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Dissociating body representations in healthy individuals: Differential effects of a kinaesthetic illusion on perception and action

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Abstract

Evidence from neuropsychological patients suggests that multiple body representations exist. The most common dissociation is between body schema to guide limb movements, and body image used to make perceptual judgements. In the current study we employed a kinaesthetic illusion in two experiments to dissociate body representations in healthy individuals. Tendon vibration creates an illusory lengthening of the muscle and an illusive displacement of the limb. In Experiment 1 two conditions were used. In the 'direct' condition the biceps of the dominant right arm of blindfolded participants was vibrated, creating illusory elbow extension. In the 'indirect' condition the right knee was held with the vibrated right arm, creating illusive lowering of the leg and knee. In both conditions, subjects performed with the non-vibrated arm a reaching as well as a matching response, theorized to be based on the body schema and body image, respectively. Results showed that the illusion was significantly larger for the matching as compared to the reaching response, with the most pronounced difference observed in the direct condition. In Experiment 2 reaching and matching without vibration and a passive matching response were implemented in the direct condition. The same differential effect of the illusion was found. Results further showed that passive and active matching were statistically similar but significantly different from the reaching response. In conclusion, these findings suggest that the effect of the kinaesthetic illusion on reaching and matching differed, consistent with the idea of separate underlying body representations for both responses.

Keywords: Body image; Body schema; Perception; Action

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1. Introduction

For almost all motor behaviour we rely on internal representations of the current spatial configuration of our body. These internal body representations enable us to guide limb movements and to make perceptual judgements about the location of different body parts with respect to each other. Disruption of body representations can result in a variety of disorders, including autotopagnosia (Buxbaum & Coslett, 2001) and phantom limb phenomena (Ramachandran, 1998).

There is now a growing body of evidence suggesting that multiple body representations exist (Paillard, 1999; Schwartz, Moran, & Reina, 2004; Schwoebel & Coslett, 2005). Neuropsychological studies have provided evidence for a dissociation between at least two body representations; one which is used during motor action and one underlying perceptual judgement (Gallagher & Cole, 1995; Graziano & Botvinick, 1999; Paillard, 1991). This dissociation is largely based on neurological patients with numbsense who are unable to perceive proprioceptive and tactile stimuli, but are nevertheless able to point to these targets (Paillard, 1999; Rossetti, Rode & Boisson, 1995, 2001), and patients with autotopagnosia who are impaired in localizing perceptually different body parts, but remain able to guide their actions (Buxbaum & Coslett, 2001).

The current most commonly used classification between different body representations is that of body schema and body image. Although there is no consensus among researchers of their definitions, body schema is generally regarded as an unconscious, bottom-up, dynamic representation, relying on proprioceptive information from the muscles, joints and skin. The body schema is thought to be used to govern posture and motor actions. The body image, on the other hand, is considered to be a more conscious, top down, cognitive representation, incorporating semantic knowledge of the body, and mostly used to make perceptual judgements (Gallagher, 1986; Head & Holmes, 1911–1912; Paillard, 1999).

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The idea of different representations underlying perceptual judgement and guiding action is not new and has previously been suggested for the visual system (Jeannerod & Rossetti, 1993; Milner & Goodale, 1995). Visual illusions have been used to dissociate between automatic, accurate calibration required for actions and conscious visual perception for perceptual judgements in healthy subjects (Aglioti, DeSouza & Goodale, 1995; Haffenden & Goodale, 2000; Westwood & Goodale, 2003) (although this is not undisputed, see for example: Dassonville & Bala, 2004; Smeets, Brenner, de Grave, & Cuijpers, 2002).

Considering the growing body of evidence from neuropsychological patients and in parallel with the application of illusions in the visual system, we reasoned that one possible way to dissociate between different body representations in healthy individuals might be to evoke a kinaesthetic illusion which affects both representations differently. One well known illusion involves tendon vibration. Vibration of ~75 Hz on the sinew of a limb causes an illusory lengthening of the muscle, creating an illusory movement and (eventually) displacement of the limb (Cordo, Gurfinkel, Brumagne, & Flores-Vieira, 2005; Eklund, 1972; Goodwin, McCloskey & Matthews, 1972). The muscle spindles excited by the vibration signals to the brain that the muscle is stretched and thus the limb must have moved, while it actually has remained stable. Although a considerable number of studies have assessed different aspects of this illusion, including the involved neural correlates (Cordo et al., 2005; de Vignemont, Ehrsson & Haggard, 2005; Naito & Ehrsson, 2001; Naito, Ehrsson, Geyer, Zilles, & Roland, 1999), it has, to our best knowledge, not yet been used to dissociate action and perception based body representations in healthy individuals.

