Is the body in the eye of the beholder? Visual processing of bodies in individuals with anomalous anatomical sensory and motor features

Corrado Corradi-Dell’Acqua\textsuperscript{a,b,*}, Alessia Tessaric\textsuperscript{c}

\textsuperscript{a} Cognitive Neuroscience Sector, Scuola Internazionale Superiore di Studi Avanzati (SISSA), Trieste, Italy
\textsuperscript{b} Swiss Centre for Affective Sciences, University of Geneva, Geneva, Switzerland
\textsuperscript{c} Department of Psychology, University of Bologna, Bologna, Italy

\textbf{ABSTRACT}

Neuropsychological and neuroimaging studies suggest distinct body representations involved in coding one’s and others’ body. Other influential theories, however, instead posit a unique model behind coding multisensory information about one’s own body and visual information about others. An efficient way to further investigate this issue can be through testing individuals with anomalous anatomical and sensorimotor bodily features. In these people, the representation of their own body is held to be different with respect to the average population due to the peculiar properties of their body, and any experimental finding supposedly mediated by this representation should reflect such difference. We reviewed the most relevant studies reporting individuals with anomalous anatomical and sensorimotor bodily features engaged in (a) handedness task, (b) visual processing of biological motion and (c) visual processing of body shape. The performance in all three kinds of cognitive processes is affected by anomalous body features of the tested populations. However, the reviewed data are also in favor of a body model extrapolated by visual experience of others which mediates processing of biological stimuli and which operates in parallel, or as an alternative, to the representation of one’s own body. In light of these results, pure visual and pure embodied accounts behind visual processing of biological stimuli should be reconsidered.

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1. One’s own vs. others’ body representation

The human brain receives information about the human body through many sources. One is the body in which it is kept: indeed, the cerebral cortex integrates sensory input (e.g., visual, somatosensory, proprioceptive, vestibular), as well as information about the outgoing movements, which are revealing of the body’s states and of the changes thereof. A second source of information is the bodies of other human beings. Thus, the body is not only something that the brain owns and regulates, but it is as well a highly familiar visual stimulus as it is seen in everyday contact with other members of one’s family, friends, colleagues, etc.

The large heterogeneity of information about the concept of human body has frequently been associated with the presence of multiple body representations in the human brain. These vary according to the reference frame which body-related informa-
of how one’s own body is at each given moment, and a representation of how the body (either one’s own or others’) is usually like.

1.1. Evidence from brain damaged patients

Recently, Felician and colleagues (Felician, Cecchaldi, Didic, Thinus-Blanc, & Poncet, 2003; Felician & Romagüera, 2008) proposed the dichotomy between One’s Own vs. Others’ Body Representation, who distinguishes between a sensorimotor map coding the relative position of one’s body parts at each given time-point, and a map coding the position that body parts have with respect to a body model built on visual experience of others. The most convincing evidence in favor of such account is offered by the observation of those patients who, following brain damage to the posterior portion of the left inferior parietal cortex, exhibit heterotopagnosia (Auclair, Noulhiane, Raibaut, & Amarenco, 2009; Cleret de Langavant, Trinkler, Cesaro, & Bachoud-Lévi, 2009; Degos & Bachoud-Levi, 1998; Felician et al., 2003). These patients are unable to point to parts of the body of the examiner, or of another person. However, they are able to identify the body parts that they cannot locate, suggesting that their deficit lies neither at the level of visual processing of isolated body parts, nor at the level of the semantic knowledge of the body. Furthermore, they are able to locate parts of a non-human object (e.g., an animal or a bicycle), ruling out the account that the deficit reflects a general spatial impairment (Auclair et al., 2009; Felician et al., 2003). These patients are also able to point to small objects placed over the examiner’s body, being still unable to point to the parts underneath (Felician et al., 2003), thus suggesting that their pointing ability was flawless as long as the aimed target was not a body part. Crucially, they show flawless performance in locating parts of their own body (Auclair et al., 2009; Cleret de Langavant et al., 2009; Degos & Bachoud-Levi, 1998; Felician et al., 2003), thus confirming that the deficit is limited to bodies of others.

The behavioral pattern exhibited by patients affected by heterotopagnosia contrasts quite sharply with the one observable in patients affected by pure autotopagnosia, who are unable to point to parts of their own body despite being flawless at pointing parts to the body of the examiner¹ (Felician et al., 2003; Pick, 1922). In particular, Felician et al. (2003) reported a double dissociation between (a) a patient with damage at the level of the left angular gyrus exhibiting heterotopagnosia, thus able to locate parts of his own (but not the examiner’s) body, and (b) a patient with damage at the level of the left superior parietal cortex with a mild proprioceptive deficit (i.e., he was unable to describe the position of his body segments when slowly and passively moved by the examiner) and exhibiting pure autotopagnosia, thus mistakenly locating parts of his own (but not the examiner’s) body. The authors suggested the presence of two independent body models, one drawing most of its information from visual experience of others, and the other from one’s sensorimotor signals. Felician et al. (2003), accordingly, advocated the psychological reality of “one’s own” and “others’” body representation.

1.2. Evidence from healthy individuals

The data from brain damaged patients converge with the findings from recent neuroimaging experiments testing healthy participants. For instance, Corradi-Dell’Acqua, Hesse, Rumiati, and Fink (2008) found significant activation of the left posterior intraparietal sulcus when participants were asked to assess the distance between body parts visual stimuli, controlling for the identification thereof and for spatial competences per se. Most recently, Felician et al. (2009) asked participants to point to parts of body visual stimuli, being this a human or a dog: they found a significant activation of the left angular gyrus specifically when the parts of a human body were located. This region was inferior with respect to the superior parietal region Felician et al. (2004) found when asking participants to point to parts to their own body, rather than to parts of the external space. Although, Felician and colleagues did not compare pointing to one’s/others’ body directly in the same experimental paradigm, the results are compatible with the ones from brain damaged patients (Felician et al., 2003), according to which superior portions of the left parietal cortex code the position of one’s own body parts, whereas more inferior portions code the spatial location of the body of others. Recently, Corradi-Dell’Acqua, Tomasino, and Fink (2005) asked participants to compare a visual stimulus of a hand with either the hand of their own body, or the hand of a visual template of a body. Authors found differential neural networks associated with the two conditions: the left parietal operculum (previously implicated in high level tactile processing, multisensory integration and coding proprioceptive signals about one’s own body—e.g., Bremmer et al., 2001; Fitzgerald, Lane, Thakur, & Hsiao, 2004, 2006a, 2006b) was specifically active whilst comparing the body part to their own body, whereas the posterior portion of the left intraparietal sulcus (over and around the regions identified by Corradi-Dell’Acqua et al., 2008) was active whilst comparing the body part to the visual template.

1.3. Shared or dissociated neural substrates?

The account of two distinct representations, one involved specifically in coding information about one’s own body, and the other involved in coding visual information about the body of others, is in apparent contradiction with many influential theories positing a unique model behind processing of both one’s own and others’ body. For instance, the common-coding theory (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997) postulates that observing an action facilitates its execution because perception and action planning share a common representational code, and that, at a neural level, perception of an action activates motor-related regions directly. This account is supported by the existence of a bilateral fronto-parietal brain network known as the mirror neuron system, which has been proposed to be engaged during both the observation and execution of purposeful actions (see Cattaneo & Rizzolatti, 2009; Decety & Grèzes, 1999; Rizzolatti, Fogassi, & Gallese, 2001, as reviews). More recently, scholars suggested that a model of one’s own body (holding information about the spatial relation between one’s parts, biomechanical constraints, the orientation of body segments in the external space, and even its kinematics—Wilson & Knoblich, 2005) might be used by the visual system as model information for either one’s own body, that of a third person, or even as top-down information to help interpret incoming visual signals (Grush, 2004; Wilson & Knoblich, 2005). Thus, perception of biological stimuli, even if pertaining others’, might be then mediated by the activation of homologous body portions of a model of one’s own body.

