Embodiment, spatial categorisation and action

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Abstract

Despite the subjective experience of a continuous and coherent external world, we will argue that the perception and categorisation of visual space is constrained by the spatial resolution of the sensory systems but also and above all, by the pre-reflective representations of the body in action. Recent empirical data in cognitive neurosciences will be presented that suggest that multidimensional categorisation of perceptual space depends on body representations at both an experiential and a functional level. Results will also be resumed that show that representations of the body in action are pre-reflective in nature as only some aspects of the pre-reflective states can be consciously experienced. Finally, a neuro-cognitive model based on the integration of afferent and efferent information will be described, which suggests that action simulation and associated predicted sensory consequences may represent the underlying principle that enables pre-reflective representations of the body for space categorisation and selection for action.

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1. Introduction

The conscious perception of a continuous external world contrasts to some extent with the conscious experience of a discontinuous action space: what we see is not what we can reach. More specifically, the world in which one moves and interacts is incredibly well organised, and is lived as homogenous and continuous both through time and space. However, it might be obvious even after only a brief second of thought that interactions with this world are constrained in some aspects by body properties. In agreement with Proffitt (2006) claim: “Perceptions are embodied; they relate body and goals to the opportunities and costs of acting in the environment”. A cup can be grasped only if our arm is long enough to reach it, and only if our fingers are strong enough to lift it. Hence, self-defined spatial boundaries must have been at some point defined, and this was very probably developed progressively through active behaviour, with the discovering of our own body
capabilities. Of course, specifying subjective spatial limits must be context dependent as the use of a tool might modify what is reachable and graspable (Berti & Frassinetti, 2000; Farne, Dematte, & Ladavas, 2005; Farne & Ladavas, 2000; Maravita, Husain, Clarke, & Driver, 2001). Under these circumstances, functional boundaries would serve as the basis for intentional selection and optimal control of motor actions. Consequently, perceptual experience and categorisation of the external world must be somehow constrained by what we know about our own motor system. In this manuscript, we will present empirical data that suggest that perceived external space depends on body representations at both an experiential and a functional level. A neuro-cognitive model based on the integration of afferent and efferent information will be proposed to describe how action simulation and associated predicted sensory consequences may represent the underlying mechanism that give rise to pre-reflective representations of the body in action. Finally, we will discuss the possibility that these representations of the body are pre-reflective in nature as only some aspects can be consciously experienced.

2. The notion of delimited action spaces

Motor acts can be performed only in a demarcated part of the surrounding space and thus, action capabilities must modulate the way we perceive and categorise the external world. This is particularly the case when considering reaching activities that are not uniform, as objects can be (1) grasped and manipulated in the near space, which is delimited by body anthropometric constraints, (2) thrown and reached in the distant space through locomotion but (3) only observed in far space. These subspaces have been investigated in terms of perceptual (Cutting & Vishton, 1995) and action potentialities (Previc, 1990; Rizzolatti, Gentilucci, & Pavesi, 1985), and have received various denominations such as personal, action and vista space (Cutting & Vishton, 1995), with action space being subdivided into peripersonal, focal-extrapersonal, action-extrapersonal and ambient-extrapersonal space (Previc, 1990; Previc, 1998).

According to Previc (1998), functional dissociations between different action spaces can be found in perceptive-motor behaviours and brain related activities. The peripersonal system (for reaching and manipulative behaviours) and the ambient-extrapersonal system (for postural control and locomotion) involve predominantly brain areas located in the dorsolateral and dorsomedial cortices. The focal-extrapersonal system (for visual scanning) and the action-extrapersonal system (for navigation and orientation control) involve brain areas predominantly located in the ventrolateral and ventromedial cortices. Furthermore, each brain hemisphere receives visual information from the contralateral visual space. Hence, the perceptual system is neurologically organised so as to differentiate near–far and right–left subspaces. As a consequence, localised brain lesions may affect an individual’s space awareness in a very specific matter. In the case of unilateral neglect syndrome for instance, brain lesion studies have revealed that patients show marked deficits in spatial tasks that are performed in near or far space but predominantly within the left egocentric hemi-field (Berti & Frassinetti, 2000; Halligan & Marshall, 1991; Heilman, Bowers, & Shelton, 1990; Weiss et al., 2000).

Though objectively evidenced, how the brain specifies these functional spaces and articulates the transition from one to the other remains an open issue. More specifically, the conditions required to dissociate those objects that are reachable from those that are not—thus, delimiting peripersonal from extrapersonal space—is an issue that needs to be properly addressed in relation to body capabilities. The line of thought that will be followed here is that the conscious (explicit) categorisation of external space relies to a great extent upon our capacity to simulate our body in action, both at an experiential and at a functional level. This goes in line with the phenomenological approach of consciousness (Legrand, 2006; Varela, Thompson, & Rosch, 1991), which argues for the existence of a pre-reflective state of consciousness. According to this perspective, perceptual experience of extrapersonal space would not be an abstract, disembodied phenomenon but would rather be shaped by pre-reflective representations of the body in action. The pre-reflective property of such representations suggests that they may influence conscious experience without the necessity to be per se the content of conscious experience. As stated so well by Gallagher (2005), “pre-reflective body-awareness is not an item of object-perception, but is an essential element of every such perception”. This necessity to link body capabilities to perceptual categorisation—and subsequently, to action intention, can be explicitly revealed through the natural case where people must make a decision that has a direct consequence on the organism’s safety. For a rock climber for instance, the selection of a reachable secure handhold must be
defined according to body capabilities, i.e., anthropometric and action characteristics. Indeed, in the eventu-
ality of a misperceived handhold in relation to these body capabilities, an inappropriate decision would be
fatal. Nevertheless, reorienting attention towards the body might provide the means to change the content
of conscious experience. Indeed, focused attention may help bring to the level of conscious awareness certain
properties of the pre-reflective representations of the body that are under most circumstances at a sub con-
scious level. This is however still a matter of debate and we will come back to this question a little later for
discussion.

