expression on the right side. The faces remained on the screen for 4000 ms and participants were instructed to make judgements by pressing either the 'J' or 'K' keys on their keyboards, with one key indicating that the top chimeric face appeared more emotional and the other key indicating the chimeric stimulus at the bottom appeared more emotional. The assignment of response keys was counterbalanced. The stimuli disappeared immediately after participant responded, followed by a fixation cross for 2000 ms which indicated the start of the next trial (see Figure 2). If participants did not respond within 4000 ms, the trial was repeated at the end of the trial block. If participants did not respond to the repeated trial, the trial was recorded as no-response.

In Experiment 1, 124 face pairs were presented in 124 trials across four test blocks. Each block contained one pair of each intensity degree (20%, 40%, 60%, 80%, 100%) for every emotion (anger, disgust, fear, happiness, sadness, surprise), as well as a neutral trial (0% intensity), where both faces presented did not display any emotions. The order of the blocks and the order of trials within a block were both randomized. The trials were counterbalanced overall for hemiface arrangement.



*Figure 2.* A schematic figure of an example trial of the Emotional Chimeric Face Task. Instructions were presented along with the faces (e.g., “Press ‘J’ for the top face or ‘K’ for the bottom face”).

In line with (Hausmann et al., 2019, Innes et al., 2016), Laterality Quotients (LQs) were calculated from left and right responses as follows:

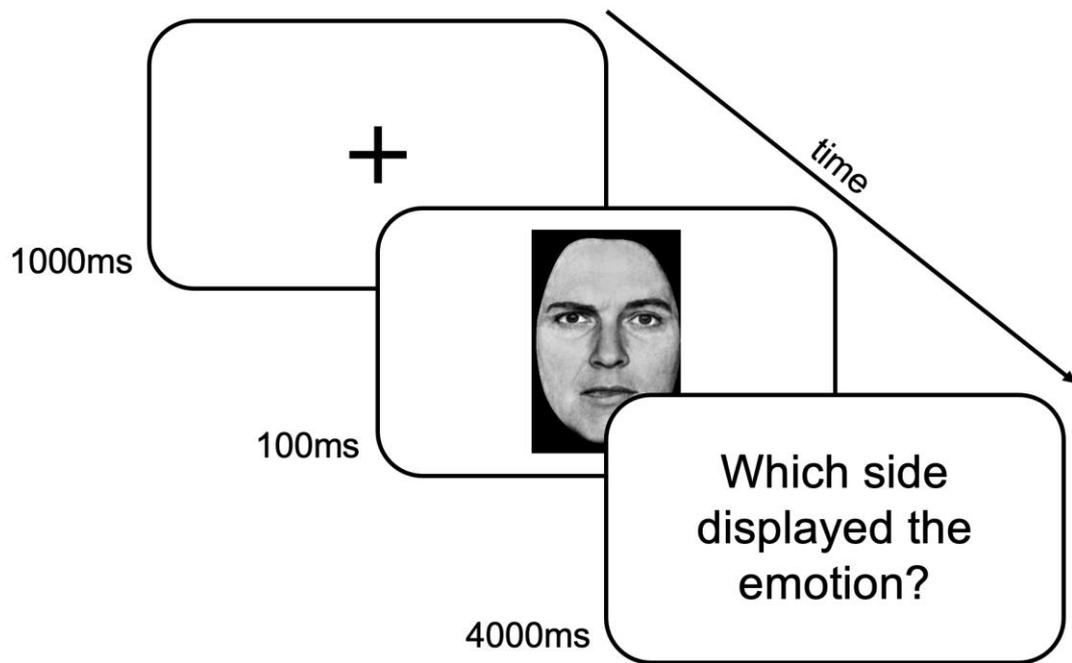
$$\frac{Left - Right}{Left + Right}$$

LQs ranged from -1 to 1, where negative values indicated a stronger right hemiface bias and positive values a stronger left hemiface bias. In addition to previous studies, we also calculated response times starting with stimulus onset.

### ***Emotional hemiface detection task (Experiment 2)***

To test participants' individual 'detection threshold' for each emotional stimulus and intensity, the emotional hemifield detection task was performed directly after participants completed the ECFT. This was done to determine if the emotional faces were being consciously processed by the participants. In the emotional hemifield detection task, after being instructed on the task, participants were presented with a fixation cross for 1000 ms before a single chimeric face was flashed in the middle of the screen for 100 ms. This was followed by a response screen, where the participants had 4000 ms to decide which side of the face had the emotional component by pressing either the 'J' or 'K' keys (see Figure 3). The assignment of the response keys was counterbalanced.

A total of 244 chimeric face stimuli trials were presented during the task in four blocks. Each block contained each of the degrees of emotionality (20%, 40%, 60%, 80%, 100%) for every basic emotion (anger, disgust, fear, happiness, sadness, surprise) with emotions being on the left and right sides of the face, along with a neutral face trial (emotionality of 0%). The order of the blocks and the order of the trials within a block were randomized.



*Figure 3.* A schematic figure of an example trial of the emotional hemifield detection task. Additional instructions were presented on the final screen (e.g., “Press ‘J’ if it was the left side or ‘K’ if it was the right side.”)

### ***Procedure***

At the start of the experimental session, participants read the participant information sheet and the privacy notice and completed a consent form. This was followed by the Edinburgh Handedness Inventory (Oldfield, 1971) and a questionnaire for basic demographic information about age, gender and ethnicity. After reading the instructions, participants performed the ECFT task (Experiment 1). Participants performed four blocks of 31 trials that matched all stimulus combinations as described earlier. The program paused after each block, allowing participants to resume the task at their own pace. After all four blocks were completed, participants were again allowed to pause before proceeding to the instructions for emotional hemifield detection task (Experiment 2). Participants were again able to pause after completing each block. Once

all emotional hemiface detection trials were completed, participants were taken to a debriefing page. Finally, participants were given their anonymized ID number, which they could use to withdraw their data from the experiment, if wanted.

### ***Transparency and openness***

We report how we determined our sample size, all data exclusions, and all measures in the study, and we follow JARS (Kazak, 2018). All data are available at <https://osf.io/yvfg4/>. This study was not pre-registered.

### **Results**

If the sphericity assumption was violated in the repeated-measures ANOVA, the degrees of freedom were epsilon-corrected by the Greenhouse-Geisser method. Bonferroni correction was used for post-hoc tests and pairwise comparisons.