Understanding to which extent visual processing of biological stimuli is mediated by a representation of one’s own body or a model of other bodies extrapolated from visual experience about others is far from being a trivial issue, as most of the times the putative properties of these models can hardly be distinguished one with respect to the other. This does not happen, however, when testing individuals whose body has physical, sensory and motoric features which diverge from the average population. This is the

¹ Pure autotopagnosia should not be confused with a much better known neuropsychological syndrome, called autotopagnosia or somatopagnosia, in which patients’ pointing inability pertains both one’s own and others’ body (see Corradi-Dell’Acqua & Rumiati, 2007, for a review).
case, for instance, of individuals born without one or more limbs, or individuals affected by growth/birth diseases which prevents them to develop a body with size, motricity and sensitivity compatible to those of healthy individuals. In these people, a representation of their own model is held to be different with respect to the average population due to the peculiar properties of their body, and any experimental finding supposedly mediated by this representation should reflect such difference. This is not the case, however, of a body representation derived by visual information about others which is not held to change in these people, as their visual experience should be, at least in principle, similar to that of the average population.

The following sections of this review will focus on the most relevant research testing visual processing of biological stimuli in individuals exhibiting body features divergent from the average population. We will first describe (a) studies employing the handedness task, a task in which participants, when asked to assess whether a hand visual stimulus is right/left, spontaneously compare the seen body part with the homologous portion of their own body (Parsons, 1987a, 1987b, 1994). We will then review (b) studies testing visual processing of body motion and (c) studies testing visual processing of body shape. Of particular interest are sections (b) and (c), which will describe aspects of visual processing of biological stimuli about which, as the following parts of the review will show, scholars still debate the true role of such a processing, whether it be a visual experience about others, a representation of one’s body and one’s motricity, or a combination of both features.

2. The handedness task

The handedness task is a widely used experimental paradigm, which is a variation of the mental rotation task introduced by Shepard (e.g., Cooper & Shepard, 1973; Shepard & Metzler, 1971). In a prototypical mental rotation task, subjects have to decide about the sameness of two objects presented at different orientations. The decision time increases linearly with the orientation-disparity. Shepard concluded that participants accomplished the task through the employment of visual imagery, imagining one of the objects rotating towards the orientation of the other, thus allowing the comparison to occur when the two stimuli are aligned in the mental space. In the handedness task, participants are asked to assess whether a hand stimulus (few studies used feet stimuli as well), displayed at different orientations, is right or left. Parsons (1987a, 1987b, 1994) documented the time necessary to make such assessment increasing with the orientation-discrepancy between the stimulus and participants' hand. This has been shown by manipulating either the orientation of the stimulus (Parsons, 1987a, 1987b, 1994) or subjects' own posture (e.g., Sirigu & Duhamel, 2001), thus confirming the presence of an imagery process, similar to the one described by Shepard, through which participants’ own hand and the hand stimulus become aligned in the mental space. Crucially, Parsons (1987a, 1987b) found that the time of response were affected as well by whether or not the movement necessary for one’s hand to reach the displayed orientation was anatomically possible, as it complied with natural joint constraints (awkwardness effect). Parsons concluded that participants accomplished the task through motor imagery, that is, by imagining the active movement of their own hand towards the orientation displayed by the stimulus. Furthermore, such imagined movement took into account one’s own posture (e.g., Sirigu & Duhamel, 2001), thus confirming that nociceptive feedback is a variation of the mental rotation task introduced by Shepard (e.g., Cooper & Shepard, 1973; Shepard & Metzler, 1971).

Although observed in most of the studies employing this paradigm, the strategy of covertly moving one’s own hand towards the position displayed by the hand stimulus is not the only one. Indeed, neuropsychological and imaging studies showed how, if adequately instructed, healthy participants could solve the task relying only on the visual shape properties of the stimulus, and not through the employment of motor imagery (Corradi-Dell'Acqua et al., 2009; Tomasino & Rumiati, 2004). Tomasino and colleagues instructed participants to refrain from imaging the movement their own hand but to imagine, instead, providing the response only through visual inspection of the stimulus (i.e., assessing the position of the thumb with respect to the other finger). Participants managed to perform the task, and found that the awkwardness effect was drastically reduced with respect to the condition in which motor imagery was allowed, thus documenting a reduced effect of one’s biomechanical constraints and, therefore, of one’s own covert motor production (Corradi-Dell’Acqua et al., 2009; Tomasino & Rumiati, 2004). Crucially, the employment of a visual strategy in the handedness task, for instance, of individuals born without one or more limbs, or individuals diagnosed with complex regional pain syndrome (CRPS), which is a chronic condition often resulting in burning or aching sensations prevalently (although not exclusively) on one’s limbs. Schwobel and colleagues (Schwoebel, Friedman, Duda, & Coslett, 2002, 2001; Schwobel, Friedman, Duda, & Coslett, 2001), for instance, tested patients with CRPS involving one arm and found decreased performance for stimuli corresponding to the painful arm, as opposed to the unaffected arm. Moreover, patients’ decreased performance correlated with the severity (Schwoebel et al., 2002) and the duration (Moseley, 2004) of the pain, whereas it improved following therapy, thus showing how assessing a hand stimulus laterality is affected by the state of nociceptive feedback on one’s homologous hand (Schwoebel et al., 2002). However, patients exhibited a significant awkwardness effect, thus confirming that nociceptive feedback delayed (but did not block) the mental simulation of one’s body movement (Schwoebel et al., 2002, 2001).

Similar results are provided by Nico, Dapprati, Rigal, Parsons, and Sirigu (2004) who tested two patients with injury to the brachial plexus (a network of nerves conducting signals from the spinal cord to the upper limbs) which lead to complete loss of one’s upper limb functionality. Whilst facing stimuli homologous to the affected hand, patients exhibited a decreased performance in the handedness task than when facing stimuli homologous to their unaffected hand. However, for both hand, participants exhibited an awkwardness effect similar to the one described by Parsons (1987a, 1987b). Likewise, Fiorio, Tinazzi, and Aglioti (2006) engaged 15 patients...
affected by writer’s cramp, one of the most common forms of focal hand dystonia (a neurological syndrome characterized by sustained muscular contractions that cause repetitive movements and abnormal postures—Bressman, 1998; Hallett, 1998), in a handedness task involving both arms and feet stimuli. Authors found a decreased performance in assessing the handedness of hands, but not feet stimuli, thus showing how assessing hand stimulus laterality is affected by the state of the muscular activity in one’s homologous hand. However, as for the case of CPRS, patients affected by dystonia exhibited a significant awkwardness effect, thus confirming a spared (although delayed) ability to employ motor imagery.

2.2. Handedness task in individuals missing a limb

Several studies have addressed the question of whether physical availability of the body part might have a crucial role in the employment of motor imagery in such task. For instance, scholars tested the handedness task in patients suffering from limb amelia, and, in particular, congenital absence of one or more arms (Brugger et al., 2000; Funk & Brugger, 2008; Nico et al., 2004). Similarly to the case of traumatic loss of one or more arms (e.g., following amputation—Flor et al., 1998; Karl, Birbaumer, Lutzenberger, Cohen, & Flor, 2001; Lotze, Flor, Grodd, Larbig, & Birbaumer, 2001; Montoya et al., 1998) or of congenital deformation thereof (e.g., cases of upper extremity dysmelia due to thalidomide embryopathy—Stoeckel, Jörgens, Witte, & Seitz, 2005), congenital absence of one or more arms is usually associated with a reorganization of the somatosensory and motor homunculi, with the representation of the tongue occupying part of what in individuals with all limbs would be the hand area (Funk et al., 2008).

