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Perceptual asymmetries and handedness: a neglected link?

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Healthy individuals tend to weigh in more the left than the right side of visual space in a variety of contexts, ranging from pseudoneglect to perceptual asymmetries for faces. Among the common explanations proposed for the attentional and perceptual advantages of the left visual field, a link with the prevalence of right-handedness in humans has never been suggested, although some evidence seems to converge in favor of a bias of spatial attention toward the region most likely coincident with another person's right hand during a face-to-face interaction. Such a bias might imply an increased efficiency in monitoring both communicative and aggressive acts, the right limb being more used than the left in both types of behavior. Although attentional and perceptual asymmetries could be linked to right-handedness at the level of phylogeny because of the evolutionarily advantage of directing attention toward the region where others' dominant hand usually operates, it is also legitimate to question whether, at the ontogenetic level, frequent exposure to right-handed individuals may foster leftward biases. These views are discussed in the light of extant literature, and a number of tests are proposed in order to assess our hypotheses.

Keywords: perceptual and attentional asymmetries, handedness, left face bias, face, body

As largely shown by past research, healthy individuals tend to weigh in more the left than the right side of visual space in a variety of contexts, ranging from pseudoneglect (for a review, see Jewell and McCourt, 2000) to perceptual and attentional asymmetries for faces (e.g., Burt and Perrett, 1997; Hsiao and Cottrell, 2008). Among the common explanations provided for the existence of such attentional and perceptual advantages of the left visual field, including hemispheric asymmetries for processing faces (Bentin et al., 1996; Kanwisher et al., 1997; Yovel et al., 2008; Prete et al., 2013), spatial information (Mesulam, 1981; Corbetta and Shulman, 2002), and social information (Brancucci et al., 2009), a possible functional link between leftward biases and the prevalence of right-handedness in human population has never been proposed, beyond a bulk of correlational studies. In fact, while it is controversial whether the right-hemispheric specialization for face processing drives the leftward bias for faces or vice versa (Dundas et al., 2012b), no one has attempted to relate such a bias to the potential advantage of better monitoring others' dominant hand. In fact, it should be noted that the region of a person's right hand and limb, with respect to an observer facing that person (assuming a face-to-face interaction), falls in the observer's left field of view, so that any leftward bias would drive the focus of attention on the most active side of others' body.

In other words, it could be not by chance that the location in space of others' right hand, from the point of view of the observer, coincides with the well-known leftward bias of spatial attention, usually indicated as pseudoneglect (Bowers and Heilman, 1980; Jewell and McCourt, 2000). This is a natural property of attention whereby the left side of visual space is more relevant than the right side, as witnessed by the more frequent leftward errors made in bisection tasks (e.g., dividing a line or a rod into two halves), or by the fact that judgments on brightness, numerosity, and size are similarly skewed in favor of the left hemisphere.

A similar advantage for the left side is also observed in face perception, consisting in a preferential reliance upon the features on the left side of an observed face, when one has to make judgments about gender, attractiveness, age, and emotional expression conveyed by that face (Burt and Perrett, 1997). This is also reflected in the higher frequency of eye movements directed to the left side of the face (Butler et al., 2005). Given their biological relevance and their indivisibility from body – and thus from arms – in ecological settings, faces offer the best subject of inquiry to test our hypothesis.

WHICH ARE THE POTENTIAL ADVANTAGES OF LEFTWARD ASYMMETRIES?

We believe that a bias of spatial attention toward the region most likely coincident with others' right hand might have a deeply rooted justification in the communicative advantage conferred by attending to the limb most frequently used in gesturing, above all by right-handers and during speech (Kimura, 1973a,b; Dalby et al., 1980; Lavergne and Kimura, 1987; Saucier and Elias, 2001). Furthermore, the left-sided attentional bias might ensure a more efficient monitoring of aggressive behavior, the right limb being more used than the left also in violent actions (Coren and Porac, 1977). The other side of the coin is that a reduced monitoring of the right side of space – the space in which falls the dominant hand of encountered left-handed individuals – could contribute to the “surprise effect” at the basis of the left-handers' advantage in fighting and sports (Raymond et al., 1996).

