

# Both right- and left-handers show a bias to attend others' right arm

Daniele Marzoli · Chiara Lucafò · Alessandra Pagliara · Romina Cappuccio · Alfredo Brancucci · Luca Tommasi

Received: 28 August 2013 / Accepted: 6 October 2014 / Published online: 16 October 2014  
© Springer-Verlag Berlin Heidelberg 2014

**Abstract** The common-coding hypothesis suggests that the more similar an observed action is to the way the observer would perform it, the stronger is the ensuing activation of motor representations. Therefore, producing actions could prime perception so that observers would be particularly responsive to (i.e. biased to perceive) actions that are related to, and share features with, their own actions. If this similarity principle also applies to handedness, right- and left-handers should be more likely to perceive actions as performed with their dominant rather than non-dominant hand. In two experiments, participants were required to indicate the perceived orientation (front or back view) of pictures of ambiguous human silhouettes performing one-handed manual actions. Experiment 1, in which 300 right-handers and 60 left-handers reported the orientation of a single silhouette seen for as much as they wished, showed that participants perceived the figures more frequently in an orientation congruent with a movement performed with the right rather than the left hand. Experiment 2, in which 12 right-handers and 12 left-handers reported the orientation of 52 silhouettes seen for 300 ms, showed similar results when multiple responses per participant were collected rather than only one. Contrary to our expectations, no difference was

observed between right- and left-handers, which might suggest an attentional bias towards the right arm of human bodies in both groups. Moreover, participants were more likely to perceive the figure as front-facing than as back-facing, possibly due to the greater adaptive relevance of approaching compared to receding individuals.

**Keywords** Common coding · Handedness · Human body · Ambiguous figures · Facing bias · Perceptual frequency effect

## Introduction

According to many studies, observing actions can directly activate the motor system, similar brain areas being recruited in action perception and execution (Buccino et al. 2001; Grèzes et al. 2003; Rizzolatti et al. 2001). The common-coding hypothesis (Hommel et al. 2001) proposes that perceiving and performing an action result in the activation of the same motor representations: this implies that, rather than understanding observed actions by mapping them onto abstract concepts, people relive those actions by mapping them onto their own action repertoire (Knoblich and Sebanz 2006). In line with the common-coding hypothesis (according to which the more similar an observed action is to the way the observer would perform it, the stronger is the ensuing activation of motor representations), Schütz-Bosbach and Prinz (2007) propose that producing actions primes perception so that observers would be particularly responsive to actions that are related to, and share features with, their own actions. A contribution of the motor system to action perception is also suggested by action simulation theories, which state that, while observing the actions of others, people simulate performing the same actions (Blakemore and Decety 2001; Jeannerod

**Electronic supplementary material** The online version of this article (doi:10.1007/s00221-014-4124-5) contains supplementary material, which is available to authorized users.

D. Marzoli (✉) · A. Pagliara · R. Cappuccio · A. Brancucci · L. Tommasi  
Department of Psychological Sciences, Humanities and Territory,  
University of Chieti, Via dei Vestini 29, 66013 Chieti, Italy  
e-mail: d.marzoli@unich.it

C. Lucafò  
Department of Neurosciences, Imaging and Clinical Sciences,  
University of Chieti, Via dei Vestini 29, 66013 Chieti, Italy

2001). The simulation hypothesis is supported by neuroimaging studies showing that similar brain areas are activated when individuals generate, imagine or observe movements (for a review, see Grèzes and Decety 2001).

The similarity of an observed action with the common codes would also affect the accuracy of action simulation, which should be the highest when one observes self-produced actions (Knoblich and Flach 2003). Thus, people might be able to identify their own past actions by relying on the differential activation of such codes, and many studies seem to support this proposal (Calvo-Merino et al. 2005; Casile and Giese 2006; Grèzes et al. 2004; Knoblich and Flach 2001). As stressed by Schütz-Bosbach and Prinz (2007), it is likely that, when individuals watch recordings of their own movements, there is a closer or almost perfect match between the observed movements and the motor representations of those same movements, which induces greater selective responsivity to (and predictive accuracy of) one's own movements. This could also explain why expert athletes are faster and more accurate than non-expert athletes when predicting the outcome of their own sport actions from body kinematics (Abernethy et al. 2000, 2008; Aglioti et al. 2008; Hohmann et al. 2011; Sebanz and Shiffrar 2009).

In our opinion, an interesting question is whether such a preferential access to action representations stored in one's own motor repertoire can also apply to handedness. Specifically, we wonder whether individuals who are differently lateralized relative to hand use are differently prone to perceive visually ambiguous human silhouettes as performing actions with their dominant rather than non-dominant hand. In this regard, recent neuroimaging research indicates that hand action representations are differently lateralized in right- and left-handed individuals not only for execution (e.g. Dassonville et al. 1997; Solodkin et al. 2001), but also for observation, imagination and verb reading (Willems and Hagoort 2009; Willems et al. 2009, 2010). In particular, Willems et al. (2009) found differential and opposite lateralization of neural activity in right- and left-handers required to imagine performing one-handed manual actions, showing that the hemisphere that primarily controls the dominant hand is also involved in mental imagery for actions that people usually perform with that hand. Also, Willems and Hagoort (2009) found an intricate neural coupling between action production and observation, showing that differences between right- and left-handers in motor production are reflected in differential neural activation during action observation, in line with studies about the effects of motor expertise on the neural correlates of action perception (Calvo-Merino et al. 2005; Cross et al. 2006; Reithler et al. 2007). Thus, neuroimaging studies investigating the neural correlates of handedness indicate that: (1) motor imagery involves generating action plans consistent with the kinematics of actions that people

would perform with their own bodies, supporting the idea that motor imagery is body-specific (that is, the way a person usually performs an action is reflected in neural activation during motor imagery) rather than merely abstract (Willems et al. 2009), and (2) observers implicitly simulate observed actions by mapping them onto their own motor system (Willems and Hagoort 2009).

