Available online at www.sciencedirect.com

Acta Psychologica 121 (2006) 317–330

acta psychologica

www.elsevier.com/locate/actpsy

Shared representations in body perception

Richard Thomas, Clare Press, Patrick Haggard *

Institute of Cognitive Neuroscience, Department of Psychology, UCL (University College London),
17, Queen Square, London WC1N 3AR, UK

Received 1 February 2005; received in revised form 4 August 2005; accepted 5 August 2005

Abstract

The ability to understand events that happen to other people is a characteristic feature of the human mind. Here, we investigate whether the links between mental representation of one's own body and the bodies of other people could form the basis of human social representations. We studied interpersonal body representation (IBR) in a series of behavioural cueing experiments. Subjects responded to tactile events on their own body after a visual event was presented in either the corresponding anatomical location on a model's body, or in a non-corresponding location. We found that reactions were faster when the visual cue was in register with the tactile stimulation. This effect was absent when identical visual events were presented on a non-body control stimulus, suggesting a body specific mechanism for interpersonal registration of purely sensory events. Similar interpersonal systems have been demonstrated previously for the coding of action and emotion, but we believe that our results provide the first behavioural evidence for interpersonal body representation at the purely sensory level. We show that a sensory processing mechanism specific for bodies is automatically activated when viewing another person. Interpersonal body representation may be an important precursor to empathy and theory of mind. In our social world, we understand the percepts of others by registering them against the representations used to perceive our own body, and this mechanism involves an interpersonal somatotopic map.
© 2005 Elsevier B.V. All rights reserved.

---

* Corresponding author. Tel.: +44 20 7679 1153; fax: +44 20 7916 8517.
E-mail addresses: richard.m.thomas@ucl.ac.uk (R. Thomas), p.haggard@ucl.ac.uk (P. Haggard).

doi:10.1016/j.actpsy.2005.08.002

PsycINFO classification: 2300; 2320; 3040

Keywords: Interpersonal; Shared representation; Body representation; Mirror-neurons; Cross-modal; Cueing

---

1. Introduction

The perception of our own body is unique because it occurs from the inside, via touch and proprioception, *and* from the outside, via vision. Cross-modal links integrate these representations to produce the coherent conscious experience of perceptual body events (Haggard, Newman, Blundell, & Allison, 2000; Sathian, Zangaladze, Hoffman, & Grafton, 1997). Moreover, association of visual and tactile information can generalise beyond the representation of our own bodies. For example, when subjects view a rubber hand being stroked while feeling simultaneous stroking of their own unseen hand, they feel the rubber hand becomes part of their own body (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). This finding suggests that the visual–tactile association mechanism important for representing our own bodies might also be used for representing the bodies of other people. For example, I might watch you bang your knee on a table leg, and associate this with a tactile representation of that feeling in my knee if I did the same thing myself. We use the term interpersonal body representation (IBR) to refer to the relation between self and other body events based on such associations.

Sensory IBR could provide an alternative explanation of some results on interpersonal links in action representation. For instance, Reed and Farah (1995) found that subjects were better able to observe changes in the posture of a model's body when they moved the corresponding part of their own body. This finding was specific to the body part being observed (arms or legs), and disappeared when non-biological objects replaced body parts. The authors proposed that subjects processed the actions associated with their own and other people's bodies using a common mechanism. Furthermore, they found an interference effect when subjects moved a different body part to that observed on the model. Reed and Farah argued that the mechanism used to represent self and others' bodies is spatially organised, vertically delineated along upper and lower portions of the body, and is sensitive to the congruence between one's own and others' bodies. Consistent with this, Tessari and Rumiati (2002) found interference between memorised observed manual actions and performing comparable actions. These findings suggest a spatially organised body representation functioning interpersonally. However, the time course and underlying psychological mechanisms were not revealed. Moreover, in contrast to the concept of IBR the focus in these studies was on a body representation, or schema, updated during *action*, rather than a purely sensory mechanism.

Neuropsychological studies have shown that patients with left parietal damage can have difficulty localising body parts (DeRenzi & Scott, 1970; Semenza, 1988). Importantly, these 'autotopagnosic' patients have difficulty locating body parts on bodies other than their own, implying that the same mechanism is used for representing the self and the body of others (Ogden, 1985; Sirigu, Grafman, Bressler, & Sunderland, 1991). In addition, the errors made by patients have revealed the spatially organised nature of body representation. For instance, they are more likely to incorrectly localise a body part to a contiguous location than to an arbitrary location (e.g., pointing to their wrist when asked to locate their elbow) (Semenza & Goodglass, 1985). Moreover, patients also exist with deficits of blurring (Kinsbourne & Warrington, 1962) and supernumerary insertion (Hari et al., 1998) of body parts within the overall body configuration. These patients' lesions are often located in the left parietal cortex, suggesting that this area maintains a spatially organised configuration of the body, or schema.

Other studies have described brain areas that could underlie IBR. For instance, Downing, Jiang, Shuman, and Kanwisher (2001) reported differential fMRI activation in a region of visual cortex they called the 'extrastriate body area' (EBA) when subjects viewed body parts, compared to when they viewed a range of non-biological images. Astafiev, Stanley, Shulman, and Corbetta (2004) showed activity in the EBA when subjects made body movements, both when the body part was viewed and when it was occluded. Keysers et al. (2004) found that secondary somatosensory cortex (SII) was activated both when subjects were touched and when they watched movies of other people being touched. However, they also found SII activity when subjects observed inanimate objects contacting each other, with no body in sight, i.e., common activity in SII was touch-specific but not body-specific.

A network of cortical regions in monkey and human brains provides interpersonal coding for object-oriented *actions*. These 'mirror neurons' are activated both when an animal performs a grasping action, and when it observes a conspecific perform the same action (see Rizzolatti & Craighero, 2004 for a recent review). This mirror system could represent others' sensory body events, and not just their actions (Gallese, 2001). Consistent with this, when subjects view another person being painfully stimulated, they themselves show significant activation of pain-related brain areas (Hutchinson, Davis, Lozano, Tasker, & Dostrovsky, 1999). Singer et al. (2004) found evidence for a common network of activity in the anterior insula and cingulate cortex both when subjects received painful stimuli, and when they observed others experiencing the same pain.

We used a cueing paradigm to investigate links between processing of perceptual events on one's own body or another person's body. Fig. 1 shows the experimental apparatus. The cue was a visual event on the body of another person (the model) shown in the same seated posture as the subject, and directly facing them. Cues were brief flashes of light at one of several locations on the model's body. The target was a tactile stimulus delivered at either the same anatomical location on the subject's body as the preceding visual cue on the model (congruent) or a different location (incongruent). We predicted that the visual cue would activate the corresponding region of the subject's mental map of his or her own body. Thus, tactile perception should be improved, i.e., fewer errors, lower reaction times (RTs), for congