RUNNING HEADING: Emotion lateralisation

Reference information:

Watling, D., Workman, L., & Bourne, Victoria J. (2012). Emotion lateralisation: Developments throughout the lifespan. *Laterality, 17*, 389-411.

Emotion lateralisation: Developments throughout the lifespan

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KEYWORDS: hemispheric lateralisation, emotion recognition, lifespan approach, neuropsychological developments

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**Abstract**

There is a great amount of research on hemispheric lateralisation for processing emotions and on the recognition of emotions across the lifespan. However, few researchers have explored the links between these two measures. This paper highlights how trends in these two research areas inform our understanding of how lateralisation for emotion processing may influence emotion recognition performance throughout the lifespan, including if the development of emotion lateralisation is a response to our environmental experiences of learning (experience dependent) or a result of having specific experiences at a particular time (experience expectant). The development of emotion lateralisation across the lifespan (infancy through to late adulthood) is explored with reference to past research and through the integration of the novel research offered within this special issue of *Laterality*. We also explore what we can learn from atypical populations. We propose that researchers need to focus on three key avenues of future research (longitudinal research, investigating the role of hormones, and research that explores the evolution of laterality) all which will provide greater insight into the development of laterality and how this may be associated with emotion processing.

**Changes in emotion lateralisation throughout the lifespan**

With the emergence of interdisciplinary fields such as social, developmental, and affective neuroscience an increasing amount of research now examines the way in which brain-behaviour interactions develop. This special issue brings together current research that examines this interaction specifically in relation to the processing of emotion, with a lifespan approach. To date there have been very few studies which have focused on exploring links between hemispheric lateralisation and the developmental trends in emotion recognition. In this special issue we will highlight how and why this is an emerging area which may explain some of the individual differences researchers have found in our recognition of emotion throughout the lifespan. Examining the way in which emotion lateralisation develops will provide vital insights that further our understanding of the relationship between brain development and social interaction. This paper will provide a review of what we already know about emotion recognition and lateralisation for processing emotion, and will discuss how the papers presented within this special issue will advance our understanding of this topic.

**Development of behavioural and neuropsychological processing of emotion**

Emotion recognition is a key social skill which we use on a daily basis to navigate successfully through our social interactions. It is known that throughout the lifespan individuals will use facial expressions to infer and make judgements about the attitudes and/or feelings of another (Cunningham & Odom, 1986) and that the judgements that one makes will be used to guide his or her future behaviour within the interaction (Gao & Maurer, 2009). While researchers have focused on exploring how emotion is lateralised within the brain during adulthood, little research has explored how the development of lateralisation for processing emotion may explain individual differences in children’s recognition of emotion throughout adulthood (early, middle, and late adulthood). We aim to highlight the importance of exploring lateralisation for emotion processing throughout the lifespan to aid our understanding of the possible biological underpinnings for how infants, children, adults, and the elderly recognize emotions.

*Developmental trends in emotion recognition*

Throughout the lifespan our ability to discriminate between and recognize emotions has been shown to be a vital skill. It is well-established that infants are able to discriminate between emotions. There has been much research investigating children’s recognition of the ‘basic’ emotions (i.e., happiness, sadness, anger, fear, disgust, and surprise; Ekman, Sorenson, & Friesen, 1969). Researchers consistently find that 7-month-old infants can discriminate between different facial expressions of emotion, such as happy, sad, anger, and surprised (e.g., Kestenbaum & Nelson, 1990; Nelson & Dolgin, 1985; Peltola, Leppänen, Palokangas, & Hietanen, 2008; Soken & Pick, 1999). Some evidence has even shown that 3-month-olds can discriminate between happy and surprised expressions, and sometimes sad expressions (e.g., Young-Browne, Rosenfeld, & Horowitz, 1977).

Children’s accuracy for recognizing facial expressions of emotion increases throughout childhood, where there are differing developmental age trends depending on the emotion being investigated. There is consistent evidence that children’s accuracy for recognizing emotions emerges gradually with accuracy increasing between 4- and 11-years-old, whereby happiness develops earliest, followed by sad or angry, and then surprise or fearful facial expressions (Herba & Phillips, 2004). In fact, Reinenbach and Masters (1983) found that 4-year-olds were fairly accurate at identifying happiness (85% accurate), while they were less proficient in their identification of sadness and anger (62% and 56% accuracy, respectively). This leads to the question of when children are able to recognize facial expressions of emotion at an adult level, which ranges from almost perfect recognition of happy emotional expression to about 80-90% accuracy for recognising negative emotions (Calvo and Lundqvist, 2008).

Durand, Gallay, Seigneuric, Robichon, and Baudouin (2007) found that children’s emotion recognition achieved adult-like levels for happy and sad at 5-years-old, fear at 7-years-old, anger at 9-years-olds, and disgust by 11- to 12-years-old. Gao and Maurer (2009, 2010) found similar developmental trends and extended Durand et al.’s work to explore if children and adults require similar baseline intensities for accurate emotion identification. They found that while for happiness and sadness, which are recognized earlier, children were able to accurately recognize the emotions at similar intensity levels as adults (20% and 30%, respectively). In comparison, for fear, anger, surprise, and disgust, which are recognized later, there were developmental trends between 5- to 10-year-olds (in comparison to adults), where with age these emotions could be recognized at lower intensities.