Besides imaging evidence, some clues of lateralized motor representations come from behavioural research. For example, Gardner and Potts (2010) found that when required to make speeded left–right judgements about which hand of a schematic human figure was holding a ball, consistent left-handers showed faster response times to the figure's left hemibody, whereas right-handers showed faster response times to the figure's right hemibody. The authors suggested that, even in the absence of actual or implied actions, one's own motor competency (and thus motor simulation) may contribute to others' whole body perception, as previously shown for the perception of body parts (e.g. when deciding whether a hand is a left or right hand, observers seem to imagine their own hand moving from its actual orientation to the stimulus orientation, and right-handers show faster responses for right than for left stimuli; Ionta et al. 2007; Parsons 1994; Takeda et al. 2010). Consistent with Gardner and Pott's (2010) results, indicating that attention is biased towards the right and left side of observed bodies, respectively, in right- and left-handers, we found that during the imagination of others' actions, right-handed movements were visualized more often by right-handers than by left-handers, and vice versa for left-handed movements (Marzoli et al. 2011a, b, 2013). This suggests that body-specific representations (Willems et al. 2009, 2010) are involved not only for one's own movements but also for somebody else's movements.

On the basis of the reviewed research, we hypothesized that observing a human silhouette (whose front/back orientation is ambiguous) performing an action could trigger motor representations stored in the observer's motor repertoire that are differently lateralized according to the observer's handedness. Therefore, when required to judge the figure's orientation, observers might be particularly prone to perceptual interpretations congruent with their own motor habits. Specifically, we predicted that: (1) overall, both right- and left-handers should perceive the figure more frequently as oriented in agreement rather than in disagreement with their own handedness (that is, in an orientation congruent with an action performed with their dominant rather than non-dominant hand); (2) when the action is represented on the figure's right side (from the observer's perspective), right-handers should perceive a back-facing figure (congruent with a right-handed action) more frequently than left-handers, and when the action is represented on the figure's left side, right-handers should

perceive a front-facing figure (again congruent with a right-handed action) more frequently than left-handers; (3) right-handers should perceive a back-facing figure more frequently when the action is represented on the figure's right side (congruent with a right-handed action) than when it is represented on the figure's left side, whereas left-handers should perceive a back-facing figure more frequently when the action is represented on the figure's left side (congruent with a left-handed action) than when it is represented on the figure's right side.

In order to test our hypotheses, we devised two experiments in which right- and left-handed participants were required to indicate the perceived orientation (front or back view) of pictures of ambiguous human silhouettes performing one-handed manual actions. In Experiment 1, each participant reported the orientation of a single silhouette shown for as much as she/he wished. This allowed to test a large sample of participants under conditions of unconstrained viewing time. In Experiment 2, each participant reported the orientation of 52 silhouettes shown for 300 ms. This allowed to replicate, in a smaller sample of participants, the results of Experiment 1 by collecting multiple responses under conditions of controlled viewing time. Experiment 1 thus provided us with a more ecological measure, which should also be unaffected by biases such as anchoring effects, order effects and alike, whereas Experiment 2 would assess the robustness of the findings capitalizing on a within-subjects experimental design.

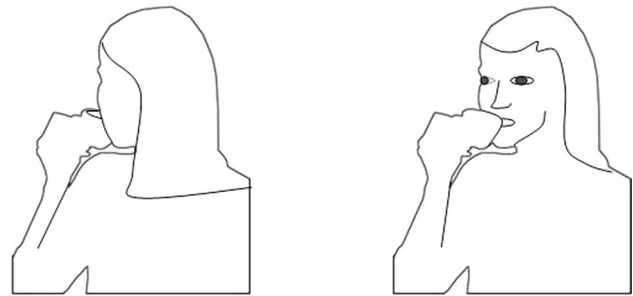
## Materials and methods

### Participants

Three hundred and sixty participants (180 females and 180 males; age 18–40 years) took part in Experiment 1. Twenty-four participants (14 females and 10 males; age 19–25 years) took part in Experiment 2 (all the participants had normal or corrected to normal vision).

### Stimuli

In Experiment 1, we employed 15 pairs of specular silhouettes of female and male persons performing one-handed manual actions (such as smoking, drinking from a glass/bottle, holding something, and waving a flag) printed in black against a white background on 21 × 15 cm white sheets (see Online Resource 1 for the complete set of stimuli). The original silhouettes (obtained by editing photographs and line drawings taken from the Web) were selected with the constraints that (1) the action was clearly represented on the figure's right or left side (from an observer's perspective) and (2) the figure's orientation



**Fig. 1** *Top* example of silhouette presented in Experiments 1 and 2. *Bottom left* left-handed interpretation (woman seen from the back). *Bottom right* right-handed interpretation (woman seen from the front)



**Fig. 2** Example of catch trial presented in Experiment 2

(front or back view) was ambiguous (see Fig. 1 for an example). Each original silhouette was mirrored horizontally in order to obtain a right-sided (from the observer's perspective) action (congruent with a right- or left-handed action if perceived as a back- or front-facing figure,

respectively) and a left-sided action (congruent with a left- or right-handed action if perceived as a back- or front-facing figure, respectively).

In Experiment 2, we employed 26 pairs of specular silhouettes of female and male persons performing one-handed manual actions depicted in black against a white background (other 11 pairs were added to the 15 pairs used in Experiment 1). The selection and editing of stimuli was the same as in Experiment 1. Moreover, 26 pairs of specular silhouettes of female and male persons who were not performing one-handed manual actions (e.g. holding objects with both hands or not performing actions; see Fig. 2 for an example) were used as catch trials. At a viewing distance of 57 cm, stimuli measured, on average, 6.8° horizontally and 10.7° vertically.