Furthermore, and similarly to the case of patients who underwent amputation, patients exhibiting congenital absence of one or more limb may report vivid sensations pertaining the missing limbs generally known as phantom limb experiences (see, Price, 2006, as a review).

Brugger et al. (2000) employed the handedness task on a woman, AZ, affected by tetra-amelia (that is congenital absence of both arms and legs), who reported vivid phantom sensations of all missing limbs as far as she could remember. The authors found that AZ’s reaction times revealed an awkwardness effect similar to the one reported by Parsons (1987a, 1987b) on healthy subjects, thus suggesting a spared ability to plan and simulate movements with the limbs that never developed, including the information about one’s biomechanical constraints. Nico et al. (2004) instead tested 19 patients with one upper limb missing in handedness judgment: 16 of them were amputees and exhibited phantom sensation of the missing limb, whereas 3 of them were amelic and never exhibited phantom sensations of the missing limbs. Authors hypothesized that if the employment of motor imagery does not require the presence of a physical counterpart, patients should be able to mentally simulate the movement of the absent body part comparatively as they do with controlateral hand. The amputees patients were described slower and less accurate in assessing the handedness of stimuli corresponding to their missing (as opposed to the controlateral) arm. Furthermore, the performance decreased furtherer when using a prosthetic limb. However, patients exhibited a significant awkwardness effect with stimuli corresponding to either the missing or the present hand, thus confirming that the physical absence of the arm might be detrimental (although not crucial) for the employment of motor imagery. Different results arise from the analysis of the three amelic patients: although authors do not provide any statistical analysis on the data from these patients, the average reaction time from these patients is suggestive of an awkwardness effect only when facing stimuli which were homologous to their present, but not absent hand. The authors interpreted their results reflective of the congenital absence of the limb precluding the ability to produce joint-constrained mental simulations for the deleted hand like those available for the present hand.

Recently, Funk and Brugger (2008) employed the handedness task to a group of 14 patients with congenital absence of one hand and 2 patients with congenital absence of both hands (one was AZ, the same patient tested by Brugger et al., 2000). Unilaterally amelic patients never exhibited phantom sensations of their missing limb. One of the bilateral amelic patients, AZ, reported phantom sensations as far as she could remember, whereas the second patient, CL, never reported phantom sensations. Consistently with what shown by Nico et al. (2004), unilaterally amelic individuals exhibited a degraded performance in the handedness task which was specific for stimuli corresponding to their absent, rather than to their existing, hand. However, and inconsistently with the results from Nico et al. (2004), for both hands patients’ exhibited a significant awkwardness effect. Of key interest, however, is the analysis of bilateral amelic patients: indeed, only AZ exhibited a significant awkwardness effect (consistently with what the same patient shown in Brugger et al., 2000), whereas CL did not.

2.3. Conclusions

The results from the studies reviewed in this section are described in Table 1 and can be summarized as follows. First, impaired sensorimotor functionalities in one’s limb does not prevent the ability to judge handedness of an homologous limb stimulus through the employment of motor strategy, although the use of such strategy is significantly delayed (Fiorio et al., 2006; Nico et al., 2004; Schwoebel et al., 2002, 2001). Secondly, the loss of a limb does not prevent (although it significantly delays) the ability to judge handedness of an homologous limb stimulus through the employment of motor strategy (note that all amputees tested

Table 1

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<thead>
<tr>
<th>Quantitative impairment</th>
<th>Qualitative impairment (loss of the awkwardness effect)</th>
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<td>Sensorimotor impairments</td>
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<td>Cronic pain</td>
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<td>Brachial plexus lesion</td>
<td>×</td>
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<td>Hand dystonia</td>
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<td>Physical absence of one’s limb</td>
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<td>Amputation (phanton sensation)</td>
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<td>Bilateral Amelia (phantom sensation)</td>
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<td>Unilateral Amelia (no phantom sensation)</td>
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<tr>
<td>Bilateral Amelia (no phantom sensation)</td>
<td>“n.r.”</td>
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</table>

“√” refers to an impairment being documented by behind quoted references, whereas “×” refers to an impairment not being documented. “n.r.” refers to non revealed information.
in the reviewed studies exhibit phantom sensations of the missing limbs either prior or during the execution of the task); furthermore, everyday use of the prosthetic arm has detrimental effects in the limbs either prior or during the execution of the task); furthermore, everyday use of the prosthetic arm has detrimental effects in the reviewed studies exhibit phantom sensations of the missing limbs (Brugger et al., 2000; Funk & Brugger, 2008). Fourth, the analysis of patients with congenital absence of one limb and no phantom sensations lead to mixed results, as one study document them unable to employ motor imagery to assess the laterality of the stimulus corresponding to the missing (but not the present) hand (Nico et al., 2004), whereas another study documents them able to do so (Funk & Brugger, 2008).

The data from individuals suffering from sensorimotor disabilities, and from amputation of the missing limb, confirm that the handedness judgment task activates the motor system and that malfunction, or even absence, of one limb does not prevent the central nervous system from programming its movements. Seminal studies in the field of sensorimotor integration agree that motor preparation is achieved by activating a predictive model on the state of one's own body (or one's body part) at a final stage of a movement; this estimate is updated during the actual execution of the movement as further copies of one's outgoing motor signals (efference copy) and sensory input arrives (Desmurget & Grafton, 2000; Wolpert, 1997; Wolpert, Goodbody, & Husain, 1998). It is conceivable for a similar process to take place in the handedness task as well: indeed, although no overt movement is being made, the motor system might predict what one's hand state would be if moved towards the orientation of the displayed stimulus, thus allowing the assessment of whether this stimulus and one's hand are the same. Indeed, the reported re-activation of extinguished phantom limb sensations in some amputees during the execution of the task strongly support the claim that motor commands to the missing limb are elicited and still effective (Nico et al., 2004). Indeed, although no overt movement is being made, the motor system might predict what one's hand state would be if moved towards the orientation of the displayed stimulus, thus allowing the assessment of whether this stimulus and one's hand are the same. Indeed, the reported re-activation of extinguished phantom limb sensations in some amputees during the execution of the task strongly support the claim that motor commands to the missing limb are elicited and still effective (Nico et al., 2004).

Although still present, the ability of issuing motor commands of one's limb is delayed by peripheral troubles. Such delay may reflect degradation of the predictive model due to the affected limb delivering, since the day in which the trouble occurred, inaccurate (or absent) sensorimotor feedback. Such degradation might explain how the poorest performance was the one from those patients wearing an aesthetic prosthesis as opposed to the case of amputation, congenital absence of a limb might prevent individuals from employing a motor strategy in assessing the laterality of a stimulus compatible with the missing one. This is the case of patient CL, who resulted unable to simulate movements with arms he never owned (Funk & Brugger, 2008). One plausible interpretation for CL’s results states that congenital absence of a body part results in the misrepresentation of the same body part in one's body representation. The motor system of CL would, therefore, be unable to program movements of a body part of which it has no knowledge. Another plausible interpretation states that, although CL's body representation might be endowed with predetermined information about the missing body part, its motor system might be unable to access such information and to put it into practical use in the assessment of hand stimulus laterality. In both case, CL would be able to solve the task only through the employment of visual strategy (Corradi-Dell'Acqua et al., 2009; Tomasino & Rumiati, 2004), that is through visual inspection of the stimulus, and its comparison with its memory-related pictorial representation.