The present paper aims at demonstrating that spatial categorisation of the external space and selection of
objects for action rests upon an up-stream (pre movement) interaction between sensory and motor compo-
nents of our body in action. The situation that will be considered in the two following sections is the partic-
ularity of the conscious and self-referenced subdivision of peripersonal space, in near–far and right–left
dimensions in relation to action. Then, those aspects of motor actions that can be consciously experienced will
be discussed so that to dissociate the characteristics of the pre-reflective experience (“what I can do”) from the
reflective experience (“what I actually did”) of the body in action. Finally, the distinction between pre-reflect-
ive and reflective experiences of the body in action will be discussed in reference to a neuro-cognitive model
based on functional integration of afferent and efferent information within the sensori-motor system. Through
this model, we will describe how predicted action consequences through the simulation of action and the emu-
lation of anticipatory sensori-motor states—thus, the pre-reflective experience of our body in action—may
represent the underlying principle that enables perceptual categorisation and selection of objects for action.

2.1. Body representations at an experiential level: Organising peripersonal space

Studies on spatial perception must consider spatial categorisation in a general sense through a multidimen-
sional approach. First, because body orientation continuously changes with respect to external space, the sepa-
ration in the left–right dimension must be evaluated at all times from an egocentric reference point. The idea
that an egocentric system of reference participates in spatial categorisation in specific contexts has been objec-
tively demonstrated by showing that the perceptual estimation of whether a visual stimulus is located to the
right or to the left according to the body mid-line is highly accurate in healthy controls (Galati et al., 2000;
Neggers, Schöllvinck, van der Lubbe, & Postma, 2005). For example, Neggers et al. (2005) reported that when
a vertical bar was presented at the centre of a horizontal bar but at different locations according to body
mid-line, the errors made when estimating the separation of right and left hemi-spaces in reference to the body
mid-line were smaller than half a degree. The estimation of the body mid-line dividing external space in two
parts has also been evaluated by simply asking blindfolded subjects to indicate with the arm the straight-ahead
direction. When required to do so, healthy subjects were accurate and errors made were very small (Jeannerod,
1988). In agreement with this, Richard, Rousseaux, Saj, and Honoré (2004) showed that when subjects were
instructed to imagine a line starting at the navel and extending away straight-ahead from the trunk, and then
adjust the position of a horizontal rod in such a way that the two extremities of the rod fall upon this virtual
line, errors in placing the centre of the rod aligned with the body mid-sagittal plane was 0.1 cm to the left, and
errors in orienting the rod was 1.2° to the left. Thus, when estimating the limits separating objects from the
right to those from the left, errors are generally small and similar whether subjects make a perceptual
discrimination task separating the right and left hemi-spaces, or whether they provide an estimation of the
straight-ahead direction.

Neuropsychological cases have suggested that such ability to organise external space along the right and left
dimensions is very dependent upon the integrity of brain areas involved in spatial coding, in particular the
parietal cortex. Indeed, patients with unilateral cerebral stroke in the right hemisphere including the posterior
parietal cortex can show signs of unilateral neglect syndrome. For these patients, case studies have reported a
lack of spontaneous response (Heilman, Watson, & Valenstein, 1985) and an abnormal reaction to stimuli that
are presented in the contra lateral position to those areas in the brain where the lesion occurred, in absence of
any particular sensory or motor deficits (Coulthard, Parton, & Husain, 2007; Shimodzono et al., 2006).
Interestingly, these patients also show a rightward deviation of the subjective straight-ahead (Heilman, Bow-
ers, & Watson, 1983; Jeannerod & Biguer, 1989; Karnath, 1994; Richard et al., 2004; Rossetti, 1998). As a
consequence, neglect patients favour the right space when exploring the environment (Karnath, Niemeier,
One interpretation for this deviation of exploratory activity was that the separation between right and left hemi-spaces is shifted to the right at a representational level (Jeannerod, 1988). According to this perspective, Richard et al. (2004) reported that when required to adjust a horizontal rod in such a way that its two extremities fall upon a virtual line starting at the navel and extending straight-ahead away from the trunk—just as described previously—neglect patients made significantly greater errors than controls in aligning the centre of the rod with the body’s mid-sagittal plane (4.8 cm to the right) whereas errors in orienting the rod remained quite small compared to healthy controls (0.6° to the left). Thus, the deviation of the straight-ahead could be related to a mis-representation of the body mid-line and more generally, a mis-representation of the whole body orientation. Following this assumption, the pre-reflective experience of the body would be biased in neglect patients and shifted in the direction of the lesion, which should influence general spatial processing. In agreement with this interpretation, we recently observed that when required to adjust a rod vertically and aligned with the body but at different heights in respect to the body, a lateral deviation of the straight-ahead (i.e., the centre of the rod) was found that depended on which body part was used as reference (Saj et al., 2006). Indeed, the lateral deviation was much greater when tested in front of the navel (5.91 cm to the right) than when tested in front of the head (2.32 cm). Thus, the body-site used as reference for determining the straight-ahead direction influenced the subjects’ estimations. Surprisingly, when computing the angle of the line joining the responses for these two body-sites according to the objective body vertical axis (5.1°), we found that it was very close to that corresponding to the vertical mis-orientation of the rod, which remained constant across the tested levels (−4.57° and −4.64° when aligned in front of the head and of the navel, respectively, see Fig. 1a). Interestingly, such mis-representation of the body was never perceived nor objectively reported by the patients. Overall, these data suggest the existence of a biased representation of body orientation in neglect patients, which can be experienced at a pre-reflective level and may influence the categorisation of the external space in the right–left dimension. In the next section, we will show that pre-reflective experience of the body can influence spatial categorisation not only at an experiential but also at a functional level.