### Procedure

In Experiment 1, each participant was approached by a female or male experimenter in various locations on the University campus, malls and other places, and was required to take part in a brief experiment. If she/he agreed, the experimenter showed her/him one of the 30 silhouettes and asked her/him to indicate: (1) the action performed by the figure, (2) whether the figure was observed from a front or back view, and (3) the sex of the figure. Data collection was scheduled so that each of the 30 silhouettes was shown to 10 right-handers (5 females and 5 males) and 2 left-handers (1 female and 1 male). Only participants who were able to provide a plausible description of the action performed by the silhouette were included. We decided to collect a single response per participant because the collection of more than one trial might have suffered from at least two main shortcomings: (1) the trials following the first might be influenced by the first response given, which could induce anchoring effects (Gehlbach and Barge 2012; Tversky and Kahneman 1974), and (2) participants might have focused more overtly on the relevant aspect of the task (handedness).

Experiment 2 was run using SuperLab 4.0 on a Windows computer with an Intel processor and a 17-inch monitor. Participants were seated comfortably in a quiet room, with their eyes about 57 cm from the computer screen, and were required to place their hands palm-down on the table and not to cross their legs, arms or even fingers throughout the experiment. The experiment consisted of 104 trials (52 target trials and 52 catch trials) in which a black fixation cross presented for 500 ms in the centre of a white screen was followed by a black silhouette presented centrally for 300 ms and then by a completely white screen. Participants were instructed to indicate the perceived orientation of the stimuli as fast as possible by saying the words “FRONTE” (the Italian word for “FRONT”) and “SPALLE” (“BACK”).

The experimenter recorded the participant’s response by pressing the key “F” or “S” on a keyboard connected to the computer, and the following trial started after an inter-stimulus interval of 1,500 ms. The 104 trials were arranged in two separate blocks (A and B), so that the right- and left-sided versions of each silhouette were shown in different blocks, thus precluding them from being presented one after the other. This expedient, along with the inclusion of catch trials, was aimed to prevent participants from focusing overtly on the relevant aspect of the task (handedness). Stimuli were presented in a random sequence within each block, and the order of block presentation was counterbalanced across participants. After completing the first block, participants were allowed to rest as long as they needed before starting the second block.

Finally, participants of both experiments provided personal data such as sex and age and completed the Italian version of the Edinburgh Handedness Inventory (Salmaso and Longoni 1985). Since neither invasive nor risky procedures were involved and since the data were analysed anonymously, participants were required to give only oral consent. When explicitly required, the experimenter debriefed the participant about the purpose of the study. The study was carried out in accordance with the principles of the Declaration of Helsinki and following the approval of the local ethical committee (Comitato Etico d’Ateneo, Università “G. d’Annunzio”-Chieti).

### Data analysis

According to the laterality score obtained in the Italian version of the Edinburgh Handedness Inventory (Salmaso and Longoni 1985), the 360 participants of Experiment 1 were divided into four categories: consistent right-handers (222 subjects with a positive laterality score greater than 0.50 [range 0.51/1.00;  $M = 0.74 \pm 0.010$  SEM]), inconsistent right-handers (78 subjects with a positive laterality score lesser than or equal to 0.50 [range 0.10/0.50;  $M = 0.38 \pm 0.012$  SEM]), consistent left-handers (35 subjects with a negative laterality score lesser than  $-0.50$  [range  $-1.00/-0.52$ ;  $M = -0.68 \pm 0.022$  SEM]) or inconsistent left-handers (25 subjects with a negative laterality score greater than or equal to  $-0.50$  [range  $-0.50/-0.04$ ;  $M = -0.30 \pm 0.025$  SEM]). Similarly, the 24 participants of Experiment 2 were divided into four categories: consistent right-handers (8 subjects with a positive laterality score greater than 0.50 [range 0.52/0.81;  $M = 0.66 \pm 0.032$  SEM]), inconsistent right-handers (4 subjects with a positive laterality score lesser than or equal to 0.50 [range 0.12/0.43;  $M = 0.34 \pm 0.072$  SEM]), consistent left-handers (6 subjects with a negative laterality score lesser than  $-0.50$  [range  $-0.85/-0.52$ ;  $M = -0.72 \pm 0.052$  SEM]) or inconsistent left-handers (6 subjects with a

negative laterality score greater than or equal to  $-0.50$  [range  $-0.48/-0.11$ ;  $M = -0.38 \pm 0.055$  SEM]).

As regards Experiment 1, the proportion of figures perceived as front-facing versus back-facing—that is, our dependent variable of interest—did not differ according to the participant's sex (front-facing vs. back-facing figures:  $\chi^2 = 0.106$  [continuity correction applied, from now on: CCA],  $df = 1$ ,  $p = 0.745$ ) or the correspondence between the participant's sex and the figure's perceived sex (front-facing vs. back-facing figures:  $\chi^2 = 2.039$  [CCA],  $df = 1$ ,  $p = 0.153$ ). Therefore, we collapsed the data across the different levels of these variables, which allowed us to meet the criteria—above all, that of a satisfactory ratio between sample size and the number of variables—for performing log-linear analysis (e.g. see Stelzl 2000). We performed a log-linear analysis with participant's handedness (right or left), participant's handedness consistency (yes or no), the side (from the observer's perspective) in which the figure's action was represented (right or left), and the perceived orientation of the figure (front view or back view). We applied the backward hierarchical method, whereby a final model that retains all significant interactions between variables is selected by removing step by step each non-significant interaction from a first model containing all potential associations between variables (saturated model). Specifically, we aimed to test whether the perceived orientation of the figure was affected by the other variables included in the log-linear analysis and/or their interactions. For each significant effect found on the basis of the  $z$  values of parameter estimates, chi-square analyses were carried out in order to specify the direction of that effect.

As regards Experiment 2, we performed a repeated measures analysis of variance (ANOVA) using participant's sex (female or male), participant's handedness (right or left) and participant's handedness consistency (yes or no) as between-subjects factors, and the side (from the observer's perspective) in which the figure's action was represented (right or left) and the perceived orientation of the figure (front view or back view) as within-subjects factors. Specifically, we aimed to test whether the perceived orientation of the figure was affected by participants' sex, handedness and handedness consistency, the side in which the figure's action was represented, and/or their interactions. When needed, post hoc  $t$  tests were carried out in order to specify the significant differences.