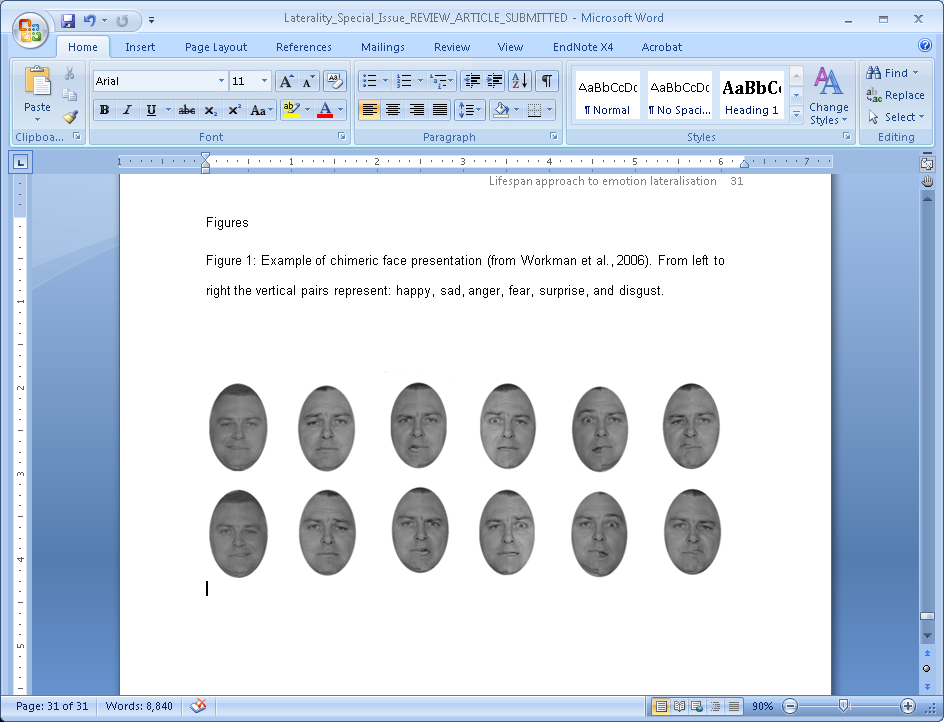
In adulthood researchers have shown that in young and middle adulthood (typically 18- to 39-years-old and 40- to 59-years-old, respectively) individuals are fairly proficient at recognizing facial expressions of emotion, but in late adulthood (typically 60-years-old and up) many researchers have found that there is a decline in one’s ability to recognize emotions. Isaacowitz and colleagues (2007) found that in middle and late adulthood there was greater difficulty in correctly identifying anger and that they made more incorrect classifications for disgust than in early adulthood. Additionally, in comparison to the young adults it was only those in late adulthood who demonstrated a decreased ability to accurately identify happiness and who made more incorrect classifications for fear. Additionally, researchers have found that older adults were less accurate in identifying fear, sadness, and anger when comparing with young adults (e.g., Keightley, Winocur, Burianova, Hongwanishkul, & Grady, 2006; Phillips, MacLean, & Allen, 2002; Sullivan & Ruffman, 2004) and this is supported across intensity levels (50%, 75%, and 100%) for these three emotions (Orgeta & Phillips, 2008).

*Developmental trends in the laterality of emotion processing*

The way in which emotion is lateralised in the brain has received a great deal of attention, with two primary hypotheses proposed: the right hemisphere hypothesis and the valence hypothesis. The right hemisphere hypothesis posits that the right hemisphere (RH) plays a dominant role in the processing of all emotions, regardless of valence. In contrast, the valence hypothesis posits that the RH is dominant for processing negative emotions (fear, anger, disgust, and sadness), while the left hemisphere (LH) is dominant for processing positive emotions (happiness and surprise). Much research has explored each of these hypotheses and researchers find overwhelming evidence that the RH is dominant for facial emotion processing[[1]](#footnote-1) both with adults (e.g., Bourne, 2005, 2010; Kucharska-Pietura & David, 2003; Nakamura et al., 1999) and with children (e.g., Aljuhanay, Milne, Burt, & Pascalis, 2010; Bava, Ballantyne, May, &Trauner, 2005; Chiang, Ballantyne, & Trauner, 2000; Failla, Sheppard, & Bradshaw, 2003; Levine & Levy, 1986; Workman, Chilvers, Yeomans, & Taylor, 2006). For instance, Batty and Taylor (2006) found that when 4- to 15-year-olds were viewing faces with emotional expressions there were hemispheric effects in brain activation. In particular, for both the P1 and N170 there was greater electrode activation over the RH than the LH, regardless of age.

There are several methods that researchers may use to explore the lateralisation of emotion processing. One key behavioural method that is used is the chimeric faces test (CFT). The CFT involves taking a neutral image and an emotive image, splitting both images down the middle and merging them together down the centre. The mirror image is then produced (e.g., if original has the emotive half of the face in the left hemifield and the neutral half of the face in the right hemifield, the mirror image will have the emotive half of the face in the right hemifield and the neutral half of the face in the left hemifield; see figure 1). The images are centrally presented and participants judge which face is more emotive. If a participant chooses the image that has the emotive half of the face in the left half face this indicates RH processing, while if the participant chooses the image that has the emotive half of the face in the right half face this indicates LH processing. The CFT has been validated with unilateral brain lesion patients. Kucharska-Pietura and David (2003) found that patients who have left hemisphere lesions and non-clinical control participants judged chimeras with the emotion in the left hemifield as more emotive than chimeras with the emotion in the right hemifield, while patients who have right hemisphere lesions were significantly less likely to have this left hemifield bias. Additionally, Bava et al. (2005) replicated these findings with children who have congenital unilateral brain damage. The CFT has been used with children as young as 5-years-old, with these children already showing a RH advantage comparable to adults when processing facial emotions of happiness (e.g., Failla et al., 2003; Levine & Levy, 1986; Workman et al., 2006). Furthermore, researchers have found that while a left hemifield (RH) bias is found at 5 years, this may continue to strengthen between 5 and 10 years, where it then appears to become stable (Chiang et al., 2000).

Figure 1. Example of chimeric face presentation (from Workman et al., 2006). From left to right the vertical pairs represent: happy, sad, anger, fear, surprise, and disgust.



Recently, researchers have begun exploring the laterality of emotion processing more widely by looking at developmental trends of different emotions. Aljuhanay and colleagues (2010) explored laterality of facial emotion processing for the expressions of happiness, sadness, and anger in a combined score and found that the left hemifield bias remained similar between the ages of 5 and 11 years. In contrast, Workman and colleagues (2006) explored 5- to 11-year-olds judgements of facial emotions for happy, sad, angry, surprise, disgust, and fear as separate measures. Similar to developmental trends in emotion recognition, they found developmental trends in the lateralisation for processing different emotions. In fact, happiness and sadness were the earliest emotions to show a RH bias in processing with no significant increase after five years. Lateralisation to the RH increased between 5 and 7 years for surprise and disgust but then remained stable, but for anger there was an increase between 5 and 7 years and it continued to increase between 7 and 11 years. With fear, there was no increase in lateralisation to the RH between 5 and 7 years, but there was an increase between 7 and 11.

Importantly, by 10-years-old it appears children’s lateralisation for processing emotion is comparable to that of adults. Researchers have found consistently a RH bias for happy emotion processing throughout adulthood (e.g., Levine & Levy, 1986; Moreno, Borod, Welkowitz, & Alpert, 1990). However, in late adulthood the strength of lateralisation appears to decline. Failla and colleagues (2003) found that while there was a significant RH bias for the 5- to 7-year-olds, 10- to 12-year-olds, and 20- to 30-year-olds, there was not for the 60- to 70-year-olds.

There are two main theories which aim to explain lateralisation changes in later life. The Right Hemisphere Decline model (Goldstein & Shelly, 1981) focuses on age associated changes in the cognitive abilities typically associated with either left or right hemispheric processing. Goldstein and Shelly had 20- to 70-year-olds complete a wide range of cognitive tests and then analysed LH tasks (e.g., language processing) and RH tasks (e.g., spatial processing). The older participants tended to be less proficient at tasks requiring RH processing, while tasks requiring LH processing were maintained until a later age. This evidence was used to suggest that the RH ages more rapidly than the LH. In contrast, the Hemispheric Asymmetric Reduction in Older Adults model (HAROLD; Cabeza, 2002; Dolcos, Rice, & Cabeza, 2002) moves away from the idea that hemispheric changes in later life affect one hemisphere to a greater extent than the other. The HAROLD model proposes that there is a more general reduction in asymmetry, with both hemispheres showing changes in later life.

*Linking emotion recognition with laterality for emotion processing: What we currently know*

Trends in the development of laterality for emotion processing are similar to the trends seen in research on emotion recognition. For instance, emotion recognition accuracy occurs at similar times to when lateralisation for emotion processing becomes lateralised to the RH. While there is evidence that children have reached adult-like levels for recognising key emotions by approximately 10-years-old and that they demonstrate adult-like degrees of laterality for emotion processing, there is very little evidence that explores developmental links between performance on emotion recognition tasks and lateralisation for emotion processing.

Studies attempting to link more advanced emotion recognition (e.g., inferring emotion) with lateralisation do show key relationships exist between the two. Workman et al. (2006) showed that children’s ability to infer emotion from the eyes was positively related to their degree of lateralisation for emotion processing (i.e., the more RH lateralised they were for emotion processing, the more accurate they were on an emotion in the eyes test). Furthermore, Watling and Bourne (2007) demonstrated that 10-year-old’s ability to recognize that facial emotional displays did not always match internal feelings could be positively predicted by their degree of RH lateralisation for happy emotion processing when the purpose was to hide what one was feeling to preserve a desired impression of the self (e.g., to not be seen as a crybaby). Importantly, these studies (Workman et al., 2006 and Watling and Bourne, 2007) demonstrate that there are links between laterality and performance; however, both studies have not made direct links with facial emotion recognition.

Throughout this special issue the selected papers explore models that may explain developmental trends in emotion recognition and laterality, as well as how variability in laterality for emotion processing may be explained through individual differences (e.g., sex differences, hormones, and handedness) that may play a role within these models.