2.2. Body representations at the functional level: Delimiting peripersonal space

Reaching for a visual object requires not only a perceptual determination of whether the object is to the right or to the left, but also a perceptual determination of whether or not the object is at a reachable distance. Thus, perceptual categorisation of external space requires the subdivision of external space following near and far dimensions, as a function of “what I can do”. In the literature, several studies have suggested that people are quite accurate in visually perceiving the limits of what is reachable. Classically, the critical test consists in placing individuals facing a horizontal surface and to present series of visual objects in increasingly near and far locations along the sagittal axis. Here, the participants’ task is simply to provide an overt verbal response about whether the visual object is thought to be reachable or not with the hand. In such perceptual task, no movement is truly performed and the mobility of the trunk is generally restricted. When using this method, the general agreement is that what is reachable with the hand depends principally on the distance of the target—object relative to the length of the arm (Bootsma, Bakker, van Snippenberg, & Tdlohref, 1992; Carello, Grososfsky, Reichel, Solomon, & Turvey, 1989; Rochat & Wraga, 1997). Thus, determining whether a visual object is reachable or not is mainly a function of the observer’s perceived body capabilities, which generally slightly overestimates the true arm length by about 10% (Carello et al., 1989; Rochat & Wraga, 1997). Such an overestimation was interpreted as originating from people’s everyday experience of reaching, which naturally requires multiple skeletal degrees of freedom, whereas they are generally tested in restricted postural situations that prevent natural body movements (Rochat & Wraga, 1997). In agreement with this interpretation, when evaluating the limit of the reaching space without postural constraints, i.e., using the torso and the arm instead of merely the arm, the overestimation significantly diminished (Carello et al., 1989), but it nevertheless persisted. It is widely acknowledge that overestimations can also have a perceptual origin. In Carello et al. (1989) experiment, participants were required to evaluate the reachability of visual objects presented in a dark environment, even if the structure of the visual scene is known to have an overall influence on the distance at which visual objects are perceived (Coello & Magne, 2000). To unravel these confounding factors, we conducted an experiment aiming at analysing the accuracy of the judgment of what is reachable, when the
informational content of the visual environment was manipulated. Nine participants (4 males and 5 females, mean age: 24.8) were requested to perform pointing movements towards visual targets but only when the target was considered as reachable, and to refrain motor initiation otherwise (motor condition). In another experimental condition, subjects were required to provide a verbal judgement about whether the target was perceived as reachable or not (perceptual condition), with no true motor activity. The experimental device was a rectangular box with the upper and lower parts divided horizontally by an upward-facing reflecting mirror. When the head rested on the upper part of the box, only the top half of the box was visible to the participants (Fig. 2a). A computer monitor was placed upside-down on the top surface of the apparatus and the image of the monitor screen was projected on the bottom surface of the box, as a consequence of the optical properties of the mirror. Hand displacements towards the targets were thus not visually perceivable although the target was always visible. The visual context varied so that the targets were presented along the sagittal axis every 5 mm from $-50$ mm to $+50$ mm according to each individual’s arm length, upon a dark (luminosity: 0 cd/m$^2$) or a textured background made of an array of grey dots (random diameter of 1–5 mm, luminosity: 4 cd/m$^2$) that were randomly positioned over the entire workspace (30 cm $\times$ 39 cm). In each condition and for each visual context, the critical limit of what is reachable was determined using a least square iterative fit