Clearly, this line of argument holds for right-handed subjects in the role of observers, and to some extent one would predict that it should also hold for left-handed observers, at least on the basis of visual experience. For example, Hagemann (2009) found that the directions of tennis strokes performed with the right hand were easier to predict compared to those performed with the left

hand, regardless of observers' handedness. Similarly, Marzoli et al. (2013) observed that, when required to report the perceived orientation (front or back view) of pictures of ambiguous human silhouettes performing one-handed manual actions, both right- and left-handers perceived the figure more frequently in an orientation congruent with a movement performed with the right rather than the left hand. However, one should not forget the possible contribution of motor representations in shaping attentional biases. In fact, the left hemispatial bias for face processing usually observed in right-handers is absent (Jaynes, 1976; Heller and Levy, 1981; Roszkowski and Snelbecker, 1982; Hoptman and Levy, 1988) or weaker (Luh et al., 1994) in left-handers. Moreover, left-handers turn out to be less affected by a leftward pseudoneglect (Brodie and Dunn, 2005; see also the meta-analysis by Jewell and McCourt, 2000). In support of a role of hand-related motor representations, attention has been reported to be biased toward the right and left side of observed bodies, regardless of their spatial orientation, respectively, in right- and left-handers (Gardner and Potts, 2010; see also Zartor et al., 2010). Analogous effects of handedness have been reported by our own group for the imagination of others' actions (Marzoli et al., 2011a,b; Marzoli et al., 2013). Noteworthy, these results seem to be in line with our proposal of a link between well-known attentional and perceptual leftward biases and an attentional bias toward the right side of others' body, both biases being affected in similar ways by handedness. However, we point out that viewing perspective seems to interact with motor experience as regards attentional asymmetries toward others' body, yielding a specific pattern of results (Marzoli et al., 2011a): when an actor is imagined as seen from the front, right-handers' attention is biased toward their own dominant hand (that is, toward the left from their own point of view), whereas left-handers' attention is biased toward their own non-dominant hand (that is, toward the left from their own point of view) or not biased at all; when an actor is imagined as seen from the back, both right-handers' and left-handers' attention is biased toward their own dominant hand (that is, toward the left from left-handers' point of view and toward the right from right-handers' point of view). Likewise, handedness does not affect perceptual and attentional asymmetries in the same direction in all tasks: form recognition and dot localization do not elicit any visual field difference between right- and left-handers, whereas letter recognition is performed better in the right visual field by right-handers, but not by left-handers (Bryden, 1973).

DEVELOPMENTAL TREND IN THE LEFT FACE BIAS: IS THERE A ROLE FOR EXPERIENCE?

In our opinion, the role of experience in the establishment of perceptual asymmetries in face processing deserves in-depth investigation. For example, the direction of reading and writing systems that characterize the various human cultures (left-to-right or right-to-left) has been called into cause as a possible factor modulating the leftward lateral bias for face exploration and attention (Vaid and Singh, 1989; Sakhuja et al., 1996; Heath et al., 2005; Megreya and Havard, 2011). Therefore, we want to highlight how, although attentional and perceptual asymmetries could be linked to right-handedness at the level of phylogeny – because of the evolutionarily adaptive advantage of directing attention toward the

region of visual space where others' dominant hand usually operates – it is also legitimate to question whether, at the ontogenetic level, frequent exposure to right-handed individuals may foster leftward biases.

In this regard, it should be stressed that, whereas the leftward bias in face perception is usually observed in children of about 5 years (e.g., Roszkowski and Snelbecker, 1982; Levine and Levy, 1986; Kolb et al., 1992; Failla et al., 2003; Workman et al., 2006; Aljuhanay et al., 2010; Taylor et al., 2012), it is often reported to increase with age and reach an adult-like level by the age of about 10 years (Chiang et al., 2000; Workman et al., 2006; Anes and Short, 2009; Balas and Moulson, 2011; Taylor et al., 2012; Watling and Bourne, 2013; for a review, see Watling et al., 2012). However, the use of different methods seems to provide data in favor of both earlier (e.g., eye tracking; Wheeler, 2010; Liu et al., 2011; Dundas et al., 2012b) and later (e.g., moving window technique; Birmingham et al., 2012) emergence of an appreciable leftward bias in face processing. Similarly, a developmental trend has been shown in studies on the right-hemispheric advantage for face processing (Reynolds and Jeeves, 1978), although it is not always observed, maybe because of procedural differences (Young and Ellis, 1976; Young and Bion, 1980). Further support to our proposal can be drawn from studies showing that a general leftward bias for both upright and inverted human faces, monkey faces, and objects in infancy becomes a specific leftward bias for upright human faces in adulthood (Guo et al., 2009), and that the increase in leftward bias is specific for human faces, which suggests its experience-dependent nature (Balas and Moulson, 2011). A leftward bias for attending human faces was also reported for laboratory-raised rhesus monkeys and domestic dogs (Guo et al., 2009; see Dahl et al., 2013 for congruent findings in chimpanzees). Interestingly, the bias was absent for monkey and dog faces in dogs, and we believe that the prolonged experience with right-handed humans could be a more plausible account for such a specificity compared to other interpretations (e.g., a right-hemispheric specialization for human but not dog faces in both humans and dogs). Although rhesus monkeys showed a leftward bias for both human and monkey faces, given that they were presented only with human and monkey faces but not with dog faces, it cannot be resolved whether such a result was due to their difficulty in differentiating between the two species, to their experience with right-handed monkeys and humans, or to a non-species-specific bias. However, there is some evidence of right-handedness at least in captive rhesus monkeys (Westergaard and Suomi, 1996), as well as in other primates such as chimpanzees, gorillas, and baboons (see Hopkins, 2006; Cochet and Byrne, 2013; Meguerditchian et al., 2013 for reviews). We point out that population-level right-handedness is observed more often in captive rather than wild primates, as well as for communicative gestures rather than non-communicative actions, which has been credited to interaction with humans (Cochet and Byrne, 2013; Meguerditchian et al., 2013). This could suggest a crucial role for social factors also in the emergence of the left face/left visual field bias observed during emotional processing in nonhuman primates (see Lindell, 2013 for a review). On the other hand, findings from animal studies should be considered with caution as regards the origin of the leftward bias for faces, given that several results are inconsistent with a crucial role of interaction with

humans even in domestic animals. For example, Racca et al. (2012) used emotional faces of both dogs and humans and found a more complex pattern of results compared to those of Guo et al. (2009), dogs showing a left gaze bias for conspecific negative expressions, a right gaze bias for conspecific positive expressions and no bias for conspecific neutral expression, as well as a left gaze bias for human negative and neutral expressions and no bias for human positive expressions. Moreover, sheep exhibit a left visual field advantage for conspecific (Peirce et al., 2000) but not for human faces (Peirce et al., 2001). Domestic chicks with no visual experience of human eyes and gaze also show a left visual field preference for monitoring a human-like dummy mask (Rosa Salva et al., 2007), which shows that even the emergence of leftward biases for human faces can be completely independent from interaction with humans.

The idea that the frequent interaction with right-handed individuals might promote leftward biases is consistent not only with both the experience-expectant and the experience-dependent view of brain development (Greenough et al., 1987), but also with previous studies showing that experience can affect the lateralization of face processing (e.g., infant holding biases; Vervloed et al., 2011; reading habits; Vaid and Singh, 1989; Sakhuja et al., 1996; Heath et al., 2005; Megreya and Havard, 2011). However, the fact that eye tracking studies reveal that a left visual field bias during face observation emerges within 9–11 months (Wheeler, 2010; Liu et al., 2011; Dundas et al., 2012b) and the fact that the leftward bias becomes more specific for upright human faces with increasing age (Guo et al., 2009) indicate that reading habits cannot account for the emergence of the bias. On the other hand, the cumulative experience with right-handed individuals might be responsible for the leftward bias increasing and becoming more selective with age. Moreover, given that the number of interactions with partners other than the primary caregiver increases with time, it should be investigated whether children of left-handed mothers show a shift from a rightward bias to a leftward one over time (in this regard, see Wheeler, 2010, who observed that in children aged 3–6 months with a rightward bias, this decreased with age).

The developmental trend in right-hemispheric specialization for faces has been credited to a parallel increase in right-hemispheric specialization for configural processing (Anes and Short, 2009). However, if the leftward bias for face processing is linked to configural processing, it should be noted that body configural information might include the knowledge (in terms of both first-order relational information and structural information; Reed et al., 2006) that the dominant hand of humans is usually placed on their right side, which could explain why face inversion, which disrupts configural processing (Maurer et al., 2002), also disrupts the leftward bias/right-hemispheric dominance in face processing (Hellis and Shepherd, 1976; Leehey et al., 1978; Luh, 1998; Coolican et al., 2008; Anes and Short, 2009; Bourne, 2011). The link between the leftward bias/right-hemispheric dominance and configural processing of faces is further corroborated by their similar developmental trends, configural processing, and face-inversion effects also reaching adult-like levels by the age of 10 years (Carey and Diamond, 1977; Diamond and Carey, 1977; Mondloch et al., 2002), as well as by the finding that face-inversion

effects appear to be stronger in the left rather than the right visual field (Leehey et al., 1978). In this regard, it is noteworthy that individuals with autism, who exhibit impaired configural processing (Behrmann et al., 2006), are less affected by both the face inversion effect (Hobson et al., 1988; Tantam et al., 1989) and the leftward bias for face processing (Dundas et al., 2012; Taylor et al., 2012; see also Dundas et al., 2012b).

Another factor reported to affect the leftward bias for faces is maternal preferred cradling side: adults whose mother had an atypical right-side preference for holding infants show a reduced left-bias for chimeric faces compared to adults whose mother had the typical left-side preference (Vervloed et al., 2011). Interestingly, the maternal cradling side is also related to children's handedness, right-cradled infants having slightly higher odds of being left-handed at 19 months of age (Scola and Vauclair, 2010). Given that children seem to imitate handedness preferences of adults (Harkins and Michel, 1988; Harkins and Uğziris, 1991; Michel, 1992; Fagard and Lemoine, 2006), imitation could also account for the greater incidence of left-handedness among right-cradled children, both because left-handed mothers are more likely to cradle on the right side (Scola and Vauclair, 2010) and because holding the infant on one side should free the opposite hand for other tasks (Huheey, 1977; see Hopkins, 2004 for similar associations between cradling side and hand preferences of both mother and infant in nonhuman primates). However, a reduced attentional bias toward the right arm might also explain the smaller leftward bias for faces observed in left-handers and in right-cradled individuals. This hypothesis deserves particular attention, above all in the light of the fact that individuals with autism, who show deficits in action imitation (see Williams et al., 2004 for a review), also exhibit a reduced leftward bias for face processing (Dundas et al., 2012a; Taylor et al., 2012; see also Dundas et al., 2012b) and a higher proportion of non-right-handedness (e.g., Escalante-Mead et al., 2003), which seems not to be accounted for by parental handedness (Tsai, 1982).

SPECIFICITY vs. GENERALIZABILITY OF LEFTWARD BIASES

Some evidence indicates that adult humans exhibit a leftward bias for upright human faces, but not for several other classes of stimuli such as vases, landscapes, and fractals (Mertens et al., 1993; Leonards and Scott-Samuel, 2005). Leonards and Scott-Samuel (2005) proposed that the leftward bias might be specific to socially relevant stimuli, and this could be in line with studies suggesting that the more the emotional load of the stimuli or tasks, the greater the leftward bias for faces (Gallois et al., 1989; Coolican et al., 2008; Thompson et al., 2009). In line with this proposal, centrally presented gaze cues (i.e., social stimuli) facilitate the detection of spatially congruent targets presented in the left visual field (that is, the region of the observed person's right hand during a face-to-face interaction) but not in the right visual field, whereas arrow cues (i.e., non-social stimuli) are effective for targets presented in both visual fields (Marotta et al., 2012; see also Greene and Zaidel, 2011).

The role of social relevance in the emergence of attentional asymmetries in favor of the left visual field is corroborated by a series of studies by Mogg and Bradley (1999, 2002) showing that threatening faces induced a greater attentional capture compared

343 to happy and neutral faces when the faces were subliminally pre- 400
344 sented in the left but not in the right visual field, and that this 401
345 effect was particularly apparent for more anxious individuals. A 402
346 study by Field (2006) found a similar pattern of results, extending 403
347 the leftward bias for threatening stimuli to a different population 404
348 (children aged 7–9 years) and different stimuli (animals). There- 405
349 fore, although the leftward bias/right hemispheric advantage could 406
350 be more evident for faces, it is not exclusive of this class of stim- 407
351 ulti, as also shown by studies generalizing the left visual field bias 408
352 to photographs of houses and cars (Levine et al., 1984) and line 409
353 drawings of common objects (Kim et al., 1990). Nonetheless, it 410
354 is not unreasonable to hypothesize that more general attentional 411
355 and perceptual asymmetries may arise from an initial leftward 412
356 bias for faces and/or bodies. Specifically, given that human bodies 413
357 and faces are the most ecologically relevant and likely the most 414
358 recurrent stimuli people deal with in everyday life, the asym- 415
359 metrical processing they elicit could generalize to some extent to 416
360 other domains. This view would be consistent with the observa- 417
361 tion that handedness and sex seem to affect the left side bias for 418
362 faces and other leftward asymmetries in similar ways: according to 419
363 a meta-analysis of line bisection studies conducted by Jewell and 420
364 McCourt (2000), in fact, males show a slightly larger pseudone- 421
365 glect compared to females and right-handers show a slightly larger 422
366 pseudoneglect compared to left-handers. Interestingly, this lat- 423
367 ter finding cannot be attributed to the mere use of the left hand, 424
368 because the authors also mentioned a relative bias in the direction 425
369 of the hand used to perform bisection, which is consistent with 426
370 the activation-orientation theory of Kinsbourne (1970). On the 427
371 contrary, the modulation of pseudoneglect by handedness could 428
372 match the way in which one's own representations seem to affect 429
373 attentional asymmetries toward humans bodies observed from the 430
374 front (e.g., Gardner and Potts, 2010; Marzoli et al., 2011a). Finally, 431
375 the fact that pseudoneglect shows a developmental trend similar to 432
376 that of the leftward bias for faces also suggest their related origin 433
377 (Bradshaw et al., 1988; Dellatolas et al., 1996; Failla et al., 2003). 434
378 However, it should be noted that a left-sided visuospatial bias has 435
379 also been found in birds (Diekamp et al., 2005), and embryonic 436
380 light stimulation has been invoked for its emergence (Chiandetti, 437
381 2011), which suggests that pseudoneglect could arise from causes 438
382 other than the social ones. 439

384 EMOTIONAL ASYMMETRIES

385 On the basis of the literature reviewed in the previous section, 440
386 social stimuli, and emotional stimuli in particular, are more likely 441
387 to induce attentional and perceptual asymmetries compared to 442
388 non social stimuli. In this section, we attempt to conciliate the 443
389 larger asymmetries observed for emotional stimuli with our main 444
390 hypothesis. As recently stressed by Watling et al. (2012), future 445
391 research should address the advantages of lateralization for emo- 446
392 tion processing, as well as related gender differences. In this regard, 447
393 a positive correlation has been observed between children's left 448
394 hemispacial advantage for emotion perception and their ability 449
395 to understand emotional states in cartoon situations and in eyes 450
396 (Workman et al., 2006), as well as in faces, although this was 451
397 shown only in male children (Watling and Bourne, 2013). How- 452
398 ever, a recent study extended the positive correlation between 453
399 left-lateralized processing and performance to the discrimination 454

400 of both human and chimpanzee faces in both species (Dahl 401
402 et al., 2013). These studies suggest a link between the lateraliza- 403
404 tion of emotional processing and the understanding of others' 405
406 emotional/cognitive states, which is bolstered by their similar 407
408 time course, theory of mind emerging by the age of 4 years 409
410 and improving during childhood (Baron-Cohen, 1995). More- 411
412 over, the leftward bias for faces approaches adult-like levels by 413
414 the age of 10 years (Chiang et al., 2000; Workman et al., 2006; 415
416 Anes and Short, 2009; Taylor et al., 2012), just before children 417
418 start to exhibit a preference for the left eye (from the observer's 419
420 viewpoint) during face scanning (Birmingham et al., 2012) and a 421
422 patent improvement in their ability to interpret emotion from eyes 423
424 (Tonks et al., 2007). 425