In the present study vibration of the biceps brachii tendon of the dominant right arm of healthy, blindfolded subjects is used to induce an illusory displacement of the forearm. Participants were required to make a reaching as well as a matching response. The matching response consisted of mirroring the position of the unstimulated arm to the perceived location of the stimulated arm. For the reaching response, subjects had to point with their left index finger to the felt location of the index fingertip of the stimulated right arm. Previous research has shown that the illusion can be transferred to another limb or body part causing a distortion of body size (de Vignemont et al., 2005; Lackner, 1988). Therefore, we also tested the effect of the illusion on both responses in an indirect condition wherein the ipsilateral knee was held with the vibrated arm, causing a transferred 'indirect' illusion of lowering of the upper leg and knee.

The idea is that within a body representation all proprioceptive information together with the knowledge we have about our body is used to minimize uncertainty about the body's spatial organisation. During the vibrotactile illusion, however, the central nervous system receives conflicting information about the movement and location of the stimulated limb, since only one tendon provides information that it is stretched while information from the joint, other tendons and the skin suggests that it has remained stable.

An important prediction of the supposition of two different body representations is that both may be differentially influenced by the illusion, since one is only based on proprioceptive information while the other also incorporates stored experiences and semantic knowledge of our body.

The body schema, on the one hand, is thought to be based solely on (conflicting) proprioceptive information. This representation might weight the proprioceptive input to minimize uncertainty about the current spatial position of the forearm, as has been suggested by optimal integration and computational models of sensory integration and action (van Beers, Sittig & Gon, 1999; van Beers, Wolpert & Haggard, 2002; Wolpert, 1997; Wolpert, Ghahramani & Jordan, 1995). Since there might be more proprioceptive input suggesting that the arm is stationary (signals from triceps, elbow joint, skin), instead of moving (signals from the biceps), the reaching movement might be more accurate towards the actual stationary arm position, rather than towards the illusory displacement.

The body image, on the other hand, is considered to be a more top down, higher order, cognitively shaped body representation (Paillard, 1999; Tsakiris & Haggard, 2005). As a consequence it might use stored knowledge from experience that stretching of the biceps is caused by lowering of the forearm, to override the conflicting information and in this way minimize uncertainty. Consequently, the body image may indeed incorporate the illusory displacement of the forearm, and the matching response may thus be lowered/dropped compared to the actual limb position. Accordingly, our first hypothesis is that the body image based matching response will be more influenced by the illusion than the body schema based reaching response. Our second hypothesis concerns the effect that transfer of the illusion to another body part might have on this dissociation. We reasoned that in the indirect condition there is even more proprioceptive input suggesting that the limb has remained stationary (since, there is no direct proprioceptive input from the knee itself suggesting that it has moved). As a consequence of this augmentation of conflict within the proprioceptive signal, we predict that the incorporation of the illusion will be less apparent for both representations in the indirect compared to the direct condition.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Twenty-five right-handed healthy subjects (21 female and 4 male, with overall group mean age 20.8 years, S.D. 1.9) participated in the study. All participants gave their informed consent prior to the experiment. Right-handedness was assessed with the Dutch handedness questionnaire (Van Strien, 1992). The inclusion criterion was an overall score of seven or more, indicating a strong preference for the right hand in daily activities. Subjects were selected without consideration of tendon vibration sensitivity. Finally, the participants were unaware of the rationale of the experiment and received a small fee for their participation. The study was in accordance with the ethical advisory committee of the Faculty of Social Sciences of the Utrecht University, the Netherlands, and with the declaration of Helsinki (1964).

2.1.2. Apparatus

The apparatus to induce the illusion was a vibration device (Brual & Kjaer type 4809) which was modified with an adapted extension containing a counterweight to keep the stimulation device steady on the right biceps brachii tendon

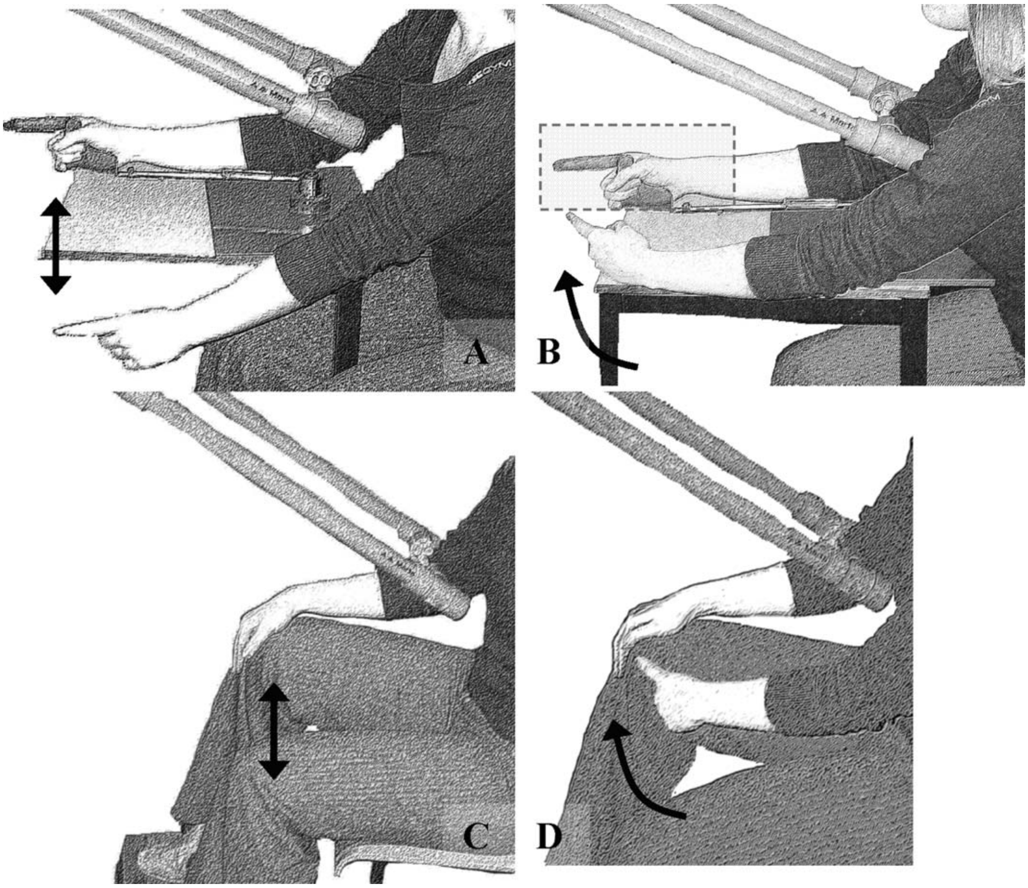

Fig. 1. Experimental setting: (A) Direct condition in which the arm was stimulated, performing a matching response, (B) Direct condition, performing a reaching response. The gray square indicates the position of the plastic board that was added in Experiment 2, (C) Indirect condition, in which the illusion was transferred to the knee, performing a matching response, and (D) Indirect condition, performing a reaching response.

while the arm was relaxed. The frequency of the vibration was set at 75 Hz with an amplitude of ~0.5 mm, which is considered to be the optimal frequency and amplitude to induce a tendon vibration illusion (Naito et al., 1999).

2.1.3. Procedure

A pilot study indicated that subjects spontaneously reported a feeling of a downward movement or displacement when the device was turned on, and an upward movement when the device was turned off. Therefore, we collected only four responses to ascertain that the subjects remained unaware of the aim of the experiment across all conditions and to maximize the illusion. In these four trials, participants were required to make a reaching response and a perceptual judgement during vibration in the direct and the indirect condition. The sequence of trials was pseudo-randomised between subjects. Because the susceptibility to the illusion differs greatly between subjects (Burrack & Brugger, in press), two procedures were included to maximize sensitivity; the vibration was administered ten seconds before the response was given to ensure that the illusion was complete (Lackner, 1988), and each trial was separated by at least two minutes without vibration to make sure the preceding stimulation would not interfere with the current performance (Rogers, Benrups & Lewis, 1985). Before each trial the subjects was blindfolded and positioned in front of the apparatus on a desk chair which was adjustable in height. This way ensuring that the angle of the vibration devise and the counter-weight was similar for each subject.

In the direct condition the stimulated, dominant right arm was placed in an armrest on the end of the table. The armrest was freely movable in the horizontal plane to provide the subject the impression that some arm movement was possible and to ensure the arm was relaxed. The left, unstimulated arm could move freely beside the table to make the perceptual (matching the position of the non-stimulated to the felt location of the stimulated forearm) and reaching (pointing to the perceived location of the fingertip of the stimulated arm) response (Fig. 1A and B). For the perceptual matching response the left arm was completely stretched and both elbows were placed at the same height by the experimenter. Subjects were instructed to move only the forearm up and down to match the position. The starting position of the left hand for the reaching response was on top of the left leg just below the hip from which point the subject was instructed to make a fast, single reaching movement without corrections. In the indirect condition, the table was removed and the subject had to place the right foot on a small platform which was 20 centimetres above the ground. The desk chair was adjusted so the angle between the upper and lower leg was 90°. The stimulated arm was placed in a relaxed position with the palm of the hand placed on the kneecap. For the perceptual response the subject also positioned the ball of the left foot on the platform. For the starting position of the perceptual response the left foot was flexed by the experimenter so the subject could subsequently match the height of both kneecaps by flexing and extending the left ankle joint. For the reaching response the left leg was placed on the floor and the subject had to point with the left index finger to the perceived location of the top of the kneecap direct under the knuckles (Fig. 1C and D). Again, for the starting position for the reaching response the hand was placed on the left leg just below the hip. After each response, the subject was asked to hold the indicated location for several seconds so the difference between the actual and indicated position of the limb in the vertical plane could be measured in centimetres using a measuring tape.

3. Results

A two-factor (condition; direct versus indirect, and response type; reaching versus matching) repeated measure ANOVA with the difference between actual and perceived limb loca-

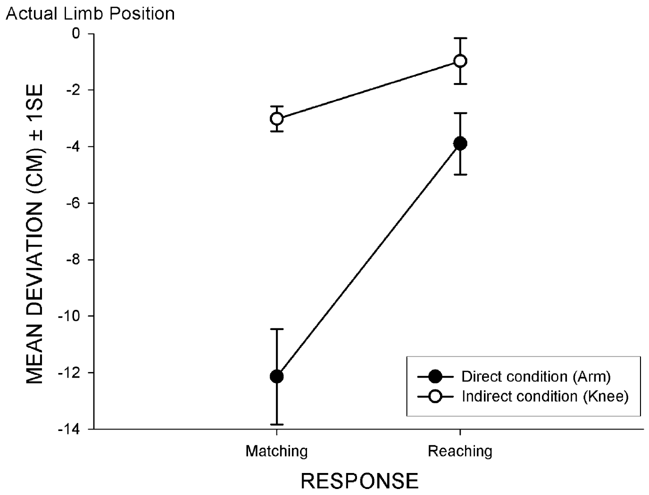

Fig. 2. Magnitude of illusory displacement. Mean difference in centimetres (and S.E.) between actual limb position (zero) and perceived limb position in the direct and indirect condition for the reaching and matching response.

tion as dependent variable, indeed showed a significant effect of condition ($F(1, 24) = 20.60$, $p < 0.001$) and response ($F(1, 24) = 52.38$, $p < 0.001$), as well as an interaction effect ($F(1, 24) = 18.64$, $p < 0.001$) (Fig. 2). A two-tailed paired samples *T*-test was employed to investigate the reliability of this difference between both responses within each condition. Results showed a significant effect for response within the direct (mean response difference direct condition ± S.E.; −8.24 cm ± 1.24; *T*-test: $t(24) = -6.66$, $p < 0.001$) as well as the indirect condition (mean response difference indirect condition ± S.E.; −2.04 cm ± 0.71; *T*-test: $t(24) = -2.86$, $p = 0.009$). The obtained interaction for condition and response type, together with the difference in magnitude of their mean, suggests that the difference between matching and reaching responses was larger for the direct condition.