**Current perspectives on the neuropsychological development of the processing of emotion**

There are two key issues to bear in mind when evaluating variability and changes in emotion lateralisation. First, how might different patterns of lateralisation impact on different patterns of emotional behaviour? Second, is there an interaction between brain development and the environmental experiences of an individual? To some extent, these two issues are highly related and can be considered with regard to mechanisms of brain development. When considering the development and plasticity of the brain, two views address the possible interaction between brain development and the environment: experience expectant and experience dependent (Greenough, Black, & Wallace, 1987). These views differ with regard to their importance for typical development and the times at which development or changes in brain function can occur.

An experience expectant view of brain development suggests that the ability of the brain to develop is entirely dependent upon the individual having the necessary experiences within the environment that the brain needs in order for typical development to occur. Plasticity and development occurs during constrained periods of development, often referred to as ‘critical’ or ‘sensitive’ periods. For example, infants with early visual deprivation, resulting from bilateral congenital cataracts, have been found to have impaired face processing abilities later in life after the cataracts have been removed (Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002). This study indicates that early experience of visual information in faces may be required for the brain to develop facial processing abilities. Therefore, if an experience expectant system does not receive the necessary input from the environment during a specific period of development the brain may develop in an atypical way that leads to impairments when processing that type of information.

In contrast to the experience expectant view, an experience dependent view suggests that brain development or plasticity occurs in response to environmental experiences of learning and that it is not dependent on a critical period. This form of brain development may reflect the fine tuning or development of skills that are reliant on the development of other skills; therefore, rather than development being constrained to any one point in time, with the experience dependent view the development of one skill will follow (or be dependent upon) the development of another skill. For example, the ability to process facial emotion requires first that the individual has the ability to perceive the visual input of facial stimuli. This view allows for development to occur throughout the lifespan and may also reflect some individual differences in brain organisation and development (Marshall & Kenney, 2009).

Relatively little research has directly examined whether early life experiences impact on the development of the neuropsychological mechanisms responsible for processing facial emotion. It is unlikely that a systematic study of this kind would ever be possible with human infants. However, research with primates has examined the consequences of manipulating early social and emotional interactions. Lyons, Afarian, Schatzberg, Sawyer-Glover, and Moseley (2002) examined how early environmental experiences might influence brain development in 39 infant monkeys (*Saimiri sciureus*) from 10- to 21-weeks-old. The monkeys were assigned to one of three environmental conditions with their mother: low foraging demands (food easily available, therefore more time for social interactions with the mother), high foraging demands (time and effort required to find food, therefore less time for social interactions with the mother), or intermittent social separations from the mother. Four years later, MRI scans showed that monkeys who had experienced intermittent social separations had more grey matter in the right ventral medial and dorsolateral areas and more white matter in the right prefrontal area. These differences showed brain areas that were between eight and 14 percent larger in monkeys who experienced early social deprivation. The authors use these findings to indicate experience dependent effects on the development of the RH, but not the LH.

Importantly, it is clear that early emotional and social experiences, at least in monkeys, can influence brain development and that these effects may be lateralised. Of course, this leaves the question open as to what extent might early emotional experiences influence brain development and the ability to process emotion in human infants?

*Neuropsychological development in infancy*

One aspect of early social interaction that has received a great deal of attention is the left cradling bias. About 80% of mothers hold their infant to the left side of their body. Studies have attempted to elucidate why there is a leftward cradling bias, with many focussing on associations with mother’s handedness (e.g., van der Meer & Husby, 2006), holding the infant near to the mother’s heartbeat (e.g., Todd & Butterworth, 1998), and mother’s patterns of emotion lateralisation in the brain (e.g., Bourne & Todd, 2004), which often point towards a stronger left cradling bias. Researchers have also explored associations with mother’s mental health and found that the left cradling bias was less apparent in mothers who were experiencing high levels of stress (e.g., Reissland, Hopkins, Helms, & Willliams, 2009). Importantly, all of these studies have explored the leftward cradling bias from the mother’s perspective with very little focus on the effects of cradling on the infant.

In this special issue, Hendriks, van Rijswijk, and Omtzigt are the first to explore how left and right side cradling affects the visual input that the infant receives. Mothers cradled a doll that had a camera within the head and therefore documented the visual input received by the infant whilst being cradled. They found that left cradled infants viewed more facial features than right cradled infants, leading Hendricks et al. to suggest that the visual input to the infant is of a higher quality when cradled to the left. This finding has important implications whereby infants who are cradled to the right may have a “suboptimal” emotional input which may impact on the infant’s future development, as was found to be the case with face processing in children who had early visual deprivation (see above discussion of Geldart et al., 2002).

Interestingly, a recent study by Vervloed, Hendriks, and van den Eijnde (2011) adds support to this relationship between cradling bias and the neuropsychological processing of emotion. Using the CFT to measure the emotion lateralisation of adults, they found that adults whose mothers had tended to left cradle showed the typical left hemifield (RH) bias, but this hemifield bias was reduced in adults whose mothers had tended to right cradle. This finding, together with Hendriks and colleagues’ (2012) finding supports the theory that infants who are left cradled may be receiving a higher quality visual input from the mother’s face, and that this influences the development of lateralisation for emotion processing in those individuals.

Research therefore suggests that left cradling has benefits for both mother and baby. The infant receives optimal emotional input, potentially leading to enhanced neuropsychological development and later emotion processing abilities, while the mother has the baby’s face in her left hemifield allowing the emotional state of the infant to initially be received and processed by the RH (Bourne & Todd, 2004).

*Neuropsychological development in early childhood*

As highlighted earlier, researchers have found that strength of lateralisation changes through childhood, with younger children having relatively symmetric brains and patterns of lateralisation strengthening through childhood (e.g., Chiang et al., 2000; Failla et al., 2003). Additionally, Workman et al. (2006) and Watling and Bourne (2007) both explored performance on more complex emotion recognition tasks, and found that children who are more accurate on the emotion tasks were also more strongly lateralised to the RH for processing emotional stimuli.

In this special issue, Barth, Boles, Giattina, and Penn contrasted patterns of lateralisation for children (4-year-olds) with undergraduate students. They explored links between lateralisation for emotional (happy emotional CFT) and linguistic (dichotic listening word task) processing with performance on emotion recognition and word recognition tasks, respectively. Interestingly, they found differing age associated relationships between lateralisation and performance on the emotion and linguistic tasks. For the linguistic processing task, which typically is lateralised to the left hemisphere in early childhood, children who were more strongly LH dominant in their processing performed better on the word recognition task, while no association existed for the adults. In contrast, for the emotion processing task, where lateralisation typically becomes more RH dominant later (between 5- and 10-years-old; discussed earlier), adults who were more RH dominant in their processing had higher emotion recognition scores. However, for the children strength of lateralisation was key (regardless of which hemisphere); the more LH or RH dominant a child was, the greater their performance on the emotion recognition task. Barth et al. interpret these findings to relate to their earlier model (see Boles, Barth, & Merrill, 2008) which states that processes that become lateralised to one hemisphere earlier become less associated with performance with age, whereas processes that become lateralised to one hemisphere later in development continue to have associations with performance, as demonstrated in the current paper.

The findings of Barth et al. (2012) raises two important issues to bear in mind in future research on the development of lateralisation: 1) that the developmental trajectories may differ across distinct cognitive functions, and 2) that the relationship between lateralisation and performance may differ as a result of the age at which lateralisation occurs.

*Neuropsychological changes through adulthood*

One limitation of the existing body of research examining changes in lateralisation is that it is focused on either end of the life span, looking either at development through childhood or in later life. It is often assumed that there are no changes in lateralisation through early and middle adulthood, but this is not necessarily the case. For example, women experience small fluctuations in functional lateralisation across the menstrual cycle (e.g., Hausmann, 2005; Hausmann & Gunturkun, 2000). While there may not be sudden or striking changes in lateralisation through adulthood, there may be some fluctuations and variability. It is therefore important to explore if and what environmental factors or emotional and social interactions might influence small changes and shifts in lateralisation during adulthood.

One paper presented in this special issue starts to address this question. Fussell, Rowe, and Mohr examined patterns of lateralisation of emotional attachment words (presented using the divided visual field methodology, where the words were presented unilaterally to either the left or the right visual field) in adults aged between 32- and 60-years-old who were either currently or previously married. Consistent with their expectations there was a RH advantage for the processing of positive attachment words. However, contrary to their expectations this finding was not more apparent in adults who were currently married than for those who were previously married. This indicates that relationship status may not influence variability in functional lateralisation. Of particular interest is that this paper has demonstrated that while emotional words are lateralised to the LH, emotional attachment related words that have personal relevance are lateralised to the RH. Most research in the past (as well as within this issue) has demonstrated that word tasks, regardless of whether the words are emotional or not, are dominant in the LH. However, it appears that if the emotional words have personal relevance, such as attachment related words, that they are processed in a more personally relevant and emotional manner.

There is little research examining fluctuations in lateralisation throughout adulthood and while it appears that marital status was not related to differences in relationships between emotional attachment words and individual differences in lateralisation, it would be interesting to explore how marital status may relate to emotional facial processing. Additionally, there are many other changes that occur throughout adulthood that may contribute to fluctuations in lateralisation (e.g., changes in women across the menstrual cycle and having children).

*Neuropsychological changes in later life*

The research considered thus far provides convincing evidence for experience influencing strength of lateralisation and the development of lateralisation from early infancy through to early adulthood. Does this interaction between brain and behaviour continue into later life? The model of changes in lateralisation in later life that receives the most support is the HAROLD model (Cabeza, 2002, described earlier). One interesting aspect of the HAROLD model, particularly for the research presented in this special issue, is the finding that the rates of asymmetry reduction in later life vary across individuals. In a PET study, Cabeza, Anderson, Locantore, and McIntosh (2002) compared patterns of activation during a memory task in three groups of participants: younger control participants, high-performing older adults and low-performing older adults. The younger participants showed a clear pattern of lateralisation, as did the low-performing older adults. However, the high-performing older adults, who were behaviourally indistinguishable from the younger adults, showed more asymmetric patterns of activation. Cabeza et al. interpreted this finding as the reduction in lateralisation being a compensatory form of plasticity whereby the changes in lateralisation enable the cognitive processing to be effectively completed by other areas of the brain. This raises the interesting possibility of an interplay between brain and behaviour for age associated changes in the brain.

In this special issue Beaton, Fouquet, Maycock, Platt, Payne, and Derrett contrasted patterns of lateralisation in younger (early 20's) and older (50+) adults. Whilst the majority of the papers presented in this special issue used behavioural measures of lateralisation, Beaton et al. used both behavioural and EEG measures. Their behavioural paradigm used the divided visual field methodology. A trial began with either a pair of eyes (condition 1) or an emotional word (condition 2) presented centrally. Subsequently a pair of eyes was presented to either the left of right visual field and participants had to respond whether the target pair of eyes was consistent with the centrally presented pair or eyes or word. No hemispheric effects were identified in the behavioural data and no differences were found between the younger and older participants. The lack of findings in the behavioural data for different patterns between the young and older adults is inconsistent with expectation and contradicts the HAROLD model; however, it must be noted that the older participants in Beaton et al.’s study were only assessed to be over 50 years and were not necessarily in late adulthood.

An additional, and novel, aspect of Beaton et al.’s (2012) work was that while the younger participants completed both the behavioural lateralisation task and an EEG task where the N170 component was analysed. In contrast to the behavioural data, the N170 showed laterality effects with a larger N170 response over the RH. This asymmetric effect is particularly interesting given the lack of lateralised findings for the behavioural data (both accuracy and reaction time). It seems possible that the behavioural measures used were not sensitive enough to pick up on the subtle lateralised effects that the EEG recordings identified. This finding raises the interesting possibility that other published research using behavioural methods which found no significant laterality effects may have just lacked the sensitivity to detect such effects with behavioural methods, and highlights the importance of combining different methods to identify the sometimes subtle laterality effects.

*Atypical neuropsychological development*

Whilst previous research and much of the research presented in this special issue characterises how lateralisation for emotion processing develops and changes across the life span, the majority of this research has only examined ‘typical’ participants. It is possible that examining emotion processing and emotion lateralisation in ‘atypical’ individuals, or people who have clinical disorders, might further our understanding of the development of emotion processing.

The processing of emotional stimuli has been examined a fair amount in individuals with autistic spectrum disorders (ASD), given that one aspect of this family of disorders is the reduced social and emotional interaction. Wallace, Coleman, and Bailey (2008) presented emotive faces to adults with ASD and found that they were significantly worse at recognising disgust, fear, and sadness. Patterns of atypical emotion processing in individuals with ASD have been attributed to the avoidance of fixating on the facial features when looking at emotional faces (e.g., Pelphrey, Sasson, Reznick, Paul, Goldman, & Piven, 2002).

Two papers in this special issue investigate emotion processing in atypical populations, both using the CFT to explore patterns of emotion lateralisation. In one paper, Taylor, Workman, and Yeomans examined children aged 11- to 15-years-old with autism and compared strength of lateralisation across the six basic emotions for these children to typically developing children (i.e., no diagnosis of autism) aged either 5- to 6-years-old or 7- to 8-years-old. They found that lateralisation for the processing of happy and angry facial emotions did not differ across the three groups. However, with the processing of disgust, fear, sadness, and surprise, children with autism showed reduced patterns of lateralisation. This weaker lateralisation was similar to the patterns found in the control children aged 5- to 6-years-old, which were also weaker than the patterns of lateralisation found in the 7- to 8-year-old control group. Taylor et al. used this finding to suggest a developmental delay in children with autism.

In a second paper, Vladeanu, Monteith-Hodge, and Bourne (2012) examined adult participants with no clinical diagnosis of autism, but who were higher or lower on autistic ‘traits’. Although clinical disorders are often treated in a categorical way (i.e., you either have the disorder or you do not), it is generally agreed that most of these disorders exist on a continuum, with people at the high extreme being given clinical diagnoses (Zachar & Kendler, 2007). In terms of autism, questionnaires have been developed to measure autistic “traits” (e.g., aloof personality, rigid personality, and pragmatic language) in individuals who do not have a diagnosed ASD. By looking at both individuals with a clinical diagnosis of autism and individuals with higher levels of autistic traits, a deeper understanding of atypical development of emotion processing and emotion lateralisation can be gained. Vladeanu et al. (2012) found a relationship between strength of lateralisation and the ‘aloofness’ scale on the Broad Autistic Phenotype Questionnaire (Hurley, Losh, Parlier, Reznick, & Piven, 2007), and that this relationship varied across the six basic emotions. For males only, the processing of fear, happiness, and surprise was more strongly lateralised in individuals with more aloof, or autistic-like, personalities.

Interestingly, there was one key difference between the findings of Taylor et al. (2012) and the findings of Vladeanu et al. (2012): the strength of the relationship between lateralisation for emotion processing and autism (or autistic traits) differed. Taylor et al. found weaker patterns of emotion lateralisation in adolescents who have autism, which they explain in terms of a developmental lag. In contrast, Vladeanu et al. found that adults with stronger autistic traits were more RH dominant for processing facial emotion. These apparently contrasting findings may give us insight into how laterality for emotion processing develops within participants with autism. There is evidence from other research (e.g., Farley et al., 2009) to support increased ability (and possibly processing) in individuals with autism with increasing age. Farley et al. (2009) conducted a study in which they examined various measures in a sample of 41 individuals with autism over a period of 20 years. They found that half of the participants showed either a substantial increase or a substantial decrease in cognitive ability, with those who showed cognitive gains being higher functioning. This is in line with the developmental delay proposal. It may be possible that the development of lateralised mechanisms for processing facial emotion starts later in individuals with autism but then develops in a more exaggerated manner, leading to the stronger patterns of lateralisation found by Vladeanu et al. However, given that the two papers also found differences in which emotions showed patterns of RH lateralisation (Taylor et al. found RH lateralisation for happy and angry emotions, while Vladeanu et al. found RH lateralisation for happy, fear, and surprise emotions), it could be that RH lateralisation develops as a result of experiences in their social environment, where with increasing age and social experiences higher functioning individuals with autism (or autistic traits) may be trained or develop strategies to look for particular features in faces to detect particular emotions, which may lead to greater lateralisation in adulthood (experience dependent). In fact, there is some evidence that children with autism pass second-order theory of mind tasks (social cognition) due to using logical strategies (e.g., Frith, Morton, & Leslie, 1991).