Fig. 1. (a) Experimental apparatus used to evaluate the vertical adjustment of a rod that can be manipulated in orientation and translation in reference to different body locations (head or navel). The deviation of the visual vertical axis in neglect patients is described in the right panel. The arrows indicate the adjustment of the orientation of the rod in reference to the true vertical axis, whereas the lines ending with a dot indicate the adjustment of the rod in translation according to the body mid-line (adapted from Saj et al., 2006). As mentioned in the text, the angular error in orienting the rod is similar to that observed when considering the angle formed by the two estimations of the straight-ahead of the body at the head and the navel levels, respectively. This suggests an erroneous representation of the orientation of the body in neglect patients. (b) Somatosensory perception in the deafferented patient GL and accuracy of pointing movements performed without direct visual control, under two experimental conditions: in darkness and in presence of a textured background.
procedure to obtain the logistic function that best fitted the motor and perceptual decision, for the various locations of the target. Results showed that the limit of what is reachable was farther in a dark environment than in the presence of a textured background under both response conditions (39.9 mm and 13.2 mm for the motor condition, 37.8 mm and 12.9 mm for the perceptual condition in the textured background and dark context, respectively—Fig. 2 b). The slope of the logistic regression, which expressed the level of uncertainty of the decision (a low value is the indicator for a low discrimination ability), was affected neither by the background nor by the response condition (0.10 and 0.16 under the motor condition, 0.07 and 0.09 under the perceptual condition, in the dark environment and the textured background condition, respectively—Fig. 1 c). Thus, decisions were not more difficult to make under one or other of the experimental conditions.

On the basis of these results, three conclusions were formulated. First, the perception that a visual object is reachable leans upon the representation of the functional body, i.e., the representation of action capabilities for the limbs and thus, spatial perception is body-scaled. Second, the critical limit of what is reachable was accurate according to action capabilities as long as it was estimated in a structured visual context; this suggests that perceptual judgements depend also on sensory constraints. Indeed, the fact that the critical limit of what is reachable recedes about 25 mm in darkness indicates that the perception of what is reachable strongly depends on the informational content of the entire visual scene. Consequently, an accurate estimation of what is reachable in darkness would require an improved model of the visual scene, providing a better understanding of the relationship between body, environment, and perception.

Fig. 2. (a) Schematic representation of the experimental apparatus and the layout of the visual targets used to estimate the limit of what is reachable in darkness and in the presence of a textured background. The critical boundary corresponded to each subject’s maximum arm length. (b) Error in estimating the limit of what is reachable in reference to arm length as provided by the logistic function when using a motor or a verbal response, in a dark or textured background for control subjects and the defferented patient GL. (c) Slope of the logistic function indicating response uncertainty for control subjects and the defferented patient GL (higher values are indicators of lower confidence levels for the reachable/not reachable decision).
The conscious experience of what is reachable and the categorisation of external space according to the near–far dimension at the reflective level seems thus, to be rooted in a pre-reflective experience of the body in action. In order to establish whether pre-reflective representations of the functional body may serve as the basis for the conscious categorisation of visual space, we designed two complementary experiments. First, we analysed the effect of modifying the relationship between body characteristics and external space on the conscious experience of what is reachable. The rational was that conscious experience of what is reachable should be influenced by the experimental manipulation only if one attributes a major role to the pre-reflective representations of the body in action. Using a similar experimental paradigm than the one described previously, 14 participants (9 males and 5 females, mean age: 28.4) were requested to judge whether the visual target presented on a horizontal surface (targets were positioned radially every 8 mm up to ±96 mm from maximum arm length) was reachable or not with the right hand. Before and after this perceptual test, participants were required to perform a pointing task towards targets presented at −10 cm, −13 cm and −16 cm from maximum arm length. Before the perceptual test, an accurate feedback was provided to the participants during the reaching task. After having executed 36 pointing movements, spatial accuracy of movements was evaluated using targets that received no feedback (placed at −11.5 cm and −14.5 cm; 16 trials). In the second reaching session following the perceptual test, participants were assigned to either an experimental (N = 7) or a control group (N = 7). In the experimental group, a biased visual feedback about reaching performances was provided (radial offset of 3 cm). In the control group, accurate feedback was provided during the entire pointing task. In the two groups, 125 trials were performed towards the three targets and again, the last 16 movements were carried out towards the two targets that received no feedback. As a consequence of the experimental manipulation, participants in the experimental group ended their movement too short (−30.4 mm) in the second series compared to the performance observed in the first series of movements (7.84 mm—Fig. 3a). Conversely, participants in the control group did not change their pointing performance (−6.21 mm and −5.13 mm for the first and second series, respectively—Fig. 3b). In the perceptual post-test following motor learning, results further revealed that the perceptual limit of what is reachable was affected by the motor adaptation to the visual bias and decreased significantly in the same direction as the pointing under the inaccurate feedback condition (pre-test: 39.87 mm, post-test: −1.64 mm; Fig. 3a). No modification of the limit of what is reachable was observed for the control group (pre-test: 42.17 mm, post-test: 36.68 mm; Fig. 3b). We also observed that the learning period induced a decrease of the felt arm length (9 mm) but only for the experimental group, which may have in turn influenced perceptual categorisation (see Fig. 3c). Perceived arm length was tested by asking subjects to indicate through the manipulation of a visual target (visual estimation) or through the use of their left index-finger (proprioceptive estimation) where in space they perceived their right index finger to be, following a passive displacement of the right arm by the experimenter.

Overall, the experimental data presented here clearly reveal that the perception of what is reachable relies, at least to a certain extent, upon pre-reflective representations of the functional body. There are numerous reasons for arguing that pre-reflective representations of the body in action involve at some stage a simulated action occurring in absence of any true objective motor event (see Jeannerod, 2001). The fact that when modifying the experienced arm properties through the adaptation paradigm, it was possible to influence the perceptual spatial categorisation, is in total agreement with this interpretation. Consequently, the function of the
simulation process may be thought as providing the self with a pre-reflective experience of body capabilities. We will return to this particular point in the last section of the manuscript.

In a second experiment, the necessity of pre-reflective representations of the functional body for an accurate perceptual categorisation was demonstrated by analysing the performance of a deafferented patient (GL) who has a complete loss of the sense of movement and of postural changes. GL has been suffering a permanent and specific loss of the large sensory myelinated fibres in the four limbs following two episodes of sensory polyneuropathy, which affected her entire body below the neck. The illness has resulted in a total loss of sense of touch, vibration, pressure and kinaesthesia (see Fig. 1b left). GL is confined to a wheelchair, but is able to perform most of her daily activities under constant visual guidance. Indeed, GL has no visual deficit and shows normal behaviour when required to describe, identify or locate visual object. Analysing pointing movements performed with or without vision of the moving arm, Nougier et al. (1996) reported that despite the lack of proprioception, both amplitude and directional errors were similar to those of control subjects. We found similar results when evaluating GL performances in a pointing task performed without direct visual guidance whether in darkness or in presence of a textured background. Again, though trajectories were less smooth and more variable than those of healthy controls, terminal spatial performance did not differ significantly (Fig. 1b right). These results indicate an absence of deficit for 3D vision and for the use of accurate
motor efference for planning goal-directed actions in GL. When evaluating the limits of what is reachable with our paradigm, the performance of GL was found to be nevertheless abnormal. Indeed, the distance at which she thought she was able to reach visual targets was only weakly related to arm-length characteristics: in the well-structured visual environment, she judged targets to be reachable when presented some 73 mm further than her own arm length (Fig. 2b right). This suggests a strong deficit in referring to representations of the functional body. However, the perceptual contraction of the visual space in darkness that was revealed in healthy controls, was also observed with GL: the limit of what is reachable was about 35 mm further out under this unstructured visual condition, thus 108 mm farther than arm length (Fig. 2b left). Finally, the decision was significantly more uncertain in GL than in healthy controls, as shown by the lower slope of the logistic regression used to determine the perceptual limit of what is reachable (Fig. 2c). Overall, these results strongly suggest that pre-reflective representations of the body in action serves as the basis for determining what is reachable and that this mechanism requires a non-impaired sensori-motor system, which is not the case for GL.

In conclusion, the data presented so far indicate that multidimensional space categorisation depends on pre-reflective representations of the experiential and the functional body. We have shown that modifying the body experiences through experimental manipulations, or by testing individuals with sensori-motor pathologies modifies significantly the way external space is categorised. Thus, spatial categorisation cannot be considered as a disembodied phenomenon but rather as constrained by both the spatial resolution of the sensory systems, and the pre-reflective representations of the body in action. Whether representations of the body in action must be considered to be pre-reflective because only some aspects of these pre-reflective states can be consciously experienced remains an open issue. The next section will investigate this question by evaluating which aspects of the functional body can reach consciousness.

3. The conscious experience of self-generated motor actions

Considering the pre-reflective nature of body experiences, on the one hand, and the need of knowledge about body capabilities for the explicit categorisation of visual space, on the other hand, one may wonder which aspects of motor acts can be consciously perceived when required to do so. In the motor literature, it has long been considered that most goal-directed movements are planned and executed in an “automatic” fashion (Johansson & Cole, 1994). For instance, Castiello, Paulignan, and Jeannerod (1991) showed in a pointing task that an unexpected target jump becomes available to consciousness some 200–300 ms after the start of the sensori-motor adjustments (see also Chua & Enns, 2005; Day & Lyon, 2000; Pelisson, Prablanc, Goodale, & Jeannerod, 1986). This could be understandable as the visual representations used for action are thought to be distinct from the conscious representations that are used for identification, as suggested by the perception–action model (Milner & Goodale, 1995). Fourneret and Jeannerod (1998) further analysed the conscious experience of goal-directed action in presence of a sensory bias. Subjects here were instructed to move their unseen hand in the direction of a visual target and only the trajectory was visible as a line superimposed to the hand-trajectory on a computer screen. In some trials, a directional bias (2°, 5° or 10° to the right or to the left) was introduced such that the visible trajectory no longer corresponded to that of the hand and thus, to reach the target, subjects had to adjust hand-trajectory in the opposite direction to the bias. At the end of each trial, subjects were asked in which direction they thought they had truly moved their hand. The authors observed that subjects tended to ignore the veridical trajectory of their hand, i.e., they ignored the non visual action-related cues. Instead, they based their report on the visual cues and adhered to the direction seen on the screen. These results and more recent ones (e.g., Chua & Enns, 2005) suggest that the visuomotor system is able to use information appropriately for producing accurate corrections, but that this information cannot be accessed consciously. Thus, for a while, it was accepted that the motor parameters for actions could not be consciously monitored, and that it is only the consequence of an action on the environment that could give rise to conscious experience.