426 Therefore, one could wonder whether the advantage of the 427
428 right-hemispheric specialization for emotion processing might 429
430 lie in monitoring other's emotional states and their subsequent 431
432 actions within the same hemisphere, and whether leftward biases 433
434 could be strengthened by the fact that interaction partners' facial 435
436 expressions and eye movements are constantly associated with 437
438 their right-handed actions. This hypothesis deserves particular 439
440 consideration, given that the leftward bias for emotion processing 441
442 could appear counterintuitive, emotions being expressed more 443
444 intensely on the left side of the face, which falls in the right visual 445
446 field of the observer in a face-to-face interaction (Sackeim and 447
448 Gur, 1978). On the other hand, there is some evidence that anger 449
450 might be expressed more intensely on the right side of the face 451
452 (Indersmitten and Gur, 2003) and that the leftward bias might be 453
454 larger for anti-social emotions (and in particular for anger) than 455
456 for pro-social emotions (Workman et al., 2000). Thus, the left- 457
458 ward bias appears to be less counterintuitive if one assumes that 459
460 both bearing a particular sensitivity to the hemiface expressing 461
462 more intense threat-related facial displays and directing attention 463
464 toward the region containing the right arm of an angry individual 465
466 could provide important ecological advantages. This could be par- 467
468 ticularly true during interactions among males, and we would like 469
470 to point out that the leftward bias has been reported to be stronger 471
472 in males than in females (Bourne, 2008; see also Godard and Fiori, 473
474 2010). Moreover, in males the leftward bias reaches its highest 475
476 degree when they observe male faces expressing anger rather than 477
478 male faces expressing the other five basic emotions or female faces 479
480 expressing all basic emotions (Rahman and Anchassi, 2012). The 481
482 uniqueness of anger among emotions has already been proposed 483
484 by Indersmitten and Gur (2003; see Workman et al., 2000 for simi- 485
486 lar considerations), who stressed both its nature of evolutionarily 487
488 important sign for action (its purpose is to prepare the organ- 489
490 ism for conflict) and its increased likelihood to be appreciated by 491
492 the perceiver (its greater intensity on the right rather than the left 493
494 hemiface enhances its impact on the hemisphere more dominant 495
496 in emotion processing). In the same vein, it is not surprising that 497
498 more anxious individuals exhibit a greater leftward bias compared 499
500 to less anxious ones (Heller et al., 1995; Keller et al., 2000; Voelz 501
502 et al., 2001; Bourne and Vladeanu, 2011), and therefore an interest- 503
504 ing experimental question is whether the former also show greater 505
506 attention toward the right limbs of human bodies compared to the 507
508 latter. 509

510 We would like to remark that the advantages of lateralization 511
512 for emotion processing discussed in this section are in agreement 513

with previous suggestions (e.g., Vallortigara and Rogers, 2005) that (i) the lateralization of cerebral functions enhances cognitive capacity and efficiency (a positive correlation existing between the leftward bias for emotion perception and performance in emotion discrimination), and (ii) the alignment of the direction of behavioral asymmetries at the population level emerges, as an evolutionary stable strategy, under social pressures (the leftward bias for emotion processing being credited to the advantage of monitoring other's emotional states and their dominant hand within the same hemisphere).

COUPLING BETWEEN FACE AND BODY PROCESSING

Our proposal that the leftward bias for faces might be associated with a similar bias for bodies is supported by several analogies between face and body processing, including the importance of configural information, the inversion effect affecting both categories (e.g., Reed et al., 2003), and embodied experience, humans being able to move both faces and bodies (Slaughter et al., 2004). On the other hand, face, and body representations are likely to differ at least to some extent (e.g., Soria Bauser et al., 2011). Moreover, although both face and body processing develop early in infancy, there is some evidence that face expertise may precede body expertise (Heron-Delaney et al., 2011; Slaughter et al., 2002). A possible account for such a differential development is that the earliest social experiences between infants and caregivers involve a face to face interaction, so that infants are exposed more often to faces than to whole bodies. Surely, face and body representations interact reciprocally (van de Riet and de Gelder, 2008; Yovel et al., 2010; Aviezer et al., 2012) and also induce similar responses (Tamietto et al., 2009).

At the neural level, the same area, the right fusiform gyrus, contains representations for both faces (Kanwisher et al., 1997) and bodies (Peelen and Downing, 2005). Although largely overlapping (Peelen and Downing, 2005), the fusiform face and body areas (FFA, FBA) turned out not to be identical (Schwarzlose et al., 2005; Peelen et al., 2006). Given that the magnitude of the asymmetry of the FFA strongly correlates with leftward asymmetries in face perception (Yovel et al., 2008), the existence of a similar association between FBA and perceptual and attentional asymmetries toward the right side of human bodies deserves investigation. Moreover, whereas the size and selectivity of the rFFA increase with age (Aylward et al., 2005; Golarai et al., 2007; Scherf et al., 2007; Peelen et al., 2009), matching the developmental trend of face-related configural processing and leftward bias, those of the rFBA do not differ between children and adults, this region not showing any development beyond the age of 7 years (Peelen et al., 2009). Thus, given that the age-related increase of the leftward bias for faces can be explained also in terms of mere maturation of the biological substrate, it could be investigated whether an age-dependent increase in the attention allocated to the right side of human bodies exists and, if so, whether it pre-exists that observed for faces. According to Peelen et al. (2009), a possible account for the differential development of rFFA and rFBA is that young children, when not looking up, usually observe the bodies rather than the faces of older (and thus taller) individuals, whereas adults are more likely to observe the faces of other individuals. For the same reason, the dominant hand might be

associated earlier to the right side of bodies rather than of faces, which could contribute to explain why the rFBA reaches adult size before the rFFA. The FFA is also more right-lateralized in right-handers than in left-handers (Willems et al., 2010), in line with the weaker left face bias observed in left-handers. Although less consistent, similar effects of handedness have been reported for the FBA (Willems et al., 2010), which could be linked to the weaker bias toward the right side of bodies observed in left-handers (Gardner and Potts, 2010; Marzoli et al., 2011a,b, 2013).

CONCLUSION AND FUTURE DIRECTIONS

Although different adaptive reasons have been proposed for the evolution of human right-handedness (Cochet and Byrne, 2013), the adaptive functions of the left face bias, as well as, broadly speaking, perceptual, and attentional asymmetries, have not received the same consideration. The present article attempts to provide a contribution in this direction, suggesting several research questions. The first prediction derived from our hypothesis is that the intensities of the leftward bias for faces and for bodies should be correlated. The leftward bias for bodies could also be modulated by the same factors affecting the leftward bias for faces, such as maternal cradling preference, age, anxiety, emotional context (for example, the presentation of angry faces or voices should increase the bias), configural processing (the bias should be reduced by inversion), and so on.

Moreover, a major topic of investigation should be the effect of experience with right-handed individuals in inducing leftward biases (for both faces and bodies). For example, it could be expected that the bias would be stronger for faces and bodies of highly familiar right-handed individuals than for faces and bodies of unfamiliar individuals. In the same respect, the discovery that dogs show a selective left face bias for human faces (Guo et al., 2009) offers an interesting opportunity to investigate the role of experience also in a nonhuman species. Specifically, it could be tested whether the bias is weakened, or even reversed, in dogs that have interacted mainly with left-handed individuals (i.e., owners, breeders, trainers). Such a study would provide useful information on the contribution of sensory experience in the manifestation and perhaps even in the origin of a perceptual asymmetry whose existence is known since several decades in human beings, but that has recently been observed also in other species.

Finally, an important field of study could address the topic of leftward biases in individuals with autism, who exhibit deficits in social communication (Klin et al., 2003) and emotion recognition from both faces and bodies (Philip et al., 2010), as well as in inferring others' complex mental states from faces and particularly by eyes (Baron-Cohen et al., 1997). These individuals are known to show impaired configural processing (Behrmann et al., 2006) and an absent (Dundas et al., 2012) – or at least delayed (Taylor et al., 2012) – perceptual bias for the left side of faces. Given the link between face and body representations, it should be investigated whether in this population the reduced leftward bias for faces is coupled with a reduced leftward bias for bodies, just as a reduced face-inversion effect (Hobson et al., 1988; Tantam et al., 1989) is coupled with a reduced body inversion effect (Reed et al., 2007).

Moreover, it would be interesting to examine whether action imitation deficits of individual with autism are positively related to non-right-handedness and negatively related to leftward biases toward faces and bodies. If so, a reduced attention toward the right side of human bodies could be responsible for the abnormal pattern of behavioral asymmetries in the autistic disorder, endorsing once again the role of body representations in social cognition.

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