Importantly, perhaps individuals on the higher functioning side of the autistic spectrum have more, or higher quality, social and emotional interactions through childhood and adolescence and are therefore more likely to develop stronger patterns of lateralisation at a later age (in comparison to typically developing children).

**Exploring future research directions in the development of emotion lateralisation**

Throughout this review we have highlighted the importance of exploring lateralisation of emotion processing throughout the lifespan and the links with between this developing lateralisation and emotion recognition performance, both aspects of which we are in the early phases of understanding. At present, we are unable to draw firm conclusions as to how lateralisation for emotion processing occurs, what the advantage would be, and why females and males may have different lateralisation patterns. It is clear that future research will want to place greater focus on what the advantages (or disadvantages) of being more strongly lateralised for emotion processing may be. Which patterns of lateralisation might lead to more efficient processing?

*Developmental approach to emotion lateralisation across the lifespan*

Throughout this paper we have highlighted how researchers have explored the development of, and individual differences in, emotion lateralisation across the lifespan. However, all of this research has investigated these questions cross-sectionally. Much of the evidence to date suggests that lateralisation for emotion processing occurs as a result of our interactions with the environment (consistent with the experience dependent view). However, to address the question of the extent to which the development of laterality for emotion processing is a result of experience dependent or experience expectant systems, we require longitudinal work.

It would be important for future research to explore individual differences in the development of lateralisation and emotional recognition throughout the time when we know both are developing (i.e., between 4 and 10-years-old). Additionally, it would be important to investigate the time leading up to this period (infancy to early childhood) and throughout the life course (i.e., through adulthood and into old age) to enable researchers to address what factors may correspond to the development of, the maintenance and modification of the relationship between laterality for emotion processing and emotion recognition performance. There is a gap in the literature with regards to developments in adolescence and across adulthood where there is surprisingly little research completed in this area. Clearly, with rich longitudinal data that covers the life span a model could be developed and tested.

In addition to research with typically developing populations, we have also seen evidence in this paper and throughout this special issue to indicate that researchers should explore the development of lateralisation longitudinally in atypical populations. It is clear that a life span approach is required to address the ‘how’ and ‘why’ lateralisation occurs for processing emotions (including how this relates to performance on various tasks).

Alongside the lifespan approach, it is important to extend the methods that are used to assess lateralisation of emotion processing. Researchers tend to use primarily behavioural methods, including the CFT and the divided visual field paradigms. However, as shown by Beaton et al. (2012) it is possible to have non-significant results in the behavioural measures, but then have significant laterality effects be found when looking at EEG results from the same participants. Additionally, while many researchers have found emotive words to be processed in the LH, we saw in Fussell et al. (2012) that positive attachment words were more likely to be processed in the RH. The work completed in this area to date clearly demonstrates that it is important to vary the methodology used with an aim to increase our understanding. With differing methodologies we can explore the processes and mechanisms involved in the development of hemispheric lateralisation for emotion processing and what mechanisms may be underlie the association between emotion lateralisation and emotion recognition performance.

*Hormonal influences on the development of emotion lateralisation*

One key question to be addressed when examining the development of lateralisation is why the brain is lateralised for emotion processing and what biological factors might influence this development? One factor that is receiving an increasing amount of attention in the current research is the role of hormonal exposure in the development of lateralisation. An early theory, proposed by Geschwind and Galaburda (1985) proposed that prenatal testosterone exposure influences how the brain develops. Specifically, they proposed that higher levels of testosterone prenatally results in delayed LH development and more rapid RH development, leading to a more asymmetric and strongly lateralised brain.

Whilst the Geschwind- Galaburda theory has little support within the contemporary literature (e.g., Bryden, McManus, & Bulman-Fleming, 1994; Cornish, 1996; Pfannkuche, Bouma, & Groothuis, 2009), it did lead to a wide range of research exploring the relationship between cerebral lateralisation and various aspects of hormonal exposure, where there is evidence supporting this relationship. In fact, there is evidence for hormones influencing lateralisation at various times across the life span: prenatally (e.g., Bourne & Gray, 2009; Cohen-Bendahan, Buitelaar, van Goozen, & Cohen-Kettenis, 2004), across the menstrual cycle (e.g., Hausmann, 2005; Hausmann & Gunturkun, 2000) and in response to hormone replacement therapy (e.g., Doty, Kisat, & Tourbier, 2008; Bayer & Erdmann, 2008). Generally, this research suggests that increased levels of testosterone tend to be associated with stronger patterns of lateralisation. Given that males tend to be more strongly lateralised (e.g., Bourne, 2005), it may be that higher levels of testosterone are associated with a more ‘masculinised’ pattern of brain lateralisation.

Whilst our understanding of the relationship between hormones and lateralisation is increasing, we still have relatively little understanding of how this relationship might impact on emotion processing and behaviours. Various questions might be addressed in future research. Might prenatal hormonal exposure predict variability in the development of emotion lateralisation and the processing of emotional stimuli? Does the onset of puberty mark the time at which the development of lateralisation stops? Might hormones be implicated in the atypical emotion processing and lateralisation reported in clinical groups such as those with autism, depression or schizophrenia? How might changes in hormones in later life, and the use of artificial hormones through hormone replacement therapies, influence changes in lateralisation, cognitive decline and possibly the development of dementia in older adults?

*Evolutionary perspectives on the development of lateralisation*

Thus far we have considered the causal and developmental aspects of lateralised patterns of emotion processing in humans. A review of the literature reveals clear developments in this field over the last 30 years. Over the same time period, however, a great deal of comparative research into the development of lateralised responses in other species has been published, much of which has also considered in the development of asymmetrical emotional responses. It is widely accepted since the time of Darwin that we share basic emotional expressions with other species (Andrew, 1963; Darwin, 1872). If we wish to fully understand the emergence of emotion lateralisation in our own species it will be necessary to incorporate functional/evolutionary explanations into our understanding by considerations of such patterns in non-human species. It would be beyond the scope of this review to examine the large and growing body of comparative literature in any depth (see Andrew & Rogers, 2002; Güntürkün, 2009), but areas of non-human research might allow us to draw parallels, and in so doing potentially provide clues as to the selective advantages that having a lateralised brain has for humans. Two areas are briefly be flagged up here as possible areas for further investigation of the evolutionary precursors of human emotion lateralisation: primates and birds.

Research on oro-facial asymmetries, including left hemimouth bias, in primates (e.g., macaques, marmosets, chimpanzees, and baboons) suggests a RH dominance for the production of emotional responses (e.g., Hauser, 1993; Wallez & Vauclair, 2011). Given our own species also demonstrates a left side bias, this might be taken as evidence that a RH bias for emotion processing has precursors in primate evolution. Interestingly, Wallez and Vauclair (2011) have recently uncovered evidence that in olive baboons (*Papio anubis*) an agonistic behaviour (screeching) demonstrates a RH bias whereas affiliative behaviours, such as copulation calls, do not. Such a finding might help to shed light on debates concerning the valence versus the RH hypothesis discussed earlier. As suggested, current evidence provides strong support for the RH hypothesis (Bourne, 2005), yet there is also some evidence for the existence of a remnant of the valence hypothesis (Workman, Peters, & Taylor, 2000). Moreover, since the work of Wallez and Vauclair suggests neuropsychological homologies between baboons and humans for lateralized emotion responses, perhaps further studies of primates will enhance our understanding of the evolutionary continuities (and discontinuities) underlying emotion responses and shed some light on the phylogenetic path leading to current patterns of human lateralization.

In relation to avian species, researchers have uncovered clear evidence of RH involvement in the control of emotion responses of the domestic chick (e.g.,Andrew & Rogers, 2002; Rogers, 2008). Interestingly, the time course for development of this RH superiority for controlling emotion responses to novelty appears to fit in well with the challenges that the chick meets as it begins to wander further from the mother hen at this point in development. Hence the chick demonstrates RH control of visually evoked responses at a time when its increased mobility means that it is more likely to encounter a wider range of (potentially emotionally-salient) environmental stimuli (Workman & Andrew, 1989). Such findings might help us to understand the functional significance of the time course for development of emotion processing. Additionally, Rogers has demonstrated that the lateralisation of emotionally evoked behaviour is dependent on the light exposure through the egg shell just prior to hatching (Rogers, 1982, 2008). The parallels with Hendriks et al.’s (2012) cradling study are fascinating in as much as the manipulation of light entering the eye also had a developmental effect on the pattern of lateralisation observed. It is feasible that avian studies might help to flesh out the functional significance for the outcome of the interaction between very early experience and the neurological substrate for the development of emotion processing in humans by comparison to the environmental factors that guide this pattern in chicks (see also Bourne & Todd, 2004, and Vervloed et al., 2011). In so doing, the work on the domestic chick might help to resolve the experience expectant versus the experience dependent systems debate.

**Conclusion**

The research presented in this paper and within the special issue clearly shows that there is variability in the strength of lateralisation for processing emotion, both across the lifespan and with regard to individual differences. It remains unclear though whether this variability might reflect an experience expectant or an experience dependent system underlying the neuropsychological processing of emotion. Additionally there is evidence that there are links between strength of lateralisation for emotion processing and performance. However, there are also gaps in our knowledge for which we have suggested that researchers could enhance our understanding through: longitudinal research and using a variety of methodologies; exploring the role of hormones to explain not only the development of lateralisation for emotion processing, but also to explore fluctuations in lateralisation throughout the lifespan; and developing further an understanding of the evolutionary and functional foundations through a greater integration of comparative findings. Importantly, the research in this special issue does go some way in addressing gaps that were within the literature and highlight where researchers in the field can focus future studies.

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1. Note that the evidence regarding asymmetry for other aspects of emotion processing, such as the production of emotional facial expressions, is somewhat more mixed (see Nicholls, Ellis, Clement, & Yoshino, 2004). [↑](#footnote-ref-1)