outcrossing, leading to the promotion of deceit pollination.

Final remarks

Pollinator-limitation and resource constraints results in only a small proportion of an orchid population giving rise to the subsequent generation. This is further limited, as most orchid populations, particularly in the tropics, are small, due to the fluid nature of the niches they occupy and the availability of mycorrhiza ‘islands’. This combined with low reproductive success results in a small effective population size (N_e), followed by genetic drift as the potential initial cause of evolution. Subsequent diversification and speciation occurs through Darwinian adaptation to the local pollinator population.

While much still remains to be learnt within orchid biology, there is now a mass of literature on their pollination biology and phylogenetic relationship. However, much of this has been the description of patterns; what is now needed are studies into the processes that drive diversification in this most remarkable of flowering plant families.

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Lateral asymmetry of bodily emotion expression

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Emotional behaviours in humans and animals, such as kissing or tail wagging, sometimes show characteristic lateral asymmetries [1,2]. Such asymmetries suggest differences in the involvement of the cerebral hemispheres in the expression of emotion. An established example is the expressiveness advantage of the left hemiface that has been demonstrated with *chimeric face stimuli*, static pictures of emotional expressions with one side of the face replaced by the mirror image of the other [3]. While this result has been interpreted as support for a right-hemisphere dominance in emotion expression [4], substantial ipsilateral innervation of the relevant facial musculature [5] and findings of reduced or reversed asymmetry for positive emotions [3,6] complicate the conclusion. It is therefore critical to investigate lateral asymmetries in emotion expression using effectors with clearly contralateral innervation. We report here a pronounced lateral asymmetry for emotional full-body movements [7], the left body side moving with higher amplitude and energy, and causing higher perceived emotional expressiveness of the left body side compared to the right. This finding provides strong support for a right-hemisphere dominance in the control of emotional expressions independent of the specific effector.

We investigated motor asymmetries in emotionally expressive walking and tested whether such asymmetries lead to differences in the perceived emotional expressiveness of the movements of the left and the right body side. Twelve right-handed lay actors were recorded, using a VICON motion capture system, during neutral walking and emotionally expressive walking (anger, happiness, sadness). Before the recording, the actors’ involvement in each effect was maximized by combining free facial and bodily expression of the emotion with a validated mood-induction paradigm based on imagining emotionally charged past life events (see Supplemental data available on-line). Gaits expressing different emotions differed along many postural and kinematic dimensions, and they were recognised with high accuracy (>88%) by 15 observers.

From the recorded trajectories the flexion angles of the shoulder, elbow, hip and knee joints were computed for the quantitative analysis of lateral asymmetries. The movements of the left and right joints were characterized by two measures: maximum joint-angle amplitudes (difference between maximum and minimum amplitude; see Supplemental data), and a measure for ‘movement energy’ defined as $E = \int x^2(t)\,dt$, where $x(t)$ denotes joint angle as a function of time. For all three emotions, both measures exhibited a pronounced lateral asymmetry (Figure 1A,B), the left body side moving with significantly higher amplitude ($F_{1,35} = 36.56$, $p < 0.001$) and energy ($F_{1,35} = 32.50$, $p < 0.001$) than the right. Emotional walking was also significantly more asymmetrical than neutral walking. For anger and happiness, both asymmetry measures were significantly higher than for neutral walking ($t_{143} > 2.69$, $p < 0.004$), and for sadness, the energy measure exceeded significantly the one for natural walking ($t_{143} = 3.01$, $p < 0.002$).

To rule out the possibility that the observed asymmetry is a consequence of handedness, we tested twelve left-handed subjects using exactly the same experimental procedure. We found comparable asymmetries across emotions, again the left side moving with higher amplitude ($F_{1,35} = 25.01$, $p < 0.001$) and energy ($F_{1,35} = 36.15$, $p < 0.001$) than the right (see Supplemental data).