### ***Emotional chimeric face task (Experiment 1)***

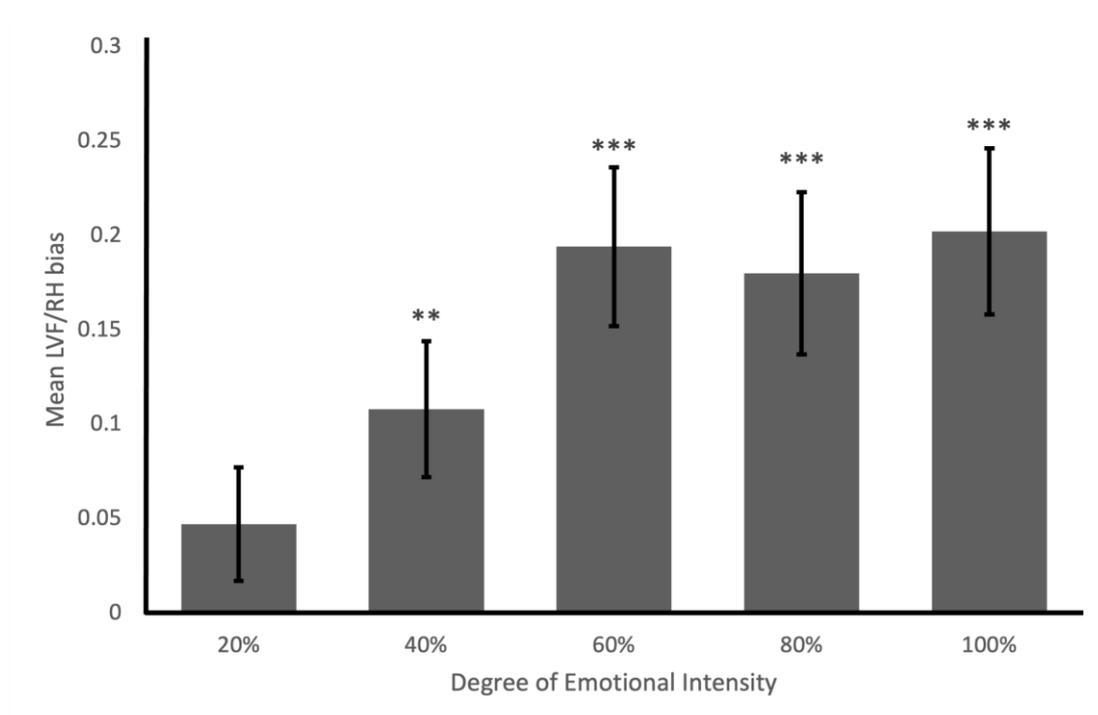
#### *Laterality quotients*

The LQs for the ECFT were subjected to a 6 x 5 repeated-measures ANOVA with Emotion (anger, disgust, fear, happiness, sadness, surprise) and Degree (20%, 40%, 60%, 80%, 100%) as the within-subjects factors. A significant main effect of the intercept was found,  $F(1, 95) = 19.069, p < .001, \eta_p^2 = .167$ , indicating the well-established and predicted overall LVF/RH bias ( $0.14 \pm 0.03$ ). The main effect of Emotion was not significant,  $F(5, 475) = 1.65, p = .145$ , indicating that the LVF/RH bias was independent of specific emotion, supporting the right hemisphere hypothesis. The main effect of Emotion Intensity was significant,  $F(2.74, 260.56) = 8.29, p < .001, \eta_p^2 = .080$ . Based on tests of within-subjects contrasts, there was a significant linear trend,  $F(1,95) = 14.309, p < .001, \eta_p^2 = .131$ , indicating that the higher the degree, the

stronger the LVF/RH bias (see Figure 4). The interaction of Emotion and Intensity was not significant,  $F(15.75, 1496.58) = 1.071, p = .378, \eta_p^2 = .011$ . The overall biases for each emotion can be found in Table 1.

|           | LVF/RH<br>Bias | Std.<br>Error | $F(1,95)$ | Sig.  | Partial Eta<br>Sq. |
|-----------|----------------|---------------|-----------|-------|--------------------|
| Anger     | 0.11           | 0.04          | 8.62      | .004  | .083               |
| Disgust   | 0.16           | 0.04          | 15.49     | <.001 | .140               |
| Fear      | 0.17           | 0.04          | 16.71     | <.001 | .150               |
| Happiness | 0.11           | 0.05          | 5.39      | .022  | .054               |
| Sadness   | 0.17           | 0.04          | 20.24     | <.001 | .176               |
| Surprise  | 0.17           | 0.04          | 20.49     | <.001 | .177               |

*Table 1.* The results of six separate repeated measures ANOVAs for all degrees of emotion intensity for each emotion showing the main effects of the models.



*Figure 4.* The mean laterality quotients (LQs) in the Emotional Chimeric Faces task for each emotional intensity averaged across all six basic emotions, the error bars represent the standard error of the model for each degree of emotion intensity. Asterisks indicate a significant difference from an LQ of 0 (\*\* $p < .01$ , \*\*\* $p < .001$ ).

A one-sample t-test with test score = 0 (virtual symmetry) revealed that the LQs for neutral faces (emotion intensity of 0%) did not achieve significance,  $t(95) = 1.23$ ,  $p = .221$ ; in other words the participants did not choose either the top or bottom neutral face more frequently than the other. Similarly, the one-sample t-test for 20% emotional intensity was not significant,  $t(95) = 1.54$ ,  $p = .127$  (uncorrected), with one exception. At 20% emotional intensity only the LQs for sadness were significantly different from 0,  $t(95) = 2.65$ ,  $p = .009$ . For intensities of 40%, 60%, 80% and 100%, one sample t-tests revealed biases significantly different from virtual symmetry, all  $t(95) > 2.99$ , all  $p < .005$ .

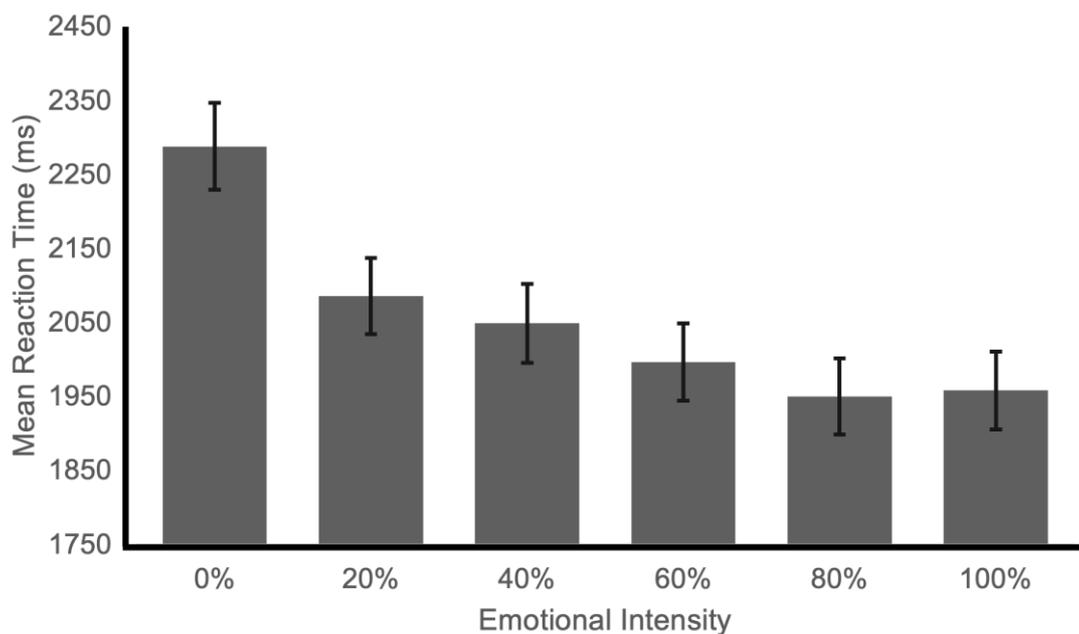
When the ANOVA was restricted to faces with only 100% degree of emotionality, the results revealed a strong overall LVF/RH bias of  $0.20 \pm 0.04$ ,  $F(1, 95) = 21.52$ ,  $p < .001$ ,  $\eta_p^2 = .185$ , which was numerically slightly smaller than the LQ of  $0.27 \pm 0.04$  and  $0.34 \pm 0.06$  in two previous studies using the same stimuli (Innes et al., 2016, and Hausmann et al., 2019, respectively). Similarly, the main effect of Emotion was not significant,  $F(5, 475) = 1.12$ ,  $p = .350$ ,  $\eta_p^2 = .012$ .