In contrast to CL, patient AZ resulted able to simulate movements with arms he never owned (Brugger et al., 2000; Funk & Brugger, 2008). The main difference between AZ and CL lays in the fact that AZ experienced since birth phantom sensations of her missing limbs. Patients such AZ have often been interpreted as due to a representation of one’s body which was hard-wired and genet-ically determined and which accounted also for the limb missing in the patients’ body (e.g., Melzack, Israel, Lacroix, & Schultz, 1997; Ramachandran & Hirstein, 1998 – please note that such interpretation cannot account patients with bilateral congenital amelia who exhibit phantom sensations of the missing limbs in late stages of life – Price, 2006). Phantom sensations in AZ (but not in CL) might reflect the ability of AZ’s motor system in using the predetermined information about the missing limb in order to simulate movements.

A final comment pertains the case of patients affected by unilateral amelia and no phantom limb who, in one study, do not show any awkwardness effect for the missing limb (although they show this effect for the present limb—Nico et al., 2004), whereas, in a second study, they exhibit such effect for both (missing and present) limbs (Funk & Brugger, 2008). Future studies testing larger amount of patients might shed light on this issue, although the results provided by Funk and Brugger (2008) seem the most reliable as they are based (1) on statistical analysis of their data and (2) on a larger sample of patients. Instead, the result from Nico et al. (2004) are the most consistent with the other data reviewed in this section, as they are reminiscent of the case of patient CL, and confirm that congenital absence of one limb (together with no experience of phantom sensation) result in the inability to simulate its movements. The results from Funk and Brugger (2008) are more troubling, as the patients described are able to simulate movement with the missing hands, consistently with the case of AZ. It should be mentioned, however, that patients affected by unilateral amelia might exhibit, in their adult life, phantom sensation of the missing limbs. Late emergence of phantom sensation in these cases have often been interpreted as mirror sensation arising from their non-missing body parts, with almost 65% of the cases described report their sensations being reminiscent of those of the contro-lateral limb (e.g., Burchard, 1965; Grouios, 1998; Price, 2006). We can, therefore, speculate that also the patients described by Funk and Brugger (2008) might have extrapolated information about the missing limb from the contralateral, non-missing arm (although, in their case, this did not lead to phantom sensations), thus providing them with spared motor imagery abilities.

3. Perception of biological motion

A wealth of studies testing visual perception of biological movement agrees that the visual system treats biological stimuli in motion differently from other displacing targets. For instance, displacing targets which exhibit kinematical properties similar to those recorded in human motion are perceived by observers as more uniform than targets who don’t exhibit such properties (Viviani & Stucchi, 1992). Likewise, it has been shown that the onset of a non-biological movement and a co-occurring color change are not detected by the visual system simultaneously but with a delay of ∼50 ms (Viviani & Aymoz, 2001). This is not the case of the onset of a biological movement and a co-occurring color change which are instead detected by the visual system as simultaneous (Aymoz & Viviani, 2004).

3.1. Apparent motion paradigm

One of the most popular examples on how biological and non-biological motions are differently processed by the visual system is provided by apparent motion paradigm (Shiffrar & Freyd, 1990). In
the original implementation of this task, observers watch pairs of photographs differing only in the position of one object. As long as the two photographs are flashed in succession at a rate proportional with their spatial separation, normal observers invariably perceive the displaced object traversing the shortest possible path of visual apparent motion (e.g., Korte, 1915; Wertheimer, 1912). In their modified version of the paradigm Shiffrar and Freyd (1990) used as photographs a human model performing simple hand actions and had their difference lying in the position of one hand segment relative to a Joint. Crucially, the experiment was built so that a putative perceived displacement through the shortest path would not be anatomically possible in a real body, as it would violate natural joint constraints. Authors found that, at a slow succession rate, observers increasingly perceive paths of apparent limb movement that violate the short-path rule but that follow natural human limb trajectories. According to the author’s interpretation of their results, knowledge about one’s own anatomical constraints binds the visual perception of human movement. Although this interpretation is strengthened by a neuroimaging study associating this effect with increased premotor and parietal activations (Stevens, Fonlupt, Shiffrar, & Decety, 2000), the knowledge about the human anatomical constraints which is behind the apparent motion might have been extrapolated by visual experience of others’ motion. In a recent study, Funk, Shiffrar, and Brugger (2005) employed the same task on two patients, AZ and CL, affected by congenital bilateral amelia (the same described in Brugger et al., 2000; Funk & Brugger, 2008). Authors found that, whereas patient AZ, who exhibited phantom sensation of the missing limbs, was susceptible to the illusion (as it was the case of controls volunteers with no amelia), the patient CL did not and always reported apparent motions following the shortest path.

3.2. Weight-assessment paradigm

Another example favoring how a representation of one’s own motricity might bind visual processing of biological motion is provided by the weight-assessment paradigm (e.g., Hamilton, Wolpert, & Frith, 2004; Runeson & Frykholm, 1981). In this task participants are required to judge the weight of a box while watching a video clip of an actor’s hand lifting it. Early implementations of this task confirmed that participants are able to infer the required information from kinematics of the actor who lifts the box (Runeson & Frykholm, 1981). Such information might be extrapolated by the observer’s motor system which simulates the other person’s behavior and, through this simulation, contributes to the observer’s understanding of the person’s movement, intentions, and goals. This hypothesis is favored by Hamilton et al. (2004), who engaged participants in the same task whilst they were either lifting a box themselves or when they were passively holding it. They found that actively lifting a box altered the perceptual judgment: whereas an observed box was judged to be heavier when subjects were lifting the light box, it was judged to be lighter when they were lifting the heavy box.

Few studies tested a variation of the weight assessment paradigm in which participants were showed video-clip of actors lifting the box. They were told that the actor could be correctly or incorrectly informed of how heavy the box was going to be, and they were instructed to assess, for each video-clip, which was the case. In order to assess whether the actor was deceived or not, participants need to assess putative mismatches between the predicted consequences of the actor preparing movements and the actual lifting gesture. In a neuroimaging study, Grèzes, Frith, and Passingham (2004) engaged participants in this task by showing video clips depicting either themselves or another person lifting the box. Although participants were equally accurate in the task irrespective of the identity of the actor, visual processing of one’s own movement (but not of others) was associated with an earlier activation of regions involved in the representation of one’s own body and one’s own motricity, such as the dorsal premotor cortex bilaterally, the left inferior parietal lobe, the left parietal operculum and the right cerebellum. The authors interpret their results in terms of a close match between one’s motor production and the perceptual input associated with one’s action. Instead, lesser match is present between one’s motor production and the input associated with others’ action. This yields to a quicker activation in the motor system when one assesses mismatches between one’s prepared and resulting action. Bosbach, Cole, Prinz, and Knoblich (2005) recently tested both healthy controls and two patients who suffered sensory neuropathy. These patients had a complete haptic deafferentation in which they lost cutaneous touch and proprioception from their body from below their head. The task had participants either lifting a box being previously informed (either correctly or incorrectly) of its weight or observing someone else who lifted a box and who was previously informed of its weight. The authors investigated the kinematic parameters of the performed movements finding that, in controls, the duration of the lifting phase was correlated with false weight expectations. It is on the basis of saying that the more the weight was unexpected, the longer the time necessary to lift it and, therefore, the greater the need to update one’s motor programs. Crucially, controls perceived movements with longer lifting phases as those in which the actors were mostly deceived. However, when the deafferented patients were engaged in the lifting task, the duration of the lifting phase was not a positive index of their false weight expectation. It is on the basis of saying that without the somatic feedback of one’s outgoing movements, unexpected events (such as weight changes in the object to be lifted) are not taken into consideration and, therefore, the motor system carries out the remaining part of the action as previously planned. Likewise, deafferented patients did not perceive movements with longer lifting phases as those in which the actors were deceived. Consequently, although patients were as good as controls in assessing the weight of the box when the actor was not deceived, they were less accurate than controls in assessing whether or not the actor was deceived, thus resulting in less sensitivity only to those on-line motor adjustments which are no longer in their motor repertoire.