In these previously mentioned studies, it is assumed that subjects’ perceptual awareness (their explicit knowledge of the goal of action) is equivalent or identical to their motor awareness (their explicit knowledge of their physical response). But, this is not necessarily the case. Indeed, if subjects have other forms of awareness, specifically motor awareness, they may be able to report their knowledge of their physical response when
tested with the appropriate methods. Motor awareness is by definition an “inner subjective state” (Searle, 2000) and thus, “it is not directly accessible from a third person viewpoint”. One means of studying motor awareness would then be to ask subjects to focus on the dynamical rather than on the observational aspect of their motor performance, e.g., by simply asking subjects to reproduce the movement characteristics of a previously performed goal-directed action. The basic assumptions of such a reproduction paradigm are that (1) the movement characteristics that can be reproduced are those of which we are aware and furthermore, (2) to reproduce a movement, awareness with a precise content is required. We will now consider experimental results that focused on motor awareness for kinematics (moving through space) and for kinetics (manipulating objects) of motor acts. We will focus on the similarities and the differences in the degree of awareness that subjects possess for these two aspects of goal-directed actions and also, in comparison to perceptual awareness.

We recently tested the possibility that motor and perceptual awareness can be dissociated. In this study, we also questioned the role of the frame of reference used to test motor and perceptual awareness (Boy, Palluel-Germain, Orliaguet, & Coello, 2005). For this purpose, we used a remote control situation (video assistance) and the subjects’ task was to reach and point to a visual target by estimating hand and target location through a vertical video display. In some trials, the visual scene was rotated by 45° counter clockwise and thus, the participants were required to compensate for the directional bias in order to reach the target. At the start of the experimental session, the initial orientation of hand-trajectory was incorrect and corresponded to the directional bias that was introduced. Within about 10 trials, participants progressively adapted to the visual bias. Throughout the experimental session, the visuo-manual performance was measured by means of a digital tablet (Wacom UD 1580). Before and after the adaptation period towards a single target, two perceptual tests were used in absence of visual information in order to gain insight in the motor awareness that subjects pos-sessed about their own reaching performances. For these two tests, two types of motor awareness were disso-ciated in reference to either a 3rd person perspective (performance estimation as evaluated from information that can be shared with an observer) or a 1st person perspective (performance estimation as evaluated from information inside the body that cannot be directly accessible by an observer). In the “space evaluation” condition (3rd person perspective), the participants were required to indicate, with either the right or the left hand, where in the workspace were the acting hand’s starting position and the target position, respectively. In the “movement evaluation” condition (1st person perspective), subjects were asked to reproduce the trajectory that they had traced in order to move their hand to reach the target. Results revealed first that all subjects learned to compensate for the directional bias. Second, a clear dissociation for motor awareness was revealed when comparing 3rd and 1st person perspectives. Indeed, under the movement evaluation condition (1st per-son perspective—Fig. 4b), there were no significant differences between end-point precision for the initial and the reproducing trials. These results are a clear indication of a good level of motor awareness. Interestingly, this finding was observed only when the reproducing trials were performed with the same limb as that used during the initial trials. Indeed, when performing with the contra lateral arm, there was a slight but significant effect of the visually biased position of the spatial relationship between hand and target positions on the sub-jects’ degree of awareness. Under the space evaluation condition (3rd person perspective—Fig. 4c), results revealed a significant effect of the biased visual feedback, and this was true whether the reproducing trials were performed with the same or the contra lateral arm than that used during the initial trials. Note worthy is the fact that subjects systematically located both hand and target positions in reference to the visually biased information.

From these results, we defend the idea that perceptual awareness must be dissociated from motor aware-ness. Furthermore, we suggest that when judging one’s own motor performance, intrinsic (proprioceptive and/ or efferent copy related signals) and extrinsic (visual) information are selectively processed depending on the perspective that one is required to adopt when reporting their conscious experience of self-generated motor actions.

1 It is worth noting that the terminology used here and in other studies to dissociate 1st and 3rd perspectives has sometimes been referred to as 1st person internal and 1st person external (observational self) perspectives (Callow & Hardy, 2004).
Interesting is the fact that the degree of motor awareness seems also to depend on the subjects’ intentional state. Using a movement reproduction paradigm in a double-step pointing task, Johnson and Haggard (2002) had subjects follow a target (pointing) or voluntarily move in the opposite direction (anti-pointing). After each initial trial, an indicator of the subjects’ awareness was obtained by asking subjects to reproduce the movement they thought they had previously executed. Results confirmed that subjects were able to make rapid corrections to an ongoing pointing movement, in response to a target shift. For anti-pointing trials, the corrections occurred later than the corrections towards the target in standard pointing. This pattern of results is consistent with the idea that a relatively slow neuronal circuit via the frontal cortices is involved when an intentional correction is required, and that conversely, a faster parietal connection is involved in automatic corrections. The interesting finding however for the present discussion was that subjects were able to perceive and reproduce the pointing corrections even in absence of a conscious perception of a target shift. For standard pointing, subjects systematically underestimated their correction-capabilities. More specifically, there was a 36 ms delay between motor correction and motor awareness, a result that was evaluated by computing the differences between initial trajectory deviations when responding to the perturbation and reproduced trajectory deviations. There was in addition an attenuated awareness of the spatial characteristics of the correction: the magnitude of the reproduced corrections was smaller than that truly performed during the initial trials. In contrast, in anti-pointing trials, subjects slightly overestimated the efficiency of their corrections but overall the reproduced corrections were rather close to that truly performed with very little awareness.

Fig. 4. (a) Schematic view of the experimental setup in the video-controlled pointing task when the directional mapping between visual space and workspace was unperturbed (0°) or rotated (45°). (b) Individual results when required to evaluate the location of initial hand position and target (spatial evaluation task) or the dynamic aspects of the performance (movement evaluation task) as a function of the active limb (ipsilateral and contralateral conditions), under the non-perturbed and rotated visual conditions. The origin (0,0) specifies the true hand starting position used for every trial. Axes are in cm and 99% confidence ellipses are superimposed onto the data points (adapted from Boy et al., 2005).
time-delay, and with rather precise spatial characteristics. Overall, these results demonstrate once more a distinction between perceptual awareness and motor awareness. Furthermore, they reveal that the awareness that subjects possess of a visuomotor adjustment might depend directly upon the role of intention in generating these adjustments.

As we live under the influence of gravity, perception of ongoing motor actions do not concern only spatial aspects of the performance but also the force developed during these goal-directed behaviours. Indeed, during object manipulation, the fine adjustment of finger force levels (further referred to here as grip force) becomes a crucial aspect of motor efficiency. To maintain a stable grip on an object during its manipulation for instance, the active grip force (muscular forces) applied upon the manipulated object needs to be sufficient to compensate for the passive forces (external forces) induced by gravity, inertia or any other destabilising forces that may act upon the object (Bernstein, 1967; Turvey, Burton, Amazeen, Butwill, & Carello, 1998). Though grip force is a motor parameter that is thought to be scaled automatically—as it was the case for movement kinematics—it appears that during some fine manipulative tasks (e.g., threading a needle) we make a conscious effort to release our grip in order to succeed in the task at hand (Delevoye-Turrell & Wing, 2005). For the question of perceptual categorisation and conscious experience of space for action in the not so rare case of object manipulation, it seems important to know what is our level of motor awareness for force adjustments, i.e., of the control of kinetics. In a recent study, it was suggested that one may have a less precise motor awareness of kinetics than that of kinematics (De Graaf et al., 2004). This might be due to the fact that for movement kinematics both intrinsic and extrinsic perceptive cues can be used to gain consciousness about the development of the goal-directed action and thus, both a 3rd person and a 1st person perspective can be adopted to build conscious experience of self initiated actions. For kinetics, however, this is not the case since force control can only be considered through a 1st person perspective. Indeed, extrinsic (visual) information plays a non significant role in force-adjustments (Delevoye-Turrell, Giersch, & Danion, 2003). In the De Graaf et al.’s study, the subjects’ motor awareness of kinetics was not directly tested. Hence, in the following, we describe a series of experiments that were conducted with the aim to assess directly the degree of motor awareness that naïve subjects may possess on the levels of grip force used during the simple act of lifting an object with a precision grip.

The protocol was the following. When an auditory signal was heard, the subjects’ task was to reach for and lift an object and maintain it in mid-air for a few seconds. After each initial trial, subjects were asked to reproduce the object, without lifting it this time, the grip force level they thought they had used in the initial true-grasping trial. Finally, to gain an insight in the role played by the subjects’ intentional state on motor awareness, we manipulated the experimental condition of the lifts. In the “automatic” condition, subjects lifted an object that was hefted with a light (100 g), a medium-heavy (225 g) or a heavy (800 g) weight. Hence, the level of active grip force required to lift the object depended directly on the levels of passive force induced to the object by the environment (gravity). In the “intentional” condition, the subjects’ task was to lift the very light object and to imagine that the manipulated object was light, medium-heavy or heavy. Hence, under this condition, the active grip force scaling depended solely on the force-scaling that subjects intentionally decided to apply. By fitting the object with a load cell (Novathech Mini40), we measured the mean grip force level in Newton (N) applied during the first 500 ms of each trial, during which the object was held steady in midair, and conducted a Pearson correlation analysis for pairs of initial and reproducing trials. Results revealed that healthy controls applied increasingly greater force when lifting light, medium-heavy and heavy objects (Fig. 5a); similar force levels were used in both the “automatic” and the “intentional” condition. Moreover, subjects were able to reproduce movement kinetics above chance level in both experimental conditions (see Fig. 5b). However, subjects’ awareness was limited as none of the subjects revealed a correlation score above 0.86. Interestingly, and in view of Johnson and Haggard (2002), motor awareness for action kinetics was significantly greater in the “intentional” condition than in the “automatic” condition. Finally, when asked to provide a verbal auto-evaluation of their capabilities to perform the reproducing trials, subjects thought that they could reproduce the “automatic” trials rather well (7/10 on an analogue scale) but that they could hardly reproduce the “intentional” trials (3/10). Overall, these results suggest that one can achieve a certain degree of motor awareness of movement kinetics without being self confident about the accuracy of the judgement. Furthermore, the intentional state in which the action is produced plays, as it did for kinematics, an important role in the level of conscious experience that subjects can pre-reflectively reveal.
The awareness of force production is also an issue of importance for discussions around the mechanisms involved in judgements of attribution (Georgieff & Jeannerod, 1998). Many patients with schizophrenia describe “passivity” experiences, in which their own actions are experienced as though made for them by some external agent (Mellors, 1970). In most cases, the actions made by the patient, although felt to be controlled by alien forces, are not discrepant with their intentions (e.g., Spence et al., 1997). Hence, these patients seem to have a problem with the functional relation between motor intention, motor control and action attribution. One might ask whether one of the causes of this mis-relation could not be related to a deficit in the awareness of their own produced muscular forces.