## Results

### Experiment 1

The log-linear analysis showed that the model including the two-way interactions between participant's handedness and

participant's handedness consistency, and between the side of action and the perceived orientation of the figure gave the best fit to the data (likelihood ratio  $\chi^2 = 2.627$ ,  $df = 9$ ,  $p = 0.977$ ).

### *Participants' handedness consistency*

Participants were classified more often as consistent rather than inconsistent handers (257 vs. 103 [71.4 %];  $p < 0.001$ ; Table 1). Moreover, a larger proportion of right-handers were classified as consistent rather than inconsistent handers (222 vs. 78 [74 %]) compared to left-handers (35 vs. 25 [58.3 %];  $p < 0.05$ ; Table 1).

### *Perceived orientation/handedness of the figures*

Participants perceived the figures more often as front-rather than back-facing (222 vs. 138 [61.7 %];  $p < 0.001$ ; Table 1; Fig. 3, top left). Moreover, a larger proportion of figures were perceived as back-facing versus front-facing when the action was represented on the right side (82 vs. 98 [45.6 %]) than when the action was represented on the left side (56 vs. 124 [31.1 %];  $p < 0.01$ ; Table 1; Fig. 3, top left). Put in other words, this result indicates that, regardless of handedness, participants perceived a larger proportion of figures oriented in agreement with a right- rather than left-handed action when the action was represented on the figure's left side (124 vs. 56 [68.9 %];  $p < 0.001$ ), but not when the action was represented on the figure's right side (82 vs. 98 [45.6 %];  $ns$ ; Table 1; Fig. 3, top right). On the whole, figures were perceived more often as right-handed than as left-handed (206 vs. 154 [57.2 %];  $p < 0.01$ ; Table 1; Fig. 3, top right).

### Experiment 2

The ANOVA showed a main effect of the perceived orientation of the figure ( $p < 0.001$ ; Table 1) and a significant two-way interaction between the side of action and the perceived orientation of the figure ( $p < 0.01$ ; Table 1).

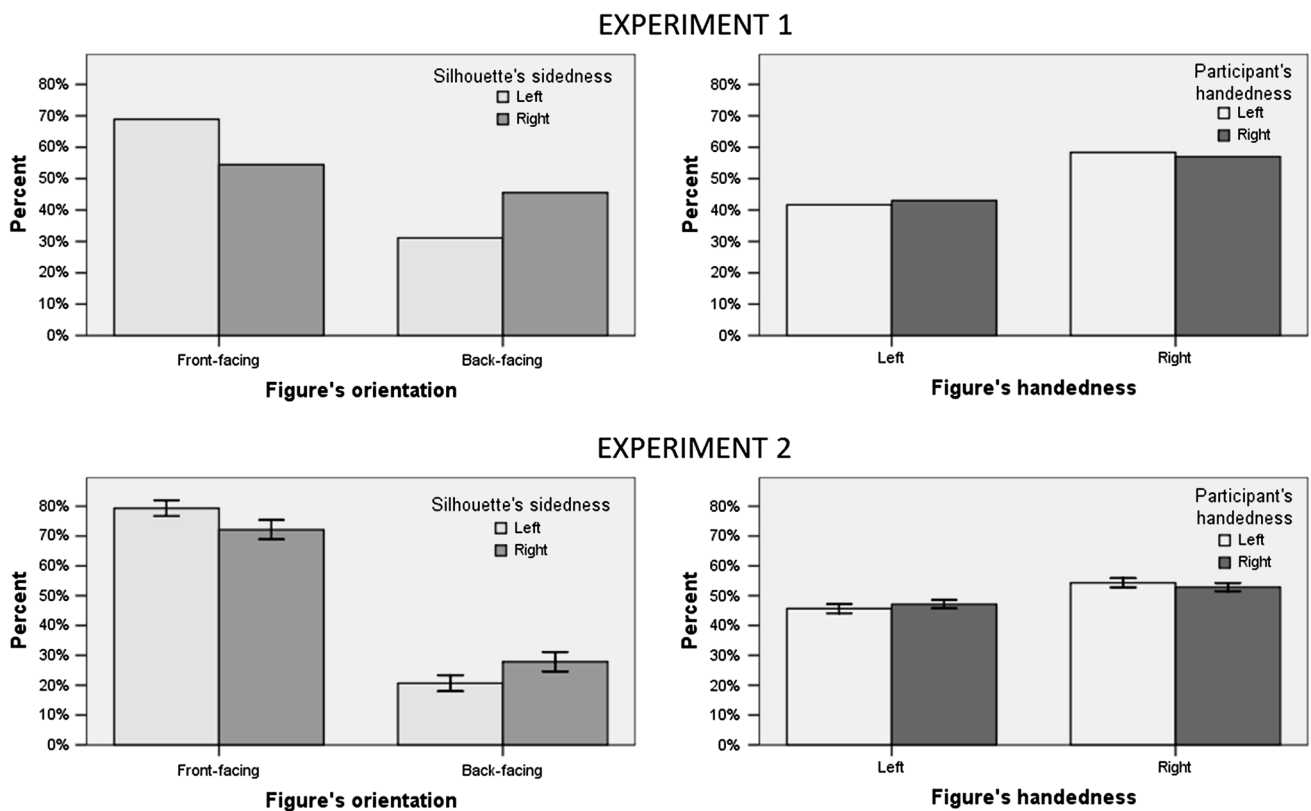
### *Perceived orientation/handedness of the figures*

Participants perceived a larger proportion of front-facing ( $M = 38.44$  [73.9 %]) rather than back-facing figures ( $M = 13.56$  [26.1 %]), and this difference held true both when the action was represented on the figure's left side (front-facing:  $M = 20.63$  [79.3 %]; back-facing:  $M = 5.38$  [20.7 %];  $p < 0.001$ ) and when the action was represented on the figure's right side (front-facing:  $M = 18.75$  [72.1 %]; back-facing:  $M = 7.25$  [27.9 %];  $p < 0.001$ ; Table 1; Fig. 3, bottom left). However, a larger proportion of figures were perceived as back-facing when the action