To test whether a systematic bias existed in performing both responses without vibration we re-tested 11 of the 25 subjects, and asked them to make a reaching and a matching response without stimulating the biceps in both conditions. A two-tailed one sample *T*-test indeed showed that there was no significant difference in the non-vibration condition between zero (the actual position) and the indicated location for the matching response in the direct condition (mean response error, ±S.E.; 0.18 cm ± 0.26; *T*-test: $t(10) = 0.69$, $p > 0.51$), for the reaching response in the direct condition (mean response error, ±S.E.; −0.23 cm ± 0.37; *T*-test: $t(10) = -0.61$, $p > 0.55$), nor for the matching response in the indirect condition (mean response error, ±S.E.; −0.55 cm ± 0.25; *T*-test: $t(10) = -2.21$, $p > 0.05$). There was, however, a significant deviation from zero for the reaching response in the indirect condition (mean response error, ±S.E.; −1.32 cm ± 0.59; *T*-test: $t(10) = -.2.24$, $p = .05$).

4. Discussion Experiment 1

The results of the Experiment 1 suggest that the effect of the illusion differs between reaching and matching responses and that this dissociation is significantly more pronounced for the direct compared to the indirect condition. However, despite the non-significant deviation from zero, for both responses in the direct condition and for the matching response in the indirect condition, the interpretation of the magnitude of the illusion of both responses remains irresolute. This is because the responses with and without vibration are averaged between subjects, while there may have been a within subject effect. Furthermore, one might argue that the matching response may be just another type of action response, since both responses require active movement and planning. To address this issue, and to re-test the assumption that there is no bias in the responses without vibration, we conducted a second experiment.

In Experiment 2 only the direct condition was employed since the response differences were more pronounced in this condition. Two changes with respect to Experiment 1 were made. First, a passive matching response was added to the reaching and matching response from Experiment 1, because passive movement has in general not been regarded as an action, since it does not require movement planning or active muscle contraction. Finally, control trials were added for all responses, with as only difference, compared to the illusion trials, that the amplitude of the vibration was reduced to zero, no longer creating the illusion. This allowed us to calculate a deviation score between the indicated position with and without vibration, constructing a more reliable measurement of the magnitude of the illusion.

5. Experiment 2

5.1. *Methods*

5.1.1. *Participants*

Twenty-five right-handed healthy subjects (22 female and 3 male, with overall group mean age 21, 1 year, S.D. 2.7) participated in the study. None of the subjects participated in Experiment 1 and all were naïve to the rationale of the experiment. Again, all participants gave their informed consent prior to the experiment. They were selected without consideration of tendon vibration sensitivity and had a score of 7 or more on the handedness questionnaire (Van Strien, 1992). Participants were paid a small fee for their participation. The study was conducted in accordance with the ethical advisory committee of the Faculty of Social Sciences of the Utrecht University, the Netherlands, and the declaration of Helsinki (1964).

5.1.2. *Apparatus*

We use the same vibration device, frequency and amplitude as describe for Experiment 1 (paragraph 2.1.2.).

5.1.3. *Procedure*

The procedure was identical to the direct condition in Experiment 1 except for the following three additions. First, a passive matching response was added in which the starting position was equivalent to the active matching response, only now the experimenter moved the forearm of the subject passively up and down until the subject verbally indicated both arms were on equal heights. Second, a control trial was added for each response, in which the tendon was not vibrated. Third, since subjects had to reach multiple times to the felt location of the vibrated arm (with and without vibration) tactile feedback from the first reaching response could be used to re-aim the next reaching response. To prevent this, the experimenter held a plastic sheet against the armrest so subject would point against this frame preventing tactile feedback (Fig. 1B, gray square). All trials were pseudo-randomised between subjects.