To assess this question, we conducted another experiment where, as above, subjects were required to lift an object with a precision grip. Each initial trial was followed by a reproducing trial where subjects were asked to reproduce on the load cell (without lifting it), the grip force level they thought they had used in the previous trial. Two pathological groups of subjects were recruited for the study in order to test the hypothesis that a deficit in motor awareness might be associated to passivity experiences in patients with schizophrenia and not general to all psychiatric patients. A group of 12 patients with schizophrenia (as defined by the DSM-IV) and a group of 6 psychiatric patients with personality disorder participated in the study. For the initial trials, results revealed that patients applied increasingly greater force when lifting light, medium-heavy and heavy objects, as did the healthy controls (Fig. 5a). Levels were similar whether lifting the object in the “automatic” or in the “intentional” conditions. Second, most patients were able to reproduce the force levels applied during the initial trials. In the “automatic” condition, motor awareness for force was statistically similar across all groups of subjects (Fig. 5b), which suggested a similar level of motor awareness when responding to passive forces. However, motor awareness for force was significantly greater in the “intentional” condition than in the “automatic” condition for the control and the non-shizophrenic pathological group only (Fig. 5b). For the patients with schizophrenia, the degree of motor awareness was not any better in the “intentional” condition than in the “automatic” condition. Overall, these results reveal a specific deficit in motor awareness of movement-kinetics for intentional actions in schizophrenia, which might be at the origin of their deficit concerning causal attribution of action for themselves and others (see also Bulot, Thomas, & Delevoye-Turrell, in press). It further suggests that the neuronal substrate that sustains motor awareness with and without intention might be different.

The results summarized here demonstrate that one can achieve a certain degree of motor awareness in both the kinematic and the kinetic dimensions of self-generated motor actions. Motor awareness is however never total. Kinematics appear to be more available to consciousness than kinetics maybe because of the fact that kinematics can be accessible both from a 1st and a 3rd person perspective, whereas kinetics are only available...
from a 1st person perspective. Furthermore, the reflective body representation that is associated with goal-directed actions might evolve towards different levels of conscious experience in function of the intention associated to the generation of the action. In the following section, we consider these experimental data in the context of a neuro-cognitive model for which the anticipatory consequences of forthcoming actions-through the mechanism of action simulation, play a central role both for the pre-reflective and the reflective experience of the body in action.

4. Neuro-cognitive model of space categorisation and selection for action

Spatial categorisation and selection for action must be viewed as articulated around three interdependent internal states: an intentional state, a pre-reflective state and a reflective state (see bottom of Fig. 6), all of which are related to the components of goal-directed action. The dominant theories of internal models (e.g., Jordan, 1995; Wolpert & Kawato, 1998) suggest that in the case of the specification of an intended goal for action (intentional state)—which may include an interaction between sensory information and representations of the experienced body, the motor centres generate an appropriate outflow signal so as to perform the planned movement (inverse model). At the same time, as the motor commands are sent to the effectors, a copy of the command is sent to an internal predictive (forward) model. By generating an efferent copy of the motor commands, the motor system can simulate the motor act and therefore, predict and anticipate the sensory consequences of self-generated movements through an emulation process (Grush, 2004). The crucial aspect of the model is that the function of the whole simulation process is not only to shape and prepare the motor system for the consequence of motor execution, but also to provide the self with information on the feasibility of...
action potentials (representation of the functional body). Thus, when a visual stimulus is presented in the peripersonal space, it evokes automatically a “potential motor action” which, regardless of whether the action is subsequently executed or not, maps pre-reflectively the spatial stimulus position in motor terms. As speculated by Jeannerod (2003), covert action includes everything that is involved in an overt action, except for the (above threshold) muscular contractions and joint rotations. A simulation theory would therefore predict a sharing, in neural terms, of the state when an action is simulated with the state that immediately precedes the execution of that action (see Fig. 6).

In the case of a simulated action, the emulation process would provide a signal that makes possible an estimation of body capabilities assuming an internal decision criterion, which in turn would provide the basis for spatial categorisation and selection for action. The fact of integrating the predicted information with endogenous true sensory feedback would contribute to motor consciousness (1st person perspective). In the same vein, integrating predicted information and true state estimation would provide the signal for perceptual consciousness (3rd person perspective). Both forms of consciousness would contribute to the reflective experience of the body in action. Finally, signals from the forward model and/or from the true state can be used to modify prior intention and subsequently action selection.

In conclusion, although our subjective experience is one of a continuous and coherent visual world, the perception of space in relation to action is necessarily constrained by the pre-reflective representations of the body in action. The empirical data that we have presented show that multidimensional categorisation of perceptual space depends on body representations at both an experiential and a functional level. In the perspective of naturalising the pre-reflective experience of the body in action, action simulation within brain motor areas may represent the underlying within brain motor areas principle that enables pre-reflective experience, which in turn may provide the support for spatial categorisation and selection for action.

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References