Do these motor asymmetries also affect perceived emotional expressiveness? To answer this question, we tested how subjects perceive ‘chimeric

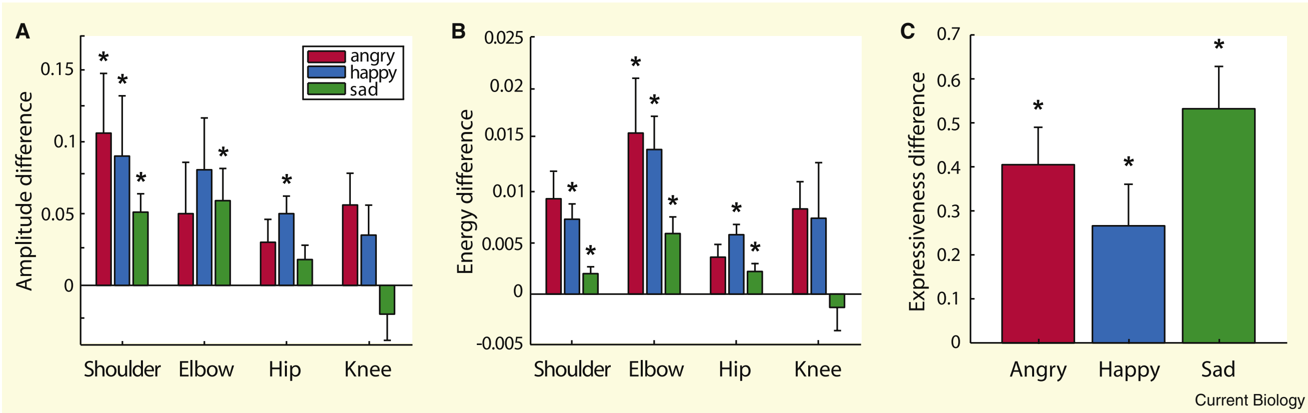

Figure 1. Motion asymmetry of bodily emotion expression (colors denote different emotions).

Analysis of motor patterns: (A) Mean amplitude difference (+/– s.e.m.) between corresponding joints on the left and right side of the body. (B) Left–right difference for the energy measure plotted in the same way. Perception: (C) Mean difference of expressiveness ratings between left–left and right–right chimeras. Stars indicate significant differences ($p < 0.05$).

walkers'. These stimuli were created by using the joint-angle trajectories of real human walkers to animate completely symmetric puppets, avoiding a possible confounding influence of anatomical asymmetries. The joint-angle trajectories of one body half were replaced by those of the other side, phase-shifted by half a gait cycle. The movements of the resulting right-right or left-left chimeric walkers were thus completely symmetric (for details see Supplemental data). These chimeric stimuli were not perceived as 'artificial', being rated as comparably natural to animations using the original trajectories (see Supplemental data).

The emotional expressiveness of the right–right and left–left chimeric walkers for each of the twelve actors was rated on a seven-point scale by 21 observers. Each walker was presented once facing 35° to the left and once 35° to the right of the view direction in order to control for view-dependence effects. The mean difference between the expressiveness ratings for left–left and right–right chimeras is shown in Figure 1C, separately for the different emotions and collapsed across view directions. Consistent with the asymmetries in the motor behaviour, the left–left chimeras were more emotionally expressive than the right–right chimeras for the three tested emotions (Wilcoxon $Z_{503} > -3.28$, one-tailed $p < 0.001$; for further statistical analysis see Supplemental data).

Our experiment provides the first demonstration of pronounced lateral asymmetries in human emotional full-body movement. These motor asymmetries influence the perceived expressiveness of emotional gait. Lateral asymmetry of emotional expression is thus not specific to the face, but extends to the movement of the human body, consistent with a general dominance of the right hemisphere in the control of emotional expression, independent of the effector. Such asymmetries in locomotion patterns seem surprising given the selection pressure towards symmetry in locomotion [8]. While clinical studies have indicated reduced expressiveness in the production of emotional face movements and speech prosody after right-hemispheric lesions [9], future imaging [10] and lesion studies will be required to isolate the cortical substrates that cause the observed asymmetry.

Supplemental data

Supplemental data including experimental procedures and supplemental video are available at http://www.current-biology.com/cgi/content/full/18/8/R329/DC1

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