**Table 1** Summary of statistical tests in Experiment 1 (*top*) and Experiment 2 (*bottom*)

<i>Experiment 1</i>			
Effect	$\chi^2$	<i>df</i>	<i>p</i>
Handedness consistency	65.878	1	<0.001
Handedness $\times$ handedness consistency	5.266 [CCA]	1	0.022
Figure's orientation	19.600	1	<0.001
Figure's sidedness $\times$ figure's orientation	7.344 [CCA]	1	0.007
Figure's handedness (all silhouettes)	7.511	1	0.006
Figure's handedness (left-sided silhouettes)	25.689	1	<0.001
Figure's handedness (right-sided silhouettes)	1.422	1	0.233
<i>Experiment 2</i>			
Effect	<i>F</i>	<i>df</i>	<i>p</i>
Figure's orientation	60.434	1, 16	<0.001
Figure's sidedness $\times$ figure's orientation	10.318	1, 16	0.005
Effect	<i>t</i>	<i>df</i>	<i>p</i>
Figure's orientation (left-sided silhouettes)	10.910	23	<0.001
Figure's orientation (right-sided silhouettes)	6.819	23	<0.001
Figure's orientation (back-facing figures in right- vs. left-sided silhouettes)	3.543	23	0.002
Figure's handedness	3.543	23	0.002

CCA continuity correction applied



**Fig. 3** *Top left* proportion of figures perceived as front-facing and back-facing for right-sided and left-sided silhouettes in Experiment 1. *Top right* proportion of figures perceived as right-handed and left-handed by right-handed and left-handed participants in Experiment

1. *Bottom left* proportion ( $\pm SE$ ) of right-sided and left-sided figures perceived as front-facing and back-facing in Experiment 2. *Bottom right* proportion ( $\pm SE$ ) of figures perceived as right-handed and left-handed by right-handed and left-handed participants in Experiment 2



was represented on the right side ( $M = 7.25$  [27.9 %]) than when the action was represented on the left side ( $M = 5.38$  [20.7 %];  $p < 0.005$ ; Table 1; Fig. 3, bottom left). Put in other words, this result indicates that, regardless of handedness, participants perceived a larger proportion of figures oriented in agreement with a right-handed action ( $M = 27.88$  [53.6 %]) than with a left-handed action ( $M = 24.13$  [46.4 %];  $p < 0.005$ ; Table 1; Fig. 3, bottom right).

## Discussion

### Biases for front-facing and right-handed figures

The present data are not consistent with our prediction that body-specific representations (Willems et al. 2009, 2010) might influence the perception, and thus the interpretation, of ambiguous stimuli consisting of human silhouettes performing one-handed manual actions. Indeed, we found that, regardless of their own motor habits, our participants were more likely to perceive the silhouette as oriented consistently with an action performed with the right rather than the left hand. Moreover, participants were also more likely to perceive front- rather than back-facing figures. These effects were not affected by participants' handedness and handedness consistency. In Experiment 1, both effects were observed only when the action was represented on the figure's left side, possibly due to the fact that the bias to perceive right-handed actions and the one to perceive front-facing figures are congruent with one another when the action is represented on the left side of the figure, whereas they are incongruent when the action is represented on the right side of the figure. In Experiment 2, the bias to perceive front-facing figures was present both when the action was represented on the figure's left side and when the action was represented on the figure's right side, and it overcame the bias to perceive right-handed actions in both conditions. A possible account is that the bias to attribute right-handedness could require more time and/or more elaborate processing to emerge compared to the bias to perceive front-facing individuals.

A possible criticism of Experiment 1 might concern the limited sample size of the left-handed group, and indeed a more balanced sampling would have been desirable because more reliable conclusions could have been drawn. On the other hand, we made our best to achieve an adequate size of the left-handed sample while at the same time looking for left-handers in an unobtrusive way, given that a manifest search of left-handed subjects could have induced participants to focus on the relevant research question. Another criticism of Experiment 1 might regard the fact that the time of inspection of the silhouettes was not

controlled. However, both issues appeared to be not so crucial, given that Experiment 2, in which a controlled inspection time was employed in two identical samples of right- and left-handers, provided similar results.

Overall, the present results are not in line with the finding by Gardner and Potts (2010) that attention is biased towards the right and left side of observed bodies, respectively, in right- and left-handers, as well as with our previous studies indicating that, during the imagination of others' actions, right-handed movements are visualized more often by right-handers than by left-handers, and vice versa for left-handed movements (Marzoli et al. 2011a, b, 2013). On the other hand, the fact that right-handers and left-handers showed the same pattern of responses rather than the opposite pattern should not appear too surprising, given that, compared to the former, the latter usually exhibit a weaker bias (e.g. during others' action imagination; Marzoli et al. 2011a, b, 2013) or even no bias (e.g. during hand laterality judgments; Conson et al. 2011; Gentilucci et al. 1998; Ni Choisdealbha et al. 2011; Takeda et al. 2010) in favour of the dominant hand. These asymmetrical findings could be due to the fact that right-handers rely on sensorimotor processes more than left-handers, whereas left-handers rely on visual processes more than right-handers (Conson et al. 2011; Gentilucci et al. 1998; Ionta and Blanke 2009; Ni Choisdealbha et al. 2011).