3.3. Point-light display paradigm

One of the most popular experimental paradigms used to investigate visual processing of biological motion is the point-light display (PLD) task (Johansson, 1973). Participants are not faced with a full human body shape, but with a set of point lights attached to the main joints of a human body. If this body is still, observers are not usually able to identify it through the point-lights; however, if the body starts moving, observers immediately identify through the displacement of the point-lights a human motion. Early works showed that subjects can perceive a variety of information from point-light biological motion, including the gender and the identity of familiar individuals (Cutting, 1978; Cutting & Kozlowski, 1977; Cutting, Moore, & Morrison, 1988; Kozlowski & Cutting, 1977), whether the individuals are walking forward or backwards (Mather, Radford, & West, 1992; Perrett et al., 1985), the mode of ambulation (Bertenthal, Profit, Spetter, & Thomas, 1985; Fox & McDaniel, 1982; Jansson & Johansson, 1973) as well as other movements such as those used sign language (Poziner, Bellugi, & Lutes-Driscoll, 1981). As for the case of the apparent motion paradigm, participants’ sensitivity to PLD biological movements has been interpreted as reflective of the perception-action coupling, whereby the observers’ motor system binds the visual system contributing to understanding the seen displacements (e.g., Prasad & Shiffrar, 2009). This is, however, ad odds with other theories (including the one put forward by Johansson, 1973) which
identify participants’ sensitivity to these stimuli as reflective of visual experience of others’ movements.

PLD paradigms have been extensively employed in individuals born with periventricular leukomacia (PVL) (Pavlova et al., 2005; Pavlova et al., 2006; Pavlova, Lutztenberger, Sokolov, Birbaumer, & Krägeloh-Mann, 2007; Pavlova, Sokolov, Birbaumer, & Krägeloh-Mann, 2006; Pavlova, Staudt, Sokolov, Birbaumer, & Krägeloh-Mann, 2003). PVL is characterized by gliosis in the white matter and tissue loss with secondary ventricular dilatation, thereby impinging on the pathways interconnecting subcortical structures with cortical regions. Former preterms with periventricular lesions often exhibit signs of motor disorders in a form of leg-dominant bilateral spastic cerebral palsy (de Vries, 1996; Krägeloh-Mann et al., 1993). Pavlova et al. (2003) employed the PLD paradigm in adolescents who were born preterm and exhibited PVL, in order to assess whether early motor disorders relate to impairments in biological motion perception. They found that, although patients exhibit decreased sensitivities to PLD human motion, this was not correlated with the magnitude of the spastic motor disorder, but rather with the severity and topography of lesions. Thus, Pavlova et al. (2003) advocated the neurological, rather than the motor, origin of the decreased sensitivity to PLD.

The data reported by Pavlova et al. (2003) are at odds with the ones of Casile and Giese (2006) who taught blindfolded subjects to produce a new action and subsequently tested subjects’ visual sensitivity to PLD versions of that newly learned action and to similar, unlearned actions. Visual sensitivity to the motorically learned, but unseen, actions was higher than sensitivity to unlearned actions, suggesting a direct influence of acquired motor programs on action perception that is independent of visual learning.

A wealthy line or research involving individuals’ sensitivity to PLD motion patterns pertains whether observers are more sensitive to familiar (rather than strangers’) motion, which would reflect an effect of visual experience, or to one’s own (rather than familiar) motions, which would instead be suggestive of the presence of a perception-motor coupling behind visual processing of human motion. Data at hand speak in favor of both effects. Indeed, a large set of data document that visual experience and perceptual learning beneficially affect performance on a variety of biological motion tasks (e.g., Giese & Poggio, 2003; Grossman, Blake, & Kim, 2004), that children’s sensitivity to PLDs increase linearly with their age (Pavlova, Krägeloh-Mann, Sokolov, & Birbaumer, 2001), that visual sensitivity to gait speed is superior for frequently observed gaits than for rarely seen gaits (Jacobs & Shiffrar, 2005), or for friends’ than strangers’ PLD motions (Cutting & Kozlowski, 1977). Furthermore, the activity of the human superior temporal sulcus (a region in the human extrastriate system known to process specifically biological motion including PLDs—e.g., Beauchamp, Lee, Haxby, & Martin, 2003; Oram & Perrett, 1994) was reported to be modulated by visual experience (Grossman & Blake, 2001). On the other hand, a wealth of studies document as well that observers demonstrate greater visual sensitivity to their own actions than to the actions of other people. For example, Beardsworth and Buckner (1981) reported that participants more accurately identified PLD of their own gaits than the gaits of their friends. More recent research indicates that enhanced sensitivity to self-generated actions generalizes across a wide variety of actions and does not depend on static cues to body shape (Knoblich & Prinz, 2001). Furthermore, observers can predict the perceptual consequences of their own actions more accurately than the consequences of other people’s actions (Knoblich & Flach, 2001).

In a recent study, Loula, Prasad, Harber, and Shiffrar (2005) tested observers’ sensitivity to a PLD human motion which could be performed either by the observers themselves, a friend of theirs or a stranger. They found that: (1) visual sensitivity to one’s own point-light movement was higher than the visual sensitivity to either well known friends’ or strangers’ movement and that (2) sensitivity for well-known friends’ motion was still greater than those for strangers’. The familiarity effect (friends > strangers) suggests that PLD motion can be recognized by experiencing the movements of others. The one’s own movement effect (self > others) is instead more complicated to interpret as it might be revealing either of a motor-perception coupling process behind visual processing of human motion or of an effect of visual experience as people perceive in everyday life their own movement through an egocentric point of view (e.g., looking at one’s toes whilst walking). This hypothesis was tested by Prasad and Shiffrar (2009) who reproduced the paradigm of Loula et al. (2005) by showing PLD motion displays both from an egocentric or an allocentric viewpoint. The authors confirmed both the “self > others” and the “friends > strangers” effects reported by Loula et al. (2005). However, the “self > other” effect was seen only through an allocentric viewpoint and disappeared in the egocentric viewpoint which is the condition in which one experiences most frequently one’s own actions. Crucially, the “self > other” survived also when point-light shows one’s own movement from the back view, which is a condition even less frequently perceived than from the front view. Prasad and Shiffrar (2009) confirmed that the enhanced visual sensitivity to self-generated actions cannot be attributed to visual experience, and speak in favor of the alternative account according to which sensitivity to self-generated actions reflects also the contributions of motor processes to action perception.