Given the large variability in hand preference scores, we also repeated the original 6 x 5 ANOVA with handedness, and the absolute values of participants' handedness scores as a covariate. However, neither the main effect of handedness nor

any of the interactions with handedness were significant, all  $F \leq 1.26$ , *ns*. Similarly, when gender was included as a between-subjects factor, no significant main effect or interaction approached significance, all  $F \leq 1.27$ , *ns*.

### *Reaction Times*

When reaction times were subjected to a 6 x 5 repeated-measures ANOVA, the main effect of Emotion was not significant,  $F(5, 475) = 1.48$ ,  $p = .196$ , suggesting that, in line with the ANOVA with LQs as dependent variable, processing times were similar across specific emotions. The main effect of Emotional intensity was significant,  $F(3.72, 310.73) = 18.22$ ,  $p < .001$ ,  $\eta_p^2 = .161$ . The reaction times increased linearly with decreasing degree of emotional intensity, as indicated by the trend analysis,  $F(1, 95) = 41.73$ ,  $p < .001$ ,  $\eta_p^2 = .305$  (see Figure 5). The interaction of Degree and Emotion was again not significant,  $F(15.53, 1475.40) = .988$ ,  $p = .473$ .



*Figure 5.* The mean reaction times (RTs) for each emotional intensity averaged across all six basic emotions.

To investigate if emotions were processed for the lowest intensity (20%) of emotional faces, pairwise comparisons of reaction times for only 20% emotional stimuli were compared to the emotionally neutral stimuli (intensity of 0%). The results revealed that reaction times for all emotions with an intensity of 20% (RTs  $\leq$  2138 ms, SE  $\leq$  625) differed significantly (faster) from the neutral faces,  $M = 2289$  ms,  $SE = 577$ , all  $t(95) \leq 3.15$ ,  $p \leq .002$ .

### ***Emotional hemifield detection task (Experiment 2)***

For the emotional hemifield detection task, accuracy of correctly localized emotions in the chimeric stimuli (left or right) and mean reaction times (correct responses) were determined for all the chimeric stimuli used in Experiment 1.

#### *Detection accuracy*

Accuracies were subjected to a 6 x 5 x 2 repeated-measures ANOVA with Emotion, Degree and Hemiface (left, right) as within-subjects factors. The main effect of Hemiface was not significant,  $F(1, 95) = .202$ ,  $p = .654$ , indicating that the performance in the emotional hemifield detection task was unaffected by side of the emotional hemiface. This finding suggests no general detection bias for either side in the chimeric stimuli. The main effect of Emotion was significant,  $F(3.34, 317.43) = 25.31$ ,  $p < .001$ ,  $\eta_p^2 = .210$ . Post hoc pairwise comparisons revealed that accuracy was significantly higher for happiness ( $M = 74.9\% \pm 2.3\%$ ) than for all other emotions, all  $p \leq .003$ . Accuracies were also significantly lower for anger ( $64.1\% \pm 1.7\%$ ) and sadness ( $60.9\% \pm 1.4\%$ ) compared to disgust ( $71.2\% \pm 2.1\%$ ), fear ( $68.7\% \pm 2.0\%$ ) and happiness ( $74.9\% \pm 2.3\%$ ), all  $p < .001$ . The accuracy for surprise ( $65.0\% \pm 2.0\%$ ) was significantly lower than disgust ( $71.2\% \pm 2.1\%$ ) and happiness ( $74.9\% \pm 2.3\%$ ). The

main effect of Emotional intensity was also significant,  $F(1.81, 172.05) = 77.17, p < .001, \eta_p^2 = .448$ . The trend analysis revealed a linear increase in accuracy as the emotionality of the stimuli increased,  $F(1, 95) = 112.45, p < .001, \eta_p^2 = .542$ . Post hoc pairwise comparisons revealed that all the intensities differed significantly from each other (i.e.,  $20\% < 40\% < 60\% < 80\% < 100\%$ , all  $p \leq .008$ ).

To investigate if the detection threshold for the emotion in chimeric face stimuli was above chance for the lowest emotional intensity level of 20%, one-sample t-tests (test score = 50%) were conducted for the 20% level of each emotion. The results showed that at emotional intensities of 20%, accuracy (all  $M \geq 53.7\%$ ) was significantly above chance (all  $p \leq .027$ ), except for surprise ( $M = 53.2\%, p = .106$ ). At 40% emotionality, the detection rate for surprise ( $M = 62.9\%$ ) was also significantly above chance ( $p < .001$ ).

### *Reaction Times*

For reaction times, the  $6 \times 5 \times 2$  repeated-measures ANOVA with Emotion, Intensity and Hemifield as within-subject factors was also run to investigate the reaction time data for this task. In line with detection accuracy, the main effect of hemifield was not significant,  $F(1, 95) = 1.74, p = .190$ . The main effect of Emotion was significant,  $F(3.22, 308.14) = 13.28, p < .001, \eta_p^2 = .123$ . Post hoc pairwise comparisons showed that Sadness ( $822 \pm 31$  ms) had a significantly slower reaction time (all  $p \leq .014$ ) than anger ( $790 \pm 28$  ms), disgust ( $756 \pm 24$  ms), fear ( $763 \pm 25$  ms) and happiness ( $736 \pm 27$  ms). Happiness also had a significantly faster reaction time (all  $p \leq .001$ ) than anger ( $790 \pm 28$  ms) and surprise ( $790 \pm 28$  ms). Finally, surprise ( $790 \pm 28$  ms) was also significantly slower ( $p = .031$ ) than fear ( $763 \pm 25$  ms). The main effect Emotional intensity was also significant,  $F(1.82, 173.06) = 29.97, p < .001, \eta_p^2 = .240$ . All emotional intensity levels differed significantly from each other, all  $p \leq .011$ , except for

80% and 100%,  $p = 1.000$  (i.e.,  $20\% < 40\% < 60\% < 80\% = 100\%$ ). Again, intensity levels indicated a linear trend,  $F(1, 95) = 40.44$ ,  $p < .001$ ,  $\eta_p^2 = .299$ . Estimated means and pairwise comparisons showed that as the emotion intensity increased, reaction time decreased linearly.

Finally, when the repeated-measures ANOVA was restricted to emotional intensities of 20% and the neutral face (intensity of 0%), the factor Emotion was significant,  $F(3.02, 286.76) = 14.55$ ,  $p < .001$ ,  $\eta_p^2 = .133$ . Pairwise comparisons revealed that all emotions had significantly faster RTs ( $M \leq 859$  ms,  $SE \leq 38$  ms,) than the RTs for the neutral faces ( $M = 1035$  ms,  $SE = 55$  ms),  $p \leq .001$

### ***Laterality-performance relationships***

To investigate the relationships between emotion lateralization (Experiment 1) and the performance in the emotional hemifield detection task, Pearson correlations between the overall LQ in ECFT and detection performance (detection accuracy and response times) were analyzed. The analysis did not reveal any significant relationship, neither for detection accuracy,  $r(96) = .07$ ,  $p = .506$ , nor response times,  $r(96) = .008$ ,  $p = .941$ .

### ***Split-half reliability***

To calculate the split-half reliability of the ECFT used in the current online study, two LQs were calculated by randomly splitting the total number of trials into two halves (odd and even trials) for each participant. A Pearson correlation was then calculated for the two sets of values, resulting in  $r = .88$ . The split-half reliability is similar to the split-half reliability of  $r = .93$  determined for standard ECFT stimuli by Levy et al. (1983).