The absence of significant differences between right- and left-handers' responses in the present study, at odds with our previous work on others' action imagination (Marzoli et al. 2011a, b, 2013), might also be attributed to the different nature of the tasks involved. In this regard, we would like to point out that perception and imagery rely primarily on brain areas involved in bottom-up and top-down processes, respectively (e.g. see Mechelli et al. 2004), although they activate similar category-specific representations (Stokes et al. 2009). On the other hand, top-down mechanisms involved in action perception could include proportionally more visual representations and less motor representations compared to top-down mechanisms involved in motor imagery (for similar considerations, see Gallese 2003; Munzert et al. 2008), which might be in line with neuroimaging studies showing that, compared to action observation, action imagination induces a greater activation in motor-related areas (Berends et al. 2013; Munzert et al. 2008), and particularly in the supplementary motor area (Grafton et al. 1996; Macuga and Frey 2012; Szameitat et al. 2012). Moreover, on the basis of a meta-analysis of previous research, Grèzes and Decety (2001) suggest a gradient of activation, at least in the precentral cortex, from observation, to simulation, to execution. Similarly, a review of previous findings by Gallese (2003) indicates that the patterns of brain activation are more similar between action execution and imagination than between

action execution and observation. In summary, if one agrees (1) that perception involves more bottom-up processes—by definition, unaffected by individual characteristics, including handedness—compared to imagery, whereas imagery involves more top-down processes compared to perception, (2) that top-down mechanisms involved in action perception include more visual representations and less motor representations compared to top-down mechanisms involved in motor imagery, and vice versa, 3) that visual representations of others' actions are biased towards right-handed movements, and 4) that motor representations are biased towards right- and left-handed movements, respectively, in right- and left-handers, then the identical pattern of responses in right- and left-handers observed in the present study, involving a perceptual judgment, does not appear in sharp contrast with the dissimilar patterns observed in our previous studies (Marzoli et al. 2011a, b, 2013), which involved motor imagery to a greater extent.

#### Consistent findings from sport studies

The fact that, according to our results, people show an attentional bias towards the right arm/hand of other individuals is in agreement with some studies dealing with the perception of sport actions, which indicate that the outcomes of movements performed by right-handed or right-footed individuals are anticipated better than those of movements performed by left-handed or left-footed individuals (Hagemann 2009; Loffing et al. 2012; McMorris and Colenso 1996; Schorer et al. 2012). Noteworthy, Hagemann (2009) showed that this difference was present in both right- and left-handed observers, which is at odds with studies indicating that the correspondence between stored representations and observed movements would foster action recognition (see Knoblich and Flach 2003 for a review). Hagemann (2009; see also Loffing et al. 2012; Schorer et al. 2012) suggested that the ability to discriminate left-handed movements is less developed than that to discriminate right-handed movements, and interpreted his findings as due to a perceptual frequency effect (see also Faurie and Raymond 2005): similarly to right-handers, left-handers more frequently play against right-handers than against left-handers, and this might facilitate the discrimination of right-handed movements by both groups in a variety of interactive sports, in line with theories emphasizing the importance of visual experience in action recognition (e.g. Jacobs et al. 2004). The crucial role of visual experience in determining the advantage in predicting the outcome of right- rather than left-handed actions is corroborated by the finding that such a difference can be attenuated or intensified by a specific perceptual training consisting in the presentation, respectively, of left- and right-handed actions (Schorer et al. 2012). It is plausible that the disadvantage

in the discrimination of left-handers' movements may give rise to their advantage in tennis (Holtzen 2000) as well as in other interactive sports (for a review, see Raymond et al. 1996).

#### Consistent findings from biological motion studies

Another branch of research that seems to provide findings consistent with ours is that employing biological motion conveyed by point-light displays (Johansson 1973). Indeed, a non-lateral view of a point-light walker without explicit depth cues, which constitutes a bistable and ambiguous stimulus in the same way as our silhouettes, is interpreted more frequently as facing towards the viewer than as facing away from the viewer (Schouten et al. 2010; Vanrie et al. 2004), in line with our results. Moreover, Thornton et al. (2003; see Williamson et al. 2008 for consistent findings) reported that a particular version of point-light walker containing equal motion cues to each side, and thus ambiguous with regard to its lateral direction, is perceived more often as right-facing than as left-facing. This finding could suggest once again an attentional bias towards the right side of others' body, given that the right limbs are in the foreground when one observes a right-facing individual.

#### Evolutionary considerations

At this point, we would like to attempt some evolutionary explanations of our results. As regards the facing bias, we agree with Schouten et al. (2010), who hypothesized that an individual facing the observer might be more socially relevant compared to an individual facing away. According to this proposal, the visual system would take into account the potential cost of misinterpreting the actions and intentions of others, and supposing that someone is approaching rather than retreating could be—obviously—more costly than supposing that someone is retreating rather than approaching (analogous processes might subtend the faster detection of point-light walkers with approaching rather than receding movement; Doi and Shinohara 2012). In particular, the facing bias has been credited to the greater level of threat potentially conveyed by approaching rather than receding human walkers, which led some authors to hypothesize a positive correlation between the facing bias and social anxiety (Heenan and Troje 2014; Van de Cruys et al. 2013). However, their results turned out to be inconsistent, and the role of the threat value of stimuli in fostering the facing bias should be considered with caution. On the other hand, the complexity of social interactions among humans prevents from drawing definite conclusions, and future studies should investigate whether and which other selective forces (e.g. sexual selection) contribute to the facing bias.



As regards the bias to perceive right-handed actions, we believe that it could indicate a tendency to attend the region most likely coincident with others' right hand, which might have a deeply rooted justification in the increased efficiency in monitoring both communicative and aggressive acts, the right limb being more used than the left in both types of behaviour (see Marzoli et al. 2014 for a more detailed discussion). The other side of the coin would be a reduced monitoring of the opposite side of the space (in which falls the dominant hand of left-handed individuals) as well as a reduced ability in discriminating left-handed movements compared to right-handed movements, which could perfectly explain the "surprise effect" at the basis of the hypothesized advantage of left-handers in fighting (Faurie and Raymond 2005). This proposal is in line with the left-handers' advantage observed in a variety of interactive sports (for a review, see Raymond et al. 1996), among which several combat sports such as boxe (Gursoy 2009), wrestling (Ziyagil et al. 2010) and fencing (Bisiacchi et al. 1985). Although the present data cannot demonstrate that directing attention towards the right hand of others increases humans' fitness, it is plausible that such a bias might be adaptive in everyday social life, entailing the biological and ecological advantage of paying more attention to the hand that usually conveys more information, most social interactions occurring with right-handed individuals.