3.4. Conclusion

The visual system treats biological stimuli in motion differently from other displacing targets. Evidence of this statement can be found in the data from three well known experimental paradigms: apparent motion task, weight assessment task and the PLD task. The results from the studies addressing these paradigms reviewed in this section are described in Table 2 and can be summarized as follows. First, visual processing of biological stimuli in motion is affected by sensorimotor information about one’s body: this has been shown both in the weight assessment paradigm (Bosbach et al., 2005; Hamilton et al., 2004) and in the PLD paradigm (Beardsworth & Buckner, 1981; Casile & Giese, 2006; Loula et al., 2005; Prasad & Shiffrar, 2009). Second, visual processing of biological stimuli in motion is affected by one’s body structure; this has been shown by the analysis of patient CL whilst engaged in the apparent motion paradigm: this patient had congenital absence of both upper limb (and no phantom limb sensation) and diverged from the control population in its apparent motion effect for stimuli depicting arms (Funk et al., 2005). Please note the case on another amelie patient AZ, who exhibited phantom sensations of the missing limbs and showed results comparable to the ones of the control population (Funk et al., 2005). Third, visual processing of biological stimuli in motion is affected by visual experience of others’ movements: this has been shown in the PLD paradigm (Cutting & Kozlowski, 1977; Giese & Poggio, 2003; Grossman et al., 2004; Loula et al., 2005; Pavlova et al., 2001; Prasad & Shiffrar, 2009).

Common-coding theory suggests that perceptual and motor systems share representations for the same actions (Hommel et al., 2001; Prinz, 1997). The core assumption is that actions are coded in terms of the perceivable effects they should generate. Moreover, the representations of the intended action effects it is held to determine both action production (by leading to a sequence of motor commands) and action perception (by allowing one to detect others’ actions goals). A wealth of studies in both experimental psychology and cognitive neuroscience revealed how such common coding might lead to a process of motor resonance, that is the process through which visual processing of action effects in others might activate the sequence of motor commands which lead to the
same effects (e.g., Wilson & Knoblich, 2005, as review). Motor resonance have been advocated frequently in everyday activities, such as imitation, understanding of what other people are doing, are about to do or even they plan to do (e.g., Iacoboni et al., 2005; Prinz, 2006; Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003). Recently, scholars argued that a resonance mechanism might not occur only in the mind of those who observe (and putatively imitate) a given action, but also in the mind of those who execute this action and expect to be imitated. Thus, common coding might lead as well to a process of perceptual resonance through which programming sequence of motor commands leading to given action effects might bias visual processing of the same effects in others (e.g., Schütz–Bosbach & Prinz, 2007, as review). We believe that large part of the data reviewed in this section can be interpreted as effects of perceptual resonance. It is indeed the case of the studies from the weight assessment paradigm which demonstrates how engaging a person in a given action biases visual processing of perceivable effects of a similar action in others (Hamilton et al., 2004). Similar results arise from the PLD paradigm, which shows that participants are most sensitive at processing the effects which are part of one’s motor (but not perceptual) history. Crucially, effects of perceptual resonance could be degraded by impaired sensorimotor functionality of one’s body. As for the case of the patients with lesion to the brachial plexus described in the previous section (Nico et al., 2004), haptic deafferentation leads to an absent sensory feedback of one’s outgoing movements, presumably yielding to a degradation of the predictive model of the perceivable effects of one’s actions. This might explain deafferented patients’ inability to assess the compatibility between others’ preparatory movements and their outcomes (Bosbach et al., 2005). A similar hypothesis was tested on PVL patients, who show an impaired sensitivity at processing PLDs (Pavlova et al., 2003): However, in this case the impairment is to be attributed to the periventricular lesion per se, and not to its consequent sensorimotor disabilities.

Information about one’s body orientation and biomechanical constraints is crucial for the prediction of one’s movements effects in the same way in which the puppeteer cannot efficiently move a puppet without knowing how this is made. Putative misrepresentation of one’s body part should prevent the motor system from programming motor commands and from predicting sensory consequences of movements pertaining this part. Therefore, no perceptual resonance effects should be documented on stimuli depicting displacements of the misrepresented part. Funk et al. (2005) engaged two bilateral amelic patients, CL and AZ (already described in the previous section), in the apparent motion task. Patient AZ (who experienced phantom sensation of the missing limbs) was able to simulate movements of the body parts he never owned, thus suggesting (1) a predetermined mental representation of the missing parts and (2) a spared ability to use the represented information for motor programming (Brugger et al., 2000; Funk & Brugger, 2008). AZ was shown as sensitive to the apparent motion paradigm as control participants with no amelia, thus suggesting spared perceptual resonance processes (Funk et al., 2005). By contrast, patient CL (who never experienced phantom sensation of the missing limbs) was unable to simulate movements with the parts he never owned, thus suggesting a misrepresentation of its limbs is one’s body representation (Funk & Brugger, 2008). CL’s results in the apparent motion task diverged significantly from the one exhibited by controls, thus suggesting an impaired perceptual resonance process. In particular, whereas AZ and control participants perceived apparent motions which followed the principle according to which the movement should be biomechanically plausible, CL perceived apparent motions which were biomechanically implausible but followed the short-path rule (Funk et al., 2005). Funk and colleagues provided the first evidence of the role played by one’s body representation in processing others’ movements.

Finally, the only paradigm documenting effects of visual experience in visual processing on human displacement is the PLD paradigm in which friends’ movements are better recognized than strangers’ (Cutting & Kozlowski, 1977; Loula et al., 2005; Prasad & Shiffrar, 2009). Humans have a lifetime of experience watching other people move, and such extensive experience selectively enhances visual sensitivity to the human movement. The coexistence of self-related and visual-related sensitivity in the PLD task is consistent with the data from the handedness task positing two independent strategies (visual vs. motor) through which visual inspection of a hand stimulus could occur.

### 4. Perception of body shape

This final section discusses studies investigating visual processing of body shape and, in particular, configurational processing of the human shape. Configural processing is defined as perception based on relations among the constituent parts of a stimulus, rather than visual processing of the parts themselves. Whereas many stimuli classes (e.g., houses, cars) appear to be analyzed on the basis of single features, stimuli such as faces and bodies appear to be coded through whether these features are correctly arranged one with respect to the other (Collishaw & Hole, 2000; Leder & Bruce, 2000; Reed, Stone, Bozova, & Tanaka, 2003; Tanaka & Farah, 1993). At variance with the previous two sections who describe well-known experimental paradigms tested through a many different groups, the paradigms described in the present section did not undergo a such extensive testing. Nevertheless, the data described, although arising from different domains and employing experimental conditions not always compatible one another, are suggestive of some
The issue of when children acquire knowledge about the canonical layout of the human body has been tested by means of a visual habituation: this paradigm demonstrates that neonates have expectations about the typical configuration of the human body, exhibited in their clear preferences for typical over scrambled body parts stimuli, from 18 months of life on (Slaughter & Heron, 2004; Slaughter, Heron, & Sim, 2002) thus confirming their sensitivity to configurational processing of bodies rather than to the mere perception of their constituent parts.

It has been questioned, however, which sensory input contributes most to the acquisition of the knowledge about the human body shape. This issue has been investigated by observing children with congenital sensory and motor deficits. Vision plays a large role in such acquisition as shown by drawings and models of human figures made by congenitally blind children (7 years and older) in which hands and arms are exaggerated in size (Critchley, 1953; Kinsbourne & Lempert, 1980), thus suggesting that, in absence of visual input, their mental representation of human form is largely biased by their somatosensory and motor experience. On the other hand, putative role of somatosensory and motor information in acquiring the knowledge about the human shape has been investigated by testing children (3 years old and older) affected by Spina Bifida. Spina Bifida is a birth defect which involves failure of the neural tube to close during the fourth week of embryogenesis. As it affects most of the time the lumbar region of the spinal cord, Spina Bifida is compatible with life, although in most of the times it results in motor and somatosensory handicap (Northrup & Volick, 2000). Several studies testing the ability of these kids in processing body parts and body shapes through length estimation tasks (Robinson, Lippold, & Land, 1986), in constructing models of human bodies (Weininger, Rotenberg, & Henry, 1972) and in spontaneous body shapes drawings (Evans, 1999) reported performances comparable to the ones of healthy age-matched children. Taken together these studies suggest a much larger contribution of visual information in the acquisition of the knowledge about the human shape in the early stages of life than of somatosensory and motor information.