## Discussion

The present study sought to investigate whether emotional intensity of the chimeric stimuli affects the LVF/RH bias in the well-established ECFT. In line with the *right hemisphere hypothesis* (Ley & Bryden, 1979), we hypothesised an LVF bias for all basic emotions, which was confirmed by the current study, further supporting the view that the right hemisphere dominantly processes emotional chimeric stimuli. The overall LVF/RH bias is in line with previous research using the same subset of emotional chimeric face stimuli with an emotional intensity of 100% (e.g., Hausmann et al., 2019; Innes et al., 2016) and also matches previous ECFT studies which used a different set of chimeric stimuli, sometimes with only a subset of basic emotions covered (e.g., Bourne, 2010, 2011; Workman et al., 2000). More importantly, the current study revealed that the intensity of the emotional facial expression was directly related to the degree of the LVF/RH bias. The strongest LVF/RH bias was found for intensities of 100% which gradually declined with decreases in emotional intensity, to the extent that the bias was entirely eliminated for the 20% emotional and neutral faces.

The results of the ECFT (Experiment 1) correspond with the findings of the Emotional hemifield detection task (Experiment 2) which showed that the detection performance decreased with emotional intensity of the chimeric stimuli. However, even with the lowest emotional intensity of 20% and extremely short presentation times of only 100ms, participants were able to detect the correct hemifield carrying the emotion. It is noteworthy that Experiment 2 did not reveal a RH bias, probably because participants were asked to decide which side of the face displayed the emotion which required participants to pay attention to both sides of single stimuli presented centrally. This is fundamentally different to Experiment 1 where participants were asked to compare the emotional degree of two similar face stimuli (presented on top of each

other) and without any reference to left and right. If we combine the results of Experiment 1 and 2, we may conclude that emotional lateralization is reduced when the emotional stimulus content is less visible and harder to detect, suggesting that emotion lateralization is less pronounced with increasing task demands.

### ***Effects of emotional salience***

As the emotion on the chimeric faces became less evident, accuracy of localization also decreased, verifying that our stimuli did indeed manipulate task difficulty. Replicating the findings of Carbary, Almerigi and Harris (2001, 2002), we found that the laterality bias decreased as task difficulty increased. Extending the results of Carbary and colleagues, we found that at the highest level of difficulty (20% emotionality), the laterality bias was entirely eliminated. Accuracy on the second task was significantly higher than chance for most of these stimuli, suggesting that this lack of lateralization was not due to a lack of emotional processing overall, but rather a recruitment of the left hemisphere. As Hirnstein et al. (2010) suggested, for some tasks it appears that a decrease in lateralization improves cognitive performance and based on our results, emotion perception is such a process. This is contrary to early evolutionary explanations for the development of cerebral asymmetry, which argued that increased laterality existed to aid cognitive performance (Corballis, 1991, 2009).

### ***Relationship between laterality and task difficulty***

There are several potential explanations as to why decreased laterality may aid performance on this emotion perception task. One explanation comes from the findings that global configural processing is thought to be more supported by the right hemisphere, while the left hemisphere is more involved in the processing of local features (e.g., Robertson, Lamb & Knight, 1998; Robertson & Lamn, 1991; VanKleeck,

1989). In their second experiment, Carbary et al. (2002) asked participants to describe the type of processing they were using for perceptual decisions. They found that for easy decisions participants mainly relied on “first impressions” (Carbary et al., 2002, p. 308), while for the more difficult conditions participants utilized a “feature search” (Carbary et al., 2002, p. 307). Bourne, Vladeanu and Hole (2009) conducted a priming study with selectively degraded faces to promote either featural or configural processing and found differences in functional cerebral asymmetries for these two different forms of perceptual processing. While configural information seemed to be processed preferentially by the right hemisphere, featural information was biased to the left hemisphere. Combined with the findings of Bombari et al. (2013), who found that perception of different emotions relied on configural and featural processing in different ratios, these results could explain the decrease in the LVF/RH bias as the need to featural processing increased with task difficulty as well as the varying levels of asymmetry for each emotion.

Alternatively, Banich (1998) proposed that the dynamic interaction of the two hemispheres can modulate the processing capacity of the brain and this determines the relationship between laterality and task difficulty. According to this model, when processing load or demand on cognitive resources is high, then the processing is spread across the hemispheres to provide more neural space for computation. Banich and colleagues demonstrated support for this across various modalities (Banich & Belger, 1990; Banich, Passarotti & Chambers, 1994; Banich & Shenker, 1994). When the computational load is light then there is no need to utilize both hemispheres of the brain and laterality biases present themselves. Hence for our experiment, in the easy conditions when emotion was very evident in the face stimuli, the right hemisphere was sufficient for perception of the emotion, but in the difficult conditions when the

emotions were less clear, the left hemisphere was recruited to aid in the perception of the emotion. This is directly supported by our results, as in the 20% emotional intensity condition the emotional hemiface was correctly identified above chance level, but the LVF/RH bias was no longer present. Since the emotional faces were still being processed, this suggests that the left hemisphere was being recruited to aid processing, thus eliminating the bias, rather than the activation in the right hemisphere decreasing on its own.

This explanation was recently developed further by Stanković (2020), who proposed the hemispheric functional-equivalence model and argued that the brain is initially right hemisphere biased for emotional face perception, but various psychophysiological factors, including stress and task demands, can activate a bilateral brain-network, which leads to a disappearance of the cerebral asymmetry. Banich (1998) stressed that the key to their model was the corpus callosum, which facilitated the modulation of processing across the hemispheres and so it would be interesting for future research to consider our task with split-brain patients and see how their lateral division of labor compares to healthy subjects.

Finally, Boles et al. (2008) conducted an analysis of tasks in various domains and found that for some, a larger degree of laterality led to better performance, while for others they found a negative relationship between laterality and performance, as we found in our study. Boles and colleagues proposed a developmental model to account for these different relationships for different tasks. They suggested that cognitive processes which are lateralized very early or very late in development will show a positive relationship between lateralization and performance in maturity, while cognitive processes which are initially lateralized in the intermediate stages of development will show a negative laterality-performance relationship in maturity.

Although researchers have shown that infants begin to recognize emotions as early as 7 months of age (Walker-Andrews, 1997, 1998), the process does not seem to be lateralized until around the age of 8 years old (Watling & Bourne, 2013) and is developed to adulthood level by ages 10-13 years (Anes & Short, 2009; Levine & Levy, 1986). For example, Workman, Chilvers, Yeomans and Taylor (2006) conducted an ECFT experiment with three groups of children (5-6, 7-8 and 10-11 years of age) and while the 5-6 year olds showed no evidence of an LVF/RH bias, the 10-11 year olds displayed a clear bias for all six basic emotions. Based on these findings, emotion perception seems to be a process lateralized in the intermediate stages of development and based on Boles and colleagues, this would suggest a negative relationship between lateralization and performance. This is indeed what we found in adults in the current study, since increasing task difficulty led to a decrease in lateralization. However, a longitudinal study from childhood to maturity is necessary to be able to address this theory of development of lateralization fully.

### ***Sex/gender differences***

Many previous studies on the laterality of emotion perception used samples of male-only participants or with large proportions of male participants (Adolphs et al., 2001; Borod, Koff, Perlman Lorch & Nicholas, 1986; Shamay-Tsoory et al., 2008), while Bourne (2005) found that female observers had weaker biases compared to male participants, which was replicated by Rahman and Anchassi (2012), and Innes et al. (2016). This is supported by a meta-analysis of 65 neuroimaging studies, which found males to be more lateralized during decoding of emotional facial expressions (Wager, Phan, Liberzon & Taylor, 2003). On the other hand, Rodway, Wright and Hardie (2003) found that females displayed a more pronounced valence-based laterality bias for emotion perception than males. As for the relationship between laterality and

performance, Hirnstein et al. (2010) were unable to draw clear conclusions about the effects of sex on the laterality-performance relationship, while Boles (2005) and Leask and Crow (2002) did not find a significant effect of sex. Including sex as a between-subjects factor in our analysis failed to find a significant main effect or interaction with any of the other factors. This suggests that sex does not have large effects on lateralization of emotion perception itself or how this may relate to cognitive performance. However, this conclusion is also limited by the distribution of men and women in our participant sample. Compared to past ECFT studies, we had a significant female proportion of participants, but conversely the male proportion of participants was relatively small (17%), potentially obscuring any significant effect due to low male sample size.