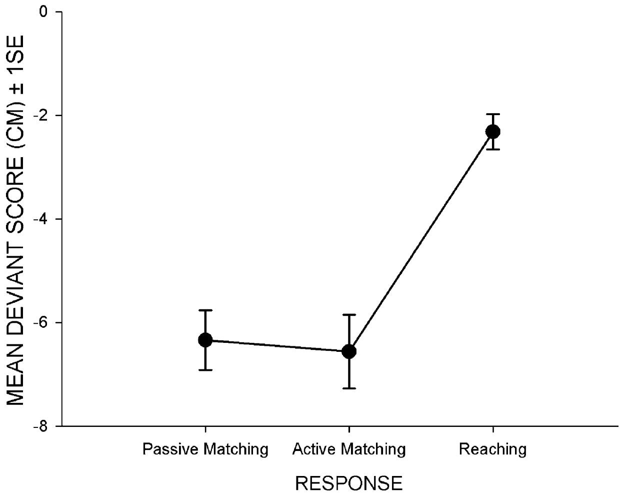

Fig. 3. Magnitude of illusory displacement. Deviant score: mean difference in centimetres and S.E., between response given during vibration minus without vibration (control trial) for the passive, active matching and reaching response in the direct condition.

6. Results

Prior to the statistical analysis we calculated the deviant score of each response by subtracting the indicated position during the control trial from that during vibration.

A one factor three level (response; reaching, active and passive matching) repeated measures ANOVA with the deviation score as dependent variable, showed a significant effect of response ($F(2, 23) = 22.14$, $p < 0.001$). A planned contrast showed a significant difference between active matching versus reaching ($F(1, 24) = 30.22$, $p < 0.001$), but no significant difference between active and passive matching ($F(1, 24) = 0.18$, $p > 0.68$) (Fig. 3).

In addition, we tested the correlation between the deviant reaching score and the deviant active/passive matching score. A paired sample correlation showed no significant correlation between active matching and reaching (Pearson correlation -0.13, $p > 0.53$) nor between passive matching and reaching (Pearson correlation 0.33, $p > 0.11$). Finally, as expected, active and passive matching significantly correlated (Pearson correlation 0.69, $p < 0.01$, $N = 25$).

7. General discussion

In the present study we aimed to dissociate body representations in healthy individuals using a kinaesthetic illusion. We hypothesized that the body image based matching response would be more influenced by the illusion than the body schema based reaching response. The results of Experiment 1 indeed showed that the illusory displacement was significantly larger for the matching as compared to the reaching response. Whereby the difference in magnitude of their mean together with the significant interaction, suggested the largest difference in the direct condition. However, several aspects were not sufficiently controlled for in Experiment 1.

First, a control trial without vibration was not implemented in Experiment 1. Instead, the given response was compared against zero (the actual limb position), since we expected subjects to perform accurate in reaching and matching without vibration. Although, this supposition was later proven to be correct for three responses, this was not the case for the reaching response in the indirect condition. To control for this we added a non-vibration trial for each response in Experiment 2. This enabled us to calculate a deviant score in which we subtracted the deviation in the control response from the magnitude of the response given during vibration. Since the difference in magnitude between both responses represented the occurrence of the kinaesthetic illusion, this resulted in a more reliable measure of illusory displacement. Results of Experiment 2 showed the same significant dissociation between matching and reaching.

Second, in Experiment 1 we assumed that the matching response was based on a perceptual representation of the arm position, while reaching involved sensorimotor processing of the arm configuration (Rossetti et al., 2001). Active matching, however, might be regarded as a form of action since it involves active muscle contraction and motor planning. Therefore, we implemented a passive matching response in Experiment 2, which did not require active planning. Results showed that passive and active matching did not differ from each other in incorporation of the illusion. Moreover, passive and active matching responses were significantly correlated across subjects suggesting a common underlying representation.

In the introduction, we formulated two general assumptions. First, we suggested that matching and reaching responses are based on different underlying body representations. Second, we proposed that the different body representations are differentially sensitive to the illusion. As theorized in our first hypothesis, the reaching responses were considerably less influenced by the kinaesthetic illusion than the perceptual judgements.

We additionally hypothesized that if both responses were based on a single body representation, the two responses should be correlated. Both matching responses correlated in Experiment 2, but we did not find a significant correlation between the matching responses and the reaching response. Although this may not provide definitive evidence, it is consistent with the idea of dissociable underlying body representations for action and perceptually based responses.