4.2. Body-inversion effect

Many studies from experimental psychology revealed that visual processing of body shapes can be affected by inversion (Reed, Stone, Grubb, & McGoldrick, 2006; Reed et al., 2003; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007): in these studies, participants find it easier to assess whether two body postures are the same or different when shown upright rather than upside-down. As for the case of visual processing of face stimuli (Maurer, Grand, & Mondloch, 2002; Yin, 1969), the inversion effect has been interpreted as revealing of a configurational processing of body shapes, according to which bodies are recognized on the basis of the spatial relations among the constituent parts in the “upright-body space” and not on that of their presence/absence. Few studies tested whether the body-inversion effect could be affected by somatic information about one’s body. The original work of Reed et al. (2003), for instance, described the inversion effect diminishing when impossible rather than possible human postures were used, leaving open the debate whether configurational processing of bodies was sensitive to implicit knowledge about biomechanical limitations of one’s own body (impossible postures violate biomechanical limitations of the body) or visual experience (impossible postures are less frequently seen than possible postures). A subsequent study (Bosbach, Knoblich, Reed, Cole, & Prinz, 2006) tested the body inversion effect for both familiar and unfamiliar postures in both healthy volunteers and a patient with complete haptic deafferentation (the same described by Bosbach et al., 2005). The authors failed to demonstrate that the size of the body inversion changed accordingly to the familiarity with the observed posture, thus discouraging purely visual accounts. However, the deafferented patient showed the same magnitude of effect than controls did, thus suggesting the cognitive processes behind the execution of this paradigm were intact in the patient.

4.3. Construction tasks

Configural processing of body parts has been tested as well through the test of Daurat-Hmeljiaj, Stambak, and Berges (1978), initially developed for children but recently used as well for brain damaged patients (Guariglia & Antonucci, 1992; Guariglia, Piccarri, Puglisi Allegre, & Trabalesi, 2002). The test involves pictures of both a full body and a full face which are decomposed in many tiles depicting isolated face/body parts. The tested person is then engaged in a construction task in which all tiles need to be spatially disposed in order to reproduce a standard, well-configured, body/facial shape. Di Russo et al. (2006) engaged a patient affected by achondroplasia in this task. Achondroplasia is a growth disorder caused by mutation in the fibroblast growth factor receptor-3 gene and which yields to a short stature with disproportionately short limbs. Individuals affected by such disease might go through surgical limb elongation (Ilizarov & Deviatov, 1971) which, in the case here described, can lead to a high shift of about 15 cm (Di Russo et al., 2006). Such procedure has shown to affect the activity patterns of the somatosensory cortex (Di Russo et al., 2006), as well as one’s locomotion pattern and estimation of locomotion distance (Dominici et al., 2009). Di Russo et al. (2006) reported changes in the performance on the Daurat-Hmeljiaj et al. (1978) test as a result of legs elongation. In particular, whereas both the patient’s performance and patient’s height (~130 cm) were comparable to the one usually exhibited by 7–8 years old children (Daurat-Hmeljiaj et al., 1978; Di Russo et al., 2006; Ogden, Fryar, Carroll, & Flegal, 2004), six months after the treatment, and consequent height elongation, the patient’s performance become comparable to the one of adults (Di Russo et al., 2006). Of particular interest are the types of errors exhibited by the patient prior to the treatment: indeed visual inspection of the human shape built (see Fig. 5 from Di Russo et al., 2006) is suggestive of overestimated horizontal distances between the body parts; however no overestimation was associated with the vertical distance between the parts, consistently with a human shape fully grown in width but not in height.

4.4. Sidedness task

In a recent set of studies, Tessari, Ottoboni and colleagues (Ottoboni, Tessari, Cubelli, & Umlità, 2005; Tessari, Ottoboni, & Bazzarin, 2007; Tessari, Ottoboni, Symes, & Cubelli, 2009) engaged participants in a modified version of the Simon paradigm (Simon, 1969), called sidedness task. Right or left arms (i.e., a hand–forearm configuration) appeared in the center of the screen superimposed by a colored circle; participants were required to ignore the arm picture and to respond according to the different colors by pressing to a right/left key placed in front of them. When the visual stimuli were presented from the hand back view, a spatial compatibility effect arose between the side of the key and the handedness of the stimulus (i.e., whether the hand was right/left); when the visual stimuli were presented from the hand palm view, a reverse effect emerged. However, such (in)compatibility effect disappeared when a hand was presented without the forearm (Ottoboni et al., 2005), or when hand and forearm were linked so that the violated anatomical/biomechanical constraints (Tessari et al., 2009). Thus, as it was not the pictorial information about the hand per se...
driving the (in)compatibility effect, but the pictorial information about the hand together with its neighboring body parts, authors suggested that the effect was revealing of a structurally configured representation of the body holding the information about the standard position of the hand with respect to the other parts (and maybe about the body’s biomechanical constraints—Tessari et al., 2009). Crucially, in their preliminary work, Tessari and Sirigu (2008) employed the sidedness task on four patients affected by unilateral upper limb amelia who never experienced phantom sensations of the missing limbs. If the stimulus was the hand corresponding to their existing limb, patients exhibited a performance comparable to the one of healthy controls with no amelia. However, if the stimulus was a hand corresponding to their missing limb, no compatibility effect was shown.

4.5. Conclusion

The present section reviewed cases of individuals with anomalous anatomical, motoric and sensory body features engaged in task tapping configurual processing of the body shape. Although the reviewed data (described in Table 2) are far from giving an exhaustive picture, they can be summarized as follows. First, configurual processing of the body shape is affected by anomalous anatomical properties of one’s own body. This has been shown both by the case of individuals with achondroplasia through the test of Daurat-Hmeljiaj et al. (1978) and by the case of unilateral amelic patients engaged in the sidedness task (Di Russo et al., 2006; Tessari & Sirigu, 2008). Second, configurual processing of the body shape is not affected by anomalous sensorimotor properties of one’s own body. This can be inferred by the case of both patients affected by spina bifida (Evans, 1999; Robinson et al., 1986; Weininger et al., 1972) and deafferented patients (Bosbach et al., 2006) who exhibited a performance compatible with the one of healthy controls. Third, data are also suggestive of a role played by visual experience, as documented by performance of congenitally blind children (Critchley, 1953; Kinsbourne & Lempert, 1980), although it should be mentioned that attempts to test differences in the inversion effect for familiar (rather than unfamiliar) body configurations failed to yield significant results (Bosbach et al., 2006).