### ***Handedness***

In discussing the effects of their study, Carbery et al. (2002) were also interested in how their conclusions could be generalized to left-handed participants, who are thought to be more variable in their cerebral organization (e.g., Harris, 1992). Additionally, Frässle, Krach, Paulus and Jansen (2016) found that handedness had an impact on the lateralization of general facial processing, specifically within the fusiform face area. However, including handedness as measured by the Edinburgh Handedness Inventory (Oldfield, 1971) in our analysis as a covariate did not reveal a significant effect or interaction. Of our sample, 14% showed a left-handedness preference, which is slightly higher than the estimated overall global prevalence of left-handedness (10.6%; Papadatou-Pastou et al., 2020), nonetheless an over-representative sample would be necessary to reveal a significant effect of handedness.

### *Advantages of online studies*

Due to the COVID-19 pandemic we were forced to adapt our study from in-person data collection to online data collection. Despite initial apprehensions, our results showed that laterality studies are entirely conceivable in an online setting and in fact confer multiple advantages. The validity of reaction time data collected in an online environment is an important concern for laterality experiments. Bridges, Pitiot, MacAskill and Peirce (preprint) conducted a battery assessment of multiple online platforms and found that many environments provided reliable and valid data similar to data collected in a laboratory. For example, the Gorilla platform (Anwyl-Irvine et al., 2018) used by our experiments showed an inter-trial variability for reaction time measurements under 6ms and visual test showed consistently low variabilities across operating systems and internet browsers. As Parker, Woodhead, Thompson and Bishop (in press) pointed out in their recent reliability assessment, online studies allow for the collection of data from a large number of participants in considerably shorter time than in-person data collection would require. This is a major benefit for laterality studies, which often suffer from a lack of statistical power due to small sample sizes. In their analysis, Parker and colleagues showed that the chimeric stimuli also used in our study have a high test-retest reliability when presented in an online environment,  $r = .88$ . For our data, we calculated a split-half reliability and found an internal reliability of  $r = .89$ , very similar to the initial split-half reliability calculated for chimeric stimuli presented in a laboratory setting of  $r = .93$  (Levy et al., 1983).

### *Summary and conclusion*

In summary, our findings showed support for the right hemisphere hypothesis, as all emotions revealed a strong laterality bias for the left visual field, processed by the right hemisphere. Our findings contribute to the robust findings of ECFT studies

revealing an LVF/RH bias. We expanded on findings from Carbary et al. (2001, 2002) and found that increasing task difficulty leads to a decrease in lateralization, suggesting that for emotion perception, lateralities did not develop to enhance cognitive processing. This may be accounted for by changes in visual processing for difficult tasks, the increased cognitive load of the difficult tasks or due to the lateralization of emotion perception in the intermediate stages of development. Further research is necessary to disentangle these potential explanations; however, our study provides a strong foundation for further investigations. The analyses suggest that gender and handedness do not have a strong effect on the lateralization of emotion perception or how the degree of emotion lateralization relates to task performance, although this may be affected by limitations in the participant sample. Finally, the present study showed that lateralization research is entirely possible in an online environment, something which should be taken advantage of for further research in the field.

## References

- Abbott, J. D., Cumming, G., Fidler, F., & Lindell, A. K. (2013). The perception of positive and negative facial expressions in unilateral brain-damaged patients: A meta-analysis. *Laterality*, *18*(4), 437–459.  
<https://doi.org/10.1080/1357650X.2012.703206>
- Adolphs, R., Damasio, H., Tranel, D., & Damasio, A. R. (1996). Cortical systems for the recognition of emotion in facial expressions. *Journal of Neuroscience*, *16*(23), 7678–7687. <https://doi.org/10.1523/JNEUROSCI.16-23-07678.1996>
- Adolphs, R., Jansari, A., & Tranel, D. (2001). Hemispheric perception of emotional valence from facial expressions. *Neuropsychology*, *15*(4), 516–524.
- Ahern, G. L., & Schwartz, G. E. (1985). Differential lateralization for positive and negative emotion in the human brain: EEG spectral analysis. *Neuropsychologia*, *23*(6), 745–755. [https://doi.org/https://doi.org/10.1016/0028-3932\(85\)90081-8](https://doi.org/https://doi.org/10.1016/0028-3932(85)90081-8)
- Alves, N. T., Aznar-Casanova, J. A., & Fukusima, S. S. (2009). Patterns of brain asymmetry in the perception of positive and negative facial expressions. *Laterality*, *14*(3), 256–272. <https://doi.org/10.1080/13576500802362927>
- Anderson, A. K., Spencer, D. D., Fulbright, R. K., & Phelps, E. A. (2000). Contribution of the anteromedial temporal lobes to the evaluation of facial emotion. *Neuropsychology*. US: American Psychological Association.  
<https://doi.org/10.1037/0894-4105.14.4.526>
- Anes, M. D., & Short, L. A. (2009). Adult-like competence in perceptual encoding of facial configuration by the right hemisphere emerges after 10 years of age. *Perception*, *38*(3), 333–342. <https://doi.org/10.1068/p6092>
- Anwyl-Irvine, A., Massonnié, J., Flitton, A., Kirkham, N., & Evershed, J. (2018). Gorilla in our Midst: An online behavioural experiment builder. *BioRxiv*, 438242. <https://doi.org/10.1101/438242>
- Banich, M. T. (1998). The missing link: The role of interhemispheric interaction in attentional processing. *Brain and Cognition*, *36*(2), 128–157.  
<https://doi.org/https://doi.org/10.1006/brcg.1997.0950>
- Banich, M. T., & Belger, A. (1990). Interhemispheric interaction: How do the hemispheres divide and conquer a task? *Cortex*, *26*(1), 77–94.  
[https://doi.org/https://doi.org/10.1016/S0010-9452\(13\)80076-7](https://doi.org/https://doi.org/10.1016/S0010-9452(13)80076-7)