Finally, we would like to stress how the bias to perceive front-facing figures was stronger than the bias to perceive right-handed figures, and even more so in Experiment 2. As already proposed, the bias to attribute right-handedness could require more time to emerge than the bias to perceive front-facing individuals, which might represent a default mode when judging the orientation of conspecifics in the human species, where social interactions play a key role in survival and fitness. On the other hand, such a default mode would be permeable to other socially relevant information (e.g. the likely handedness of others), above all when the stimulus is intact and available for deep processing (e.g. under unconstrained viewing time as in Experiment 1) rather than degraded (e.g. under restricted viewing time as in Experiment 2). On the basis of the present findings, future studies should address two main issues as regards the processing of others' bodies: (1) whether tasks mainly involving motor representations are affected by observer's own handedness more than those mainly involving visual representations, and (2) whether the social relevance of the task may influence the emergence of the bias to perceive right-handed figures, as well as its relative weight compared to other adaptive biases such as the one to perceive front-facing figures.

**Acknowledgments** We thank Matteo D'Orazio for his help in collecting data.

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Abernethy B, Gill DP, Parks SL, Packer ST (2000) Expertise and the perception of kinematic and situational probability information. *Perception* 30:233–252
- Abernethy B, Zawi K, Jackson RC (2008) Expertise and attunement to kinematic constraints. *Perception* 37:931–948
- Aglioti SM, Cesari P, Romani M, Urgesi C (2008) Action anticipation and motor resonance in elite basketball players. *Nat Neurosci* 11:1109–1116
- Berends HI, Wolkorte R, Ijzerman MJ, van Putten MJAM (2013) Differential cortical activation during observation and observation-and-imagination. *Exp Brain Res* 229:337–345
- Bisiacchi PS, Ripoll H, Stein J, Simonet P, Azemar G (1985) Left-handedness in fencers: an attentional advantage? *Percept Mot Skills* 61:507–513
- Blakemore S-J, Decety J (2001) From the perception of action to the understanding of intention. *Nat Rev Neurosci* 2:561–567
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci* 13:400–404
- Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P (2005) Action observation and acquired motor skills. *Cereb Cortex* 15:1243–1249
- Casile A, Giese MA (2006) Non-visual motor learning influences the recognition of biological motion. *Curr Biol* 16:69–74
- Conson M, Mazzarella E, Trojano L (2011) Self-touch affects motor imagery: a study on posture interference effect. *Exp Brain Res* 215:115–122
- Cross ES, Hamilton AF, Grafton ST (2006) Building a motor simulation de novo: observation of dance by dancers. *NeuroImage* 31:1257–1267
- Dassonville P, Zhu X-H, Ugurbil K, Kim S-G, Ashe J (1997) Functional activation in motor cortex reflects the direction and the degree of handedness. *Proc Natl Acad Sci USA* 94:14015–14018
- Doi H, Shinohara K (2012) Bodily movement of approach is detected faster than that of receding. *Psychon Bull Rev* 19:858–863
- Faurie C, Raymond M (2005) Handedness, homicide and negative frequency-dependent selection. *Proc Biol Sci* 272:25–28
- Gallese V (2003) The manifold nature of interpersonal relations: the quest for a common mechanism. *Philos Trans R Soc Lond B Biol Sci* 358:517–528
- Gardner M, Potts R (2010) Hand dominance influences the processing of observed bodies. *Brain Cogn* 73:35–40
- Gehlbach H, Barge S (2012) Anchoring and adjusting in questionnaire responses. *Basic Appl Soc Psychol* 34:417–433
- Gentilucci M, Daprati E, Gangitano M (1998) Right-handers and left-handers have different representations of their own hand. *Cogn Brain Res* 6:185–192
- Grafton ST, Arbib MA, Fadiga L, Rizzolatti G (1996) Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp Brain Res* 112:103–111
- Grèzes J, Decety J (2001) Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum Brain Mapp* 12:1–19
- Grèzes J, Armony JL, Rowe J, Passingham RE (2003) Activations related to "mirror" and "canonical" neurones in the human brain: an fMRI study. *NeuroImage* 18:928–937