Despite these results, the question concerning the nature of the two body representations remains. As mentioned before, the most commonly used dissociation is that of body image and body schema. However, at this point, the definitions of the two are critical to whether the dissociated body representations in this study indeed reflect the body schema and body image. Yet, currently there is no real clear cut definition of the two. Recently, Gallagher (2005) tried to clarify the definitions by contrasting the body schema as a non-conscious, anonymous, coherent and holistic representation at a sub-personal level which is in interaction with the environment and involved in action, against the body image as an available to consciousness, abstract and partial representation which provides a sense of ownership and is involved in perception. In other words, the body schema is suggested to be a representation of sensorimotor abilities that are used without conscious awareness or perceptual intervention and the body image is a representation of conscious perceptions and beliefs related to one's own body (Gallagher, 2005). Other researchers, however, have suggested that there might be more body representations than just the body schema and the body image, or that there may be different representations within the body schema or image (de Vignemont, 2005; Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler, & Sunderland, 1991). The results of the current study are consistent with the idea of a dissociation between (at least) two body representations, one used for action and one for perceptual judgements.

Our second hypothesis concerned the effect that transfer of the illusion to another body part might have on the magnitude of the illusion. We reasoned that in the indirect condition additional missing sensory information about the movement of the knee and leg causes augmentation of conflicting proprioceptive input. Therefore, we presumed that the magnitude of the illusory displacement would be less for both representations in the indirect compared to the direct condition. This implies, however, that both representations use the same conflicting afferent information, yet transformed it differently to minimize uncertainty about the current spatial configuration of the body. The results of Experiment 1 showed a declined illusory displacement in the indirect compared to the direct condition, confirming our second hypothesis.

This leaves us with a final question; how do the different body representations interpret or weight the conflicting information? On the one hand, we theorized that the body schema weights the signal from the biceps, saying that the forearm has moved, with the information from the joint, skin and other muscles signalling that the forearm has remained stable. The idea of weighting information has already been described in several models (Ernst & Banks, 2002; Ernst & Bulthoff, 2004; van Beers et al., 1999, 2002; Wolpert, 1997; Wolpert et al., 1995). Most of these models are multimodal. In the present experiments, however, the somatosenses are the only source of information about the current state of the body. Nevertheless, many definitions of the body schema also underline the multisensory sources of this representation. For example, Haggard and Wolpert (2005) point out that this representation is spatially coded and thus combines visual and somatosensory information to program an action. Although, this seems to some extent consistent with our theory of weighting conflicting proprioceptive information within the body schema, they generally define the body schema as a conscious representation required for multisensory integration. Recently, Press, Taylor-Clarke, Kennett and Haggard (2004) have showed there is indeed weighting of multisensory information by demonstrating that vision can enhance touch in spatial representations of the body. Additionally, both representations as defined by Gallagher (2005) are multimodal as well. Consequently, the interaction between vision, proprioception and touch is important for both representations. In addition, the results of the current study suggest that the dissociation between the two representations can also be observed within one modality. On the other hand, we reasoned that although the body image receives the same information as the body schema, the knowledge of our body characteristics in the body image will cause increased weighting of the signal of the stimulated biceps tendon. This because our stored experiences tell us stretching of the biceps is normally accompanied by elbow extension. Evidence that cognitive top down control can shape or influence our perception of experienced body configuration comes, for example, from Kitada, Naito and Matsumura (2002). They investigated the effect of motor imagery on illusory wrist flexion angles and found that kinaesthetic motor imagery perceptually changed the illusion in the absence of real movement (Kitada et al., 2002). In other words, knowledge about the body's configuration and movement parameters influenced the magnitude of the kinaesthetic illusion. Moreover, in a recent experiment de Vignemont et al. (2005) hypothesized that judgements concerning tactile distance might be the result of weighting information between the body schema and body image. This implies that not only information within each representation is weighted, but also between both representations, depending on the task characteristics.

In other words, many outstanding questions remain. More research is needed not only in healthy individuals but also in patients to answer the outstanding questions concerning the existence, the number and definitions of multiple body representations, and the mechanisms by which different information is weighted. Nevertheless, based on the present results we may concluded that reaching and matching responses are differentially influenced by the kinaesthetic illusion, which may provide evidence for an underlying body representation guiding action and a body representation underlying perceptual judgements in healthy subjects.

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