- Banich, M. T., & Shenker, J. I. (1994). Investigations of interhemispheric processing: Methodological considerations. *Neuropsychology*. US: American Psychological Association. <https://doi.org/10.1037/0894-4105.8.2.263>
- Banich, M. T., Passarotti, A., & Chambers, C. (1994). The role of the corpus callosum in attentional processing. In *Poster presented at the Inaugural Meeting of the Cognitive Neuroscience Society, San Francisco, USA*.
- Boles, D. B. (2005). A large-sample study of sex differences in functional cerebral lateralization. *Journal of Clinical and Experimental Neuropsychology*, 27(6), 759-768. <https://doi.org/10.1081/13803390590954263>
- Boles, D. B., Barth, J. M., & Merrill, E. C. (2008). Asymmetry and performance: toward a neurodevelopmental theory. *Brain and Cognition*, 66(2), 124–139. <https://doi.org/10.1016/j.bandc.2007.06.002>
- Bombardi, D., Schmid, P. C., Schmid Mast, M., Birri, S., Mast, F. W., & Lobmaier, J. S. (2013). Emotion recognition: the role of featural and configural face information. *Quarterly Journal of Experimental Psychology*, 66(12), 2426–2442. <https://doi.org/10.1080/17470218.2013.789065>
- Borod J. C. (1992). Interhemispheric and intrahemispheric control of emotion: a focus on unilateral brain damage. *Journal of Consulting and Clinical Psychology*, 60(3), 339–348. <https://doi.org/10.1037//0022-006x.60.3.339>
- Borod, J. C., Bloom, R. L., Brickman, A. M., Nakhutina, L., & Curko, E. A. (2002). Emotional processing deficits in individuals with unilateral brain damage. *Applied Neuropsychology*, 9(1), 23–36. [https://doi.org/10.1207/S15324826AN0901\\_4](https://doi.org/10.1207/S15324826AN0901_4)
- Borod, J. C., Cicero, B. A., Obler, L. K., Welkowitz, J., Erhan, H. M., Santschi, C., ... Whalen, J. R. (1998). Right hemisphere emotional perception: evidence across multiple channels. *Neuropsychology*, 12(3), 446–458. <https://doi.org/10.1037//0894-4105.12.3.446>
- Borod, J. C., Koff, E., Perlman Lorch, M., & Nicholas, M. (1986). The expression and perception of facial emotion in brain-damaged patients. *Neuropsychologia*, 24(2), 169–180. [https://doi.org/10.1016/0028-3932\(86\)90050-3](https://doi.org/10.1016/0028-3932(86)90050-3)
- Bourne, V. J. (2005). Lateralised processing of positive facial emotion: sex differences in strength of hemispheric dominance. *Neuropsychologia*, 43(6), 953–956. <https://doi.org/https://doi.org/10.1016/j.neuropsychologia.2004.08.007>

- Bourne, V. J. (2008). Chimeric faces, visual field bias, and reaction time bias: Have we been missing a trick? *Laterality*, *13*, 92–103.  
<https://doi.org/10.1080/13576500701754315>
- Bourne, V. J. (2010). How are emotions lateralised in the brain? Contrasting existing hypotheses using the Chimeric Faces Test. *Cognition and Emotion*, *24*(5), 903–911. <https://doi.org/10.1080/02699930903007714>
- Bourne, V. J. (2011). Examining the effects of inversion on lateralisation for processing facial emotion. *Cortex*, *47*(6), 690–695.  
<https://doi.org/https://doi.org/10.1016/j.cortex.2010.04.003>
- Bourne, V. J., Vladeanu, M., & Hole, G. J. (2009). Lateralised repetition priming for featurally and configurally manipulated familiar faces: Evidence for differentially lateralised processing mechanisms. *Laterality*, *14*(3), 287–299.  
<https://doi.org/10.1080/13576500802383709>
- Brechmann, A., & Angenstein, N. (2019). The impact of task difficulty on the lateralization of processing in the human auditory cortex. *Human Brain Mapping*, *40*(18), 5341–5353. <https://doi.org/https://doi.org/10.1002/hbm.24776>
- Bridges, D., Pitiot, A., MacAskill, M. R., & Peirce, J. W. (2020, January 20). The timing mega-study: comparing a range of experiment generators, both lab-based and online. *Brain, Cognition and Mental Health*.  
<https://doi.org/10.7717/peerj.9414>
- Burt, D. M., & Perrett, D. I. (1997). Perceptual asymmetries in judgements of facial attractiveness, age, gender, speech and expression. *Neuropsychologia*, *35*(5), 685–693. [https://doi.org/10.1016/S0028-3932\(96\)00111-X](https://doi.org/10.1016/S0028-3932(96)00111-X)
- Carbary, T. J., Almerigi, J. B., & Harris, L. J. (2001). The left visual hemispace bias for the perception of chimeric faces: A further test of the difficulty of discrimination hypothesis. *Brain and Cognition*, *46*(1), 57–62.  
[https://doi.org/https://doi.org/10.1016/S0278-2626\(01\)80034-8](https://doi.org/https://doi.org/10.1016/S0278-2626(01)80034-8)
- Carbary, T. J., Almerigi, J. B., & Harris, L. J. (2002). Task difficulty reduces the left visual hemispace bias for judgments of emotion in chimeric faces. *Brain and Cognition*, *48*(2–3), 304–311.
- Christman, S. D., & Hackworth, M. D. (1993). Equivalent perceptual asymmetries for free viewing of positive and negative emotional expressions in chimeric faces. *Neuropsychologia*, *31*(6), 621–624. [https://doi.org/https://doi.org/10.1016/0028-3932\(93\)90056-6](https://doi.org/https://doi.org/10.1016/0028-3932(93)90056-6)

- Cicone, M., Wapner, W., & Gardner, H. (1980). Sensitivity to emotional expressions and situations in organic patients. *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior*. Italy: Masson Italia.  
[https://doi.org/10.1016/S0010-9452\(80\)80029-3](https://doi.org/10.1016/S0010-9452(80)80029-3)
- Corballis, M. C. (1991). The lopsided ape: Evolution of the generative mind. *The Lopsided Ape: Evolution of the Generative Mind*. New York, NY: Oxford University Press.
- Corballis, M. C. (2009). The evolution and genetics of cerebral asymmetry. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 364(1519), 867–879. <https://doi.org/10.1098/rstb.2008.0232>
- David, A. S. (1989). Perceptual asymmetry for happy-sad chimeric faces: Effects of mood. *Neuropsychologia*, 27(10), 1289–1300.  
[https://doi.org/https://doi.org/10.1016/0028-3932\(89\)90041-9](https://doi.org/https://doi.org/10.1016/0028-3932(89)90041-9)
- Davidson, R. J., Ekman, P., Saron, C. D., Senulis, J. A., & Friesen, W. V. (1990). Approach-withdrawal and cerebral asymmetry: emotional expression and brain physiology. I. *Journal of Personality and Social Psychology*, 58(2), 330–341.
- Davidson, R. J., & Hugdahl, K. (Eds.). (1995). Brain asymmetry. *Brain asymmetry*. Cambridge, MA: MIT Press.
- DeKosky, S. T., Heilman, K. M., Bowers, D., & Valenstein, E. (1980). Recognition and discrimination of emotional faces and pictures. *Brain and Language*, 9(2), 206–214. [https://doi.org/https://doi.org/10.1016/0093-934X\(80\)90141-8](https://doi.org/https://doi.org/10.1016/0093-934X(80)90141-8)
- Demaree, H. A., Everhart, D. E., Youngstrom, E. A., & Harrison, D. W. (2005). Brain lateralization of emotional processing: historical roots and a future incorporating “dominance”. *Behavioral and Cognitive Neuroscience Reviews*, 4(1), 3–20. <https://doi.org/10.1177/1534582305276837>
- Dimond, S. J., & Farrington, L. (1977). Emotional response to films shown to the right or left hemisphere of the brain measured by heart rate. *Acta Psychologica*, 41(4), 255–260. [https://doi.org/https://doi.org/10.1016/0001-6918\(77\)90020-8](https://doi.org/https://doi.org/10.1016/0001-6918(77)90020-8)
- Ekman, P., & Friesen, W. V. (1975). Unmasking the face: A guide to recognizing emotions from facial clues. *Unmasking the Face: A Guide to Recognizing Emotions from Facial Clues*. Oxford, England: Prentice-Hall.
- Everts, R., Lidzba, K., Wilke, M., Kiefer, C., Mordasini, M., Schroth, G., ... Steinlin, M. (2009). Strengthening of laterality of verbal and visuospatial functions