- Grèzes J, Frith CD, Passingham RE (2004) Inferring false beliefs from the actions of oneself and others: an fMRI study. *NeuroImage* 21:744–750
- Gursoy R (2009) Effects of left- or right-hand preference on the success of boxers in Turkey. *Br J Sports Med* 43:142–144
- Hagemann N (2009) The advantage of being left-handed in interactive sports. *Atten Percept Psychophys* 71:1641–1648
- Heenan A, Troje NF (2014) Both physical exercise and progressive muscle relaxation reduce the facing-the-viewer bias in biological motion perception. *PLoS ONE* 9:e99902
- Hohmann T, Troje NF, Olmos A, Munzert J (2011) The influence of motor expertise and motor experience on action and actor recognition. *J Cogn Psychol* 23:403–415
- Holtzen DW (2000) Handedness and professional tennis. *Int J Neurosci* 105:101–119
- Hommel B, Müsseler J, Aschersleben G, Prinz W (2001) The theory of event coding (TEC): a framework for perception and action. *Behav Brain Sci* 24:849–937
- Ionta S, Blanke O (2009) Differential influence of hands posture on mental rotation of hands and feet in right and left handers. *Exp Brain Res* 195:207–217
- Ionta S, Fourkas A, Fiorio M, Aglioti SM (2007) The influence of hands posture on mental rotation of hands and feet. *Exp Brain Res* 183:1–7
- Jacobs A, Pinto J, Shiffrar M (2004) Experience, context, and the visual perception of human movement. *J Exp Psychol Hum Percept Perform* 30:822–835
- Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage* 14:S103–S109
- Johansson G (1973) Visual perception of biological motion and a model for its analysis. *Percept Psychophys* 14:201–211
- Knoblich G, Flach R (2001) Predicting the effects of actions: interactions of perception and action. *Psychol Sci* 12:467–472
- Knoblich G, Flach R (2003) Action identity: evidence from self-recognition, prediction, and coordination. *Conscious Cogn* 12:620–632
- Knoblich G, Sebanz N (2006) The social nature of perception and action. *Curr Dir Psychol Sci* 15:99–104
- Loffing F, Schorer J, Hagemann N, Baker J (2012) On the advantage of being left-handed in volleyball: further evidence of the specificity of skilled visual perception. *Atten Percept Psychophys* 74:446–453
- Macuga KL, Frey SH (2012) Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *NeuroImage* 59:2798–2807
- Marzoli D, Mitaritonna A, Moretto F, Carluccio P, Tommasi L (2011a) The handedness of imagined bodies in action and the role of perspective-taking. *Brain Cogn* 75:51–59
- Marzoli D, Palumbo R, Di Domenico A, Penolazzi B, Garganese P, Tommasi L (2011b) The relation between self-reported empathy and motor identification with imagined agents. *PLoS ONE* 6:e14595
- Marzoli D, Menditto S, Lucafò C, Tommasi L (2013) Imagining others' handedness: visual and motor processes in the attribution of the dominant hand to an imagined agent. *Exp Brain Res* 22:37–46
- Marzoli D, Prete G, Tommasi L (2014) Perceptual asymmetries and handedness: a neglected link? *Front Psychol* 5:163
- McMorris T, Colenso S (1996) Anticipation of professional soccer goalkeepers when facing right- and left-footed penalty kicks. *Percept Mot Skills* 82:931–934
- Mechelli A, Price CJ, Friston KJ, Ishai A (2004) Where bottom-up meets top-down: neuronal interactions during perception and imagery. *Cereb Cortex* 14:1256–1265
- Munzert J, Zentgraf K, Stark R, Vaitl D (2008) Neural activation in cognitive motor processes: comparing motor imagery and observation of gymnastic movements. *Exp Brain Res* 188:437–444
- Ni Choisdealbha Á, Brady N, Maguinness C (2011) Differing roles for the dominant and non-dominant hands in the hand laterality task. *Exp Brain Res* 211:73–85
- Parsons LM (1994) Temporal and kinematic properties of motor behaviour reflected in mentally simulated action. *J Exp Psychol Hum* 20:709–730
- Raymond M, Pontier D, Dufour AB, Moller AP (1996) Frequency-dependent maintenance of left handedness in humans. *Proc Biol Sci* 263:1627–1633
- Reithler J, van Mier HI, Peters JC, Goebel R (2007) Nonvisual motor learning influences abstract action observation. *Curr Biol* 17:1201–1207
- Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci* 2:661–670
- Salmaso D, Longoni AM (1985) Problems in the assessment of hand preference. *Cortex* 21:533–549
- Schorer J, Loffing F, Hagemann N, Baker J (2012) Human handedness in interactive situations: negative perceptual frequency effects can be reversed! *J Sports Sci* 30:507–513
- Schouten B, Troje NF, Brooks A, van der Zwan R, Verfaillie K (2010) The facing bias in biological motion perception: effects of stimulus gender and observer sex. *Atten Percept Psychophys* 72:1256–1260
- Schütz-Bosbach S, Prinz W (2007) Perceptual resonance: action-induced modulation of perception. *Trends Cogn Sci* 11:349–555
- Sebanz N, Shiffrar M (2009) Detecting deception in a bluffing body: the role of expertise. *Psychon B Rev* 16:170–175
- Solodkin A, Hlustik P, Noll DC, Small SL (2001) Lateralization of motor circuits and handedness during finger movements. *Eur J Neurol* 8:425–434
- Stelzl I (2000) What sample sizes are needed to get correct significance levels for log-linear models? A Monte Carlo study using the SPSS procedure “Hiloglinear”. *Methods Psychol Res Online* 5:95–116
- Stokes M, Thompson R, Cusack R, Duncan J (2009) Top-down activation of shape-specific population codes in visual cortex during mental imagery. *J Neurosci* 29:1565–1572
- Szameitat AJ, Shen S, Conforto A, Sterr A (2012) Cortical activation during executed, imagined, observed, and passive wrist movements in healthy volunteers and stroke patients. *NeuroImage* 62:266–280
- Takeda K, Shimoda N, Sato Y, Ogano M, Kato H (2010) Reaction time differences between left- and right-handers during mental rotation of hand pictures. *Laterality* 15:415–425
- Thornton IM, Vuong QC, Bühlhoff HH (2003) A chimeric point-light walker. *Perception* 32:377–383
- Tversky A, Kahneman D (1974) Judgment under uncertainty: heuristics and biases. *Science* 185:1124–1131
- Van de Cruys S, Schouten B, Wagemans J (2013) An anxiety-induced bias in the perception of a bistable point-light walker. *Acta Psychol* 144:548–553
- Vanrie J, Dekeyser M, Verfaillie K (2004) Bistability and biasing effects in the perception of an ambiguous point-light walker. *Perception* 33:547–560
- Willems RM, Hagoort P (2009) Hand preference influences neural correlates of action observation. *Brain Res* 1269:90–104
- Willems RM, Toni I, Hagoort P, Casasanto D (2009) Body-specific motor imagery of hand actions: neural evidence from right- and left-handers. *Front Hum Neurosci* 3:1–9
- Willems RM, Hagoort P, Casasanto D (2010) Body-specific representations of action verbs: neural evidence from right- and left-handers. *Psychol Sci* 21:67–74
- Williamson KE, Jakobson LS, Troje NF (2008) A right-facing bias in the processing of biological motion? *J Vis* 8:913
- Ziyagil MA, Gursoy R, Dane Ş, Yuksel R (2010) Left-handed wrestlers are more successful. *Percept Mot Skills* 111:65–70