Literature from object recognition states that highly familiar objects might be represented not only in terms of mere presence/absence of their constituent parts, but also in terms of spatial relations between these parts. Notions such as structural description models, or configurual representations, revolving in stating that the overall representation of the item can be seen as an organized model which combines the spatial positions of parts into a whole (Biederman, 1987; Marr & Nishihara, 1978; see Peissig & Tarr, 2007, as a review). The body shape is indeed a visual stimulus of high familiarity and, therefore, it is conceivable to be represented in the human brain in a similar fashion. However, the evidence in favor of visual experience in configurual processing of the body is faint. The only exception arise from the case of congenitally blind children, which conclusively state that the mental representation of the body shape is distorted by absence of any visual input, as children draw their information about the body structure from available sensorimotor input (Critchley, 1953; Kinsbourne & Lempert, 1980). More troubling evidence arises from the analysis of the inversion effect. Indeed, whereas Reed et al. (2003) described the inversion effect diminishing whilst facing impossible (and, therefore, unfamiliar) configurations, Bosbach et al. (2006) fails to find a significant familiarity effect. One plausible interpretation sees the study from Bosbach et al. (2006) as less powerful than the one from Reed et al. (2003) in detecting a significant effect. Thus, denying a role of visual experience in the inversion effect based on Bosbach’s findings would lead to inflation of the Type II error. Consistently, a recent study tested the inversion effect in expert ballet dancers and non-expert controls (Calvo-Merino, Ehrenberg, Leung, & Haggard, 2009): a stronger inversion effect was found in dancers than non-experts, not only whilst seeing body configurations which were in the observer’s motor repertoire (which could be interpreted through a resonance mechanism), but also when facing body configurations which were exclusively in the repertoire of other dancers (e.g., a male observes a configuration typical of a female dancer). Unfortunately, although the effect described is indeed modulated by visual experience about the ballet environment, the authors did not use as stimuli static snapshots of one body posture (as previous studies did), but rather dynamic PLDs. Thus, we cannot disentangle whether the effect of visual experience described by Calvo-Merino et al. (2009) affects the configurational processing of a body shape, or the visual processing of biological motion.

It might also be that the diminished inversion effect described by Reed et al. (2003) for impossible configurations might not reflect visual experience, but rather a failed compliance with one’s body biomechanical constraints. In is unclear, however, why information about one’s body structure (including one’s biomechanical constraints) should bias visual processing of body shapes. Indeed, perceptual resonance effects, documented in the domain of processing biological motion (Schütz-Bosbach & Prinz, 2007), have been advocated to serve social purposes, as it might render individuals further sensitive to conspecific actions similar to one’s own, thus facilitating the detection of imitators and reciprocators in the community. It is plausible for a similar mechanism to operate as well in the domain of visual processing of the body shape: indeed, structural information about the body might not be exclusively a bottom-up process (as for the case of other objects) but might be mediated as well from predetermined information about one’s own body filtering out visual inputs which are inconsistent with one’s body conformation (e.g., they violate human biomechanical constraints). Data such the one from Reed et al. (2003) would fit nicely this account. So would data from Tessari & Sirigu (2008) who showed how implicit coding of a hand stimulus in terms of its spatial position in a standard full body occurs only if the observer owns a hand compatible to the one seen. This interpretation would be in line also with the study from Di Russo et al. (2006) in which a patient’s physical anomalies bias the construction of a standard, well-organized, body shape. However, the most conclusive result in favor of this account would see unilateral amelic patients exhibiting a smaller inversion effect for body configurations exhibiting changes in the arm corresponding to their missing (but not present) limb. Unfortunately, at least to our knowledge, no study has ever addressed this issue.

5. Concluding remarks

We reviewed the most relevant findings involving individuals with anomalous anatomic and sensorimotor bodily features, who were engaged in (a) a sidedness task, (b) visual processing of body motion and (c) visual processing of body shape. All three tasks were affected by anatomical and (in the case of biological movement processing) motor properties of one’s body, thus implicating the role of one’s body representation in the observation of others. However, this review documents as well a role played by visual experience. The effect of one’s body (in all three tasks) and of one’s motricity (in case of visual processing of biological motion) is consistent with theories positing shared mechanisms involved in processing oneself and others (e.g., Hommel et al., 2001; Prinz, 1997; Rizzolatti et al., 2001; Schütz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005). According to these theories, both one’s own or others’ actions share a unique representation in which biological displacements (either intended or perceived) are seen in terms of their perceptual effects.
This might explain why active movement and visual processing of biological motion are coupled so that the occurrence of one resonates in the other. This might well explain why, in the case of the handedness task, visual processing of a hand stimulus could easily be mediated by a representation of the perceptual effect that one’s hand would have if moved towards the stimulus’ position. Instead, shared action representations do not predict a similar coupling between the configurational properties of one’s own and others’ body. Such coupling would be reflective of shared representations between one’s own and others’ body configuration as the reviewed data suggest.

The effect of visual experience is consistent with theories positing independent mechanisms involved in processing oneself and others. Indeed, without positing the presence of a visual-based representation of a hand, one could not explain why the handedness task could be accomplished without the employment of motor imagery (Corradi-Dell’Acqua et al., 2009; Funk & Brugger, 2008; Tomasoni & Rumiati, 2004). Likewise, enhanced sensitivity for movements which are not within one’s own motor repertoire cannot be explained without positing the presence of visual-based representation of most frequently seen actions (Calvo-Merino et al., 2009; Cutting & Kozlowski, 1977; Loula et al., 2005; Prasad & Shiffrar, 2009). A similar argument could be raised for configural processing of body shape, although in this case evidence in favor of effects of visual experience are faint (please note, however, that spontaneous drawings from congenitally blind children speak in favor of a role of vision—Critchley, 1953; Kinsbourne & Lempert, 1980).

Shared mechanism theories are effective at explaining the associations between representations of one’s own body and one’s motricity and visual processing of others’ body and others’ movements. Dissociated mechanisms are instead effective at explaining the independence between these processes. Although no unitary theory has been yet provided in order to explain all results (see, Mahon, 2008; Rumiati, Papeo, & Corradi-Dell’Acqua, in press, for a similar argument), shared and dissociated mechanisms are not, at least in principle, mutually exclusive. The co-presence of both types of mechanisms would explain effects of perceptual resonance and visual experience, but at cost. It would assume that information about the body of others would be coded by the human brain at lease twice, once through mechanisms originally designed to process one’s own body and once through mechanisms designed to process complex visual stimuli. Thus, the human brain would code bodily stimuli in a way which is both redundant and flexible; flexibility would be indeed necessary for the brain to cross, when needed, traditional boundaries of cognition and, therefore, to acquire information in multiple (thus redundant) representations of the same feature.

Scholars have already identified redundancy and flexibility in the human motor system and in the human brain in general. For instance, Bernstein introduced the problem of motor redundancy by showing how simple reaching gestures could be achieved through many solutions of joint rotations. Despite this, the human motor is quite efficient at selecting one solution over the many available (see, Latash, 2002, for more details). Recently, notions of brain redundancy and flexibility have been advocated to explain the link between representations of actions in the motor and lexical system: although these representations seem independent (as they can be selectively impaired in brain damaged patients), information coded in each of these mechanisms might, if necessary, flow into the other, thus explaining why motor-related regions are found involved whilst processing action-related words (see, Rumiati et al., in press; Willems & Hagoort, 2007, for more details on this topic). A similar line of thought could be applied also to our case. Indeed, bodies and body movements are represented redundantly in the brain, that is in both the visual system and the motor system (together with those mechanisms holding predetermined information about one’s body structure and position); thus, the human brain might decide to process body and body movements visual stimuli through either representation, the selection of which might depend from factors such as task demands, attention, or perceived similarity between the seen stimulus and oneself. Redundancy and flexibility might well explain why the data reviewed in this paper are suggestive of both shared and independent mechanisms.

Neuropsychological and neuroimaging studies posit independent representations of one’s and others’ body (Corradi-Dell’Acqua et al., 2009; Felician et al., 2003; Felician & Ramaüguere, 2008). Other theories, suggest instead that a model of one’s own body is behind visual processing of others as well (e.g., Grush, 2004; Wilson & Knoblich, 2005). The data reviewed here speak in favor of both accounts. Indeed visual processing of biological stimuli is mediated by a representation of one’s body. However, data as well speak as well in favor of a body model extrapolated by visual experience about others which operates either in parallel (biological motion) or alternatively (the handedness task) a representation of one’s body. In light of these results, pure visual and pure embodied accounts behind visual processing of biological stimuli should be reconsidered.

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References