- during childhood and adolescence. *Human Brain Mapping*, 30(2), 473–483.  
<https://doi.org/10.1002/hbm.20523>
- Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G\*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39, 175–191.
- Frässle, S., Krach, S., Paulus, F. M., & Jansen, A. (2016). Handedness is related to neural mechanisms underlying hemispheric lateralization of face processing. *Scientific Reports*, 6, 27153. <https://doi.org/10.1038/srep27153>
- Fox, N. A. (1991). If it's not left, it's right: Electroencephalograph asymmetry and the development of emotion. *American Psychologist*, 46(8), 863–872. <https://doi.org/10.1037/0003-066X.46.8.863>
- Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., ... Politi, P. (2009). Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *Journal of Psychiatry & Neuroscience*, 34(6), 418–432.
- Gainotti, G. (2019). Emotions and the right hemisphere: Can new data clarify old models? *The Neuroscientist*, 25(3), 258–270. <https://doi.org/10.1177/1073858418785342>
- Gazzaniga, M. S., & Smylie, C. S. (1983). Facial recognition and brain asymmetries: clues to underlying mechanisms. *Annals of Neurology*, 13(5), 536–540.  
<https://doi.org/10.1002/ana.410130511>
- Harmon-Jones E. (2004). Contributions from research on anger and cognitive dissonance to understanding the motivational functions of asymmetrical frontal brain activity. *Biological psychology*, 67(1-2), 51–76.  
<https://doi.org/10.1016/j.biopsycho.2004.03.003>
- Harris, L. J. (1992). Left-handedness. In I. Rapin & S. J. Segalowitz (Eds.), *Handbook of neuropsychology, child neuropsychology* (Vol. 6, Section 10, Part 1, pp.145–208) (Series editors: F. Boller & J. Grafman). Amsterdam: Elsevier.
- Hausmann, M., Innes, B. R., Birch, Y. K., & Kentridge, R. W. (2021). Laterality and (in)visibility in emotional face perception: Manipulations in spatial frequency content. *Emotion*, 21(1), 175–183. <https://doi.org/10.1037/emo0000648>
- Hirnstein, M., Hausmann, M., & Güntürkün, O. (2008). The evolutionary origins of functional cerebral asymmetries in humans: Does lateralization enhance parallel

- processing? *Behavioural Brain Research*, 187(2), 297–303.  
<https://doi.org/https://doi.org/10.1016/j.bbr.2007.09.023>
- Hirnstain, M., Hugdahl, K., & Hausmann, M. (2014). How brain asymmetry relates to performance – a large-scale dichotic listening study. *Frontiers in Psychology*, 4, 997. Retrieved from  
<https://www.frontiersin.org/article/10.3389/fpsyg.2013.00997>
- Hirnstain, M., Leask, S., Rose, J., & Hausmann, M. (2010). Disentangling the relationship between hemispheric asymmetry and cognitive performance. *Brain and Cognition*, 73, 119–127. <https://doi.org/10.1016/j.bandc.2010.04.002>
- Innes, B. R., Burt, D. M., Birch, Y. K., & Hausmann, M. (2016). A leftward bias however you look at it: Revisiting the emotional chimeric face task as a tool for measuring emotion lateralization. *Laterality*, 21(4–6), 643–661.  
<https://doi.org/10.1080/1357650X.2015.1117095>
- Jansari, A., Rodway, P., & Goncalves, S. (2011). Identifying facial emotions: valence specific effects and an exploration of the effects of viewer gender. *Brain and Cognition*, 76(3), 415–423. <https://doi.org/10.1016/j.bandc.2011.03.009>
- Kazak, A. E. (2018). Editorial: Journal article reporting standards. *American Psychologist*, 73(1), 1-2. <http://dx.doi.org/10.1037/amp0000263>
- Killgore, W. D., & Yurgelun-Todd, D. A. (2007). The right-hemisphere and valence hypotheses: could they both be right (and sometimes left)? *Social Cognitive and Affective Neuroscience*, 2(3), 240–250. <https://doi.org/10.1093/scan/nsm020>
- Kolb, B., Milner, B., & Taylor, L. (1983). Perception of faces by patients with localized cortical excisions. *Canadian Journal of Psychology*, 37, 8-18.
- Leask, S., & Crow, T. (2002). Word acquisition reflects lateralization of hand skill. *Trends in Cognitive Sciences*, 5, 513–516. [https://doi.org/10.1016/S1364-6613\(00\)01795-2](https://doi.org/10.1016/S1364-6613(00)01795-2)
- Levine, S. C., & Levy, J. (1986). Perceptual asymmetry for chimeric faces across the life span. *Brain and Cognition*, 5(3), 291–306.  
[https://doi.org/https://doi.org/10.1016/0278-2626\(86\)90033-3](https://doi.org/https://doi.org/10.1016/0278-2626(86)90033-3)
- Levy, J., Heller, W., Banich, M. T., & Burton, L. A. (1983). Asymmetry of perception in free viewing of chimeric faces. *Brain and Cognition*, 2(4), 404–419.  
[https://doi.org/https://doi.org/10.1016/0278-2626\(83\)90021-0](https://doi.org/https://doi.org/10.1016/0278-2626(83)90021-0)

- Ley, R. G., & Bryden, M. P. (1979). Hemispheric differences in processing emotions and faces. *Brain and language*, 7(1), 127–138. [https://doi.org/10.1016/0093-934x\(79\)90010-5](https://doi.org/10.1016/0093-934x(79)90010-5)
- Mandal, M., Tandon, S. C., & Asthana, H. (1991). Right brain damage impairs recognition of negative emotions. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, 27, 247–253. [https://doi.org/10.1016/S0010-9452\(13\)80129-3](https://doi.org/10.1016/S0010-9452(13)80129-3)
- Moreno, C. R., Borod, J. C., Welkowitz, J., & Alpert, M. (1990). Lateralization for the expression and perception of facial emotion as a function of age. *Neuropsychologia*, 28(2), 199–209. [https://doi.org/https://doi.org/10.1016/0028-3932\(90\)90101-S](https://doi.org/https://doi.org/10.1016/0028-3932(90)90101-S)
- Najt, P., Bayer, U., & Hausmann, M. (2013). Models of hemispheric specialization in facial emotion perception--a reevaluation. *Emotion*, 13(1), 159–167. <https://doi.org/10.1037/a0029723>
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113. [https://doi.org/https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/https://doi.org/10.1016/0028-3932(71)90067-4)
- Papadatou-Pastou, M., Schmitz, J., Martin, M., Munafo, M. R., Ocklenburg, S., & Paracchini, S. (2020). Human handedness: A meta-analysis. *Psychological Bulletin*, 146(6), 481-524. <http://dx.doi.org/10.1037/bul0000229>
- O'Regan, L., & Serrien, D. J. (2018). Individual differences and hemispheric asymmetries for language and spatial attention . In *Frontiers in Human Neuroscience* (Vol. 12, p. 380). <https://www.frontiersin.org/article/10.3389/fnhum.2018.00380>
- Parker, A. J., Woodhead, Z. V. J., Thompson, P. A., & Bishop, D. V. M. (2020). Assessing the reliability of an online behavioural laterality battery: A pre-registered study. *Laterality*, 26(4), 359-397. <https://doi.org/10.1080/1357650X.2020.1859526>
- Prete, G., Laeng, B., Fabri, M., Foschi, N., & Tommasi, L. (2015). Right hemisphere or valence hypothesis, or both? The processing of hybrid faces in the intact and callosotomized brain. *Neuropsychologia*, 68, 94–106. <https://doi.org/10.1016/j.neuropsychologia.2015.01.002>

- Prete, G., Laeng, B., & Tommasi, L. (2014). Lateralized hybrid faces: Evidence of a valence-specific bias in the processing of implicit emotions. *Laterality, 19*(4), 439–454. <https://doi.org/10.1080/1357650X.2013.862255>
- Qi, T., Schaadt, G., & Friederici, A. D. (2019). Cortical thickness lateralization and its relation to language abilities in children. *Developmental Cognitive Neuroscience, 39*, 100704. <https://doi.org/https://doi.org/10.1016/j.dcn.2019.100704>
- Rahman, Q., & Anchassi, T. (2012). Men appear more lateralized when noticing emotion in male faces. *Emotion, 12*(1), 174-179. <https://doi.org/10.1037/a0024416>
- Reuter-Lorenz, P., & Davidson, R. J. (1981). Differential contributions of the two cerebral hemispheres to the perception of happy and sad faces. *Neuropsychologia, 19*(4), 609–613. [https://doi.org/https://doi.org/10.1016/0028-3932\(81\)90030-0](https://doi.org/https://doi.org/10.1016/0028-3932(81)90030-0)
- Robertson, L. C., & Lamb, M. R. (1991). Neuropsychological contributions to theories of part/whole organization. *Cognitive Psychology, 23*(2), 299–330. [https://doi.org/https://doi.org/10.1016/0010-0285\(91\)90012-D](https://doi.org/https://doi.org/10.1016/0010-0285(91)90012-D)
- Robertson, L., Lamb, M., & Knight, R. (1988). Effects of lesions of temporal-Parietal junction on perceptual and attentional processing in humans. *Journal of Neuroscience, 8*, 3757–3769. <https://doi.org/10.1523/JNEUROSCI.08-10-03757.1988>
- Rodway, P., Wright, L., & Hardie, S. (2003). The valence-specific laterality effect in free viewing conditions: The influence of sex, handedness, and response bias. *Brain and Cognition, 53*, 452–463. [https://doi.org/10.1016/S0278-2626\(03\)00217-3](https://doi.org/10.1016/S0278-2626(03)00217-3)
- Ross, E. D., Homan, R. W., & Buck, R. (1994). Differential hemispheric lateralization of primary and social emotions implications for developing a comprehensive neurology for emotions, repression, and the subconscious. *Cognitive and Behavioral Neurology, 7*(1).
- Rueckert, L. (2005). A Web-based study of cerebral asymmetry for perception of emotion. *Behavior Research Methods, 37*(2), 271-276. <https://doi.org/10.3758/BF03192694>

- Sackeim, H. A., & Gur, R. C. (1978). Lateral asymmetry in intensity of emotional expression. *Neuropsychologia*, *16*(4), 473–481.  
[https://doi.org/https://doi.org/10.1016/0028-3932\(78\)90070-2](https://doi.org/https://doi.org/10.1016/0028-3932(78)90070-2)
- Sackeim, H. A., Greenberg, M. S., Weiman, A. L., Gur, R. C., Hungerbuhler, J. P., & Geschwind, N. (1982). Hemispheric asymmetry in the expression of positive and negative emotions. Neurologic evidence. *Archives of Neurology*, *39*(4), 210–218. <https://doi.org/10.1001/archneur.1982.00510160016003>
- Safer, M. A. (1981). Sex and hemisphere differences in access to codes for processing emotional expressions and faces. *Journal of Experimental Psychology: General*, *110*(1), 86–100. <https://doi.org/10.1037//0096-3445.110.1.86>
- Shamay-Tsoory, S. G., Lavidor, M., & Aharon-Peretz, J. (2008). Social learning modulates the lateralization of emotional valence. *Brain and Cognition*, *67*(3), 280–291. <https://doi.org/10.1016/j.bandc.2008.02.001>
- Springer, J. A., Binder, J. R., Hammeke, T. A., Swanson, S. J., Frost, J. A., Bellgowan, P. S. F., Brewer, C. C., Perry, H. M., Morris, G. L., & Mueller, W. M. (1999). Language dominance in neurologically normal and epilepsy subjects: A functional MRI study. *Brain*, *122*(11), 2033–2046.  
<https://doi.org/10.1093/brain/122.11.2033>
- Stanković, M. (2020). A conceptual critique of brain lateralization models in emotional face perception: Toward a hemispheric functional-equivalence (HFE) model. *International Journal of Psychophysiology*.  
<https://doi.org/https://doi.org/10.1016/j.ijpsycho.2020.11.001>
- Suberi, M., & McKeever, W. F. (1977). Differential right hemispheric memory storage of emotional and non-emotional faces. *Neuropsychologia*, *15*(6), 757–768.  
[https://doi.org/10.1016/0028-3932\(77\)90006-9](https://doi.org/10.1016/0028-3932(77)90006-9)
- Sutton, S. K., & Davidson, R. J. (1997). Prefrontal brain asymmetry: A biological substrate of the behavioral approach and inhibition systems. *Psychological Science*, *8*(3), 204–210. <https://doi.org/10.1111/j.1467-9280.1997.tb00413.x>
- Tiddeman, B., Burt, M., & Perrett, D. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications*, *21*(5), 42–50. doi:10.1109/38.946630
- Van Kleeck, M. H. (1989). Hemispheric differences in global versus local processing of hierarchical visual stimuli by normal subjects: New data and a meta-analysis of

- previous studies. *Neuropsychologia*, 27(9), 1165–1178.  
[https://doi.org/https://doi.org/10.1016/0028-3932\(89\)90099-7](https://doi.org/https://doi.org/10.1016/0028-3932(89)90099-7)
- Wager, T. D., Phan, K. L., Liberzon, I., & Taylor, S. F. (2003). Valence, gender, and lateralization of functional brain anatomy in emotion: a meta-analysis of findings from neuroimaging. *NeuroImage*, 19(3), 513–531.  
[https://doi.org/10.1016/s1053-8119\(03\)00078-8](https://doi.org/10.1016/s1053-8119(03)00078-8)
- Wagner, N. M., & Harris, L. J. (1994). Effects of typeface characteristics on visual field asymmetries for letter identification in children and adults. *Brain and Language*, 46, 41-58.
- Walker-Andrews, A. S. (1997). Infants' perception of expressive behaviors: Differentiation of multimodal information. *Psychological Bulletin*. US: American Psychological Association. <https://doi.org/10.1037/0033-2909.121.3.437>
- Walker-Andrews, A. S. (1998). Emotions and social development: Infants' recognition of emotions in others. *Pediatrics*, 102(5 Suppl E), 1268–1271.
- Watling, D., & Bourne, V. J. (2013). Sex differences in the relationship between children's emotional expression discrimination and their developing hemispheric lateralization. *Developmental Neuropsychology*, 38(7), 496–506.  
<https://doi.org/10.1080/87565641.2013.826660>
- Workman, L., Chilvers, L., Yeomans, H., & Taylor, S. (2006). Development of cerebral lateralisation for recognition of emotions in chimeric faces in children aged 5 to 11. *Laterality*, 11(6), 493–507. <https://doi.org/10.1080/13576500600724963>
- Workman, L., Peters, S., & Taylor, S. (2000). Lateralisation of perceptual processing of pro- and anti-social emotions displayed in chimeric faces. *Laterality*, 5(3), 237-249. doi: 10.1080/713754378
- Wyczesany, M., Capotosto, P., Zappasodi, F., & Prete, G. (2018). Hemispheric asymmetries and emotions: Evidence from effective connectivity. *Neuropsychologia*, 121, 98–105.  
<https://doi.org/https://doi.org/10.1016/j.neuropsychologia.2018.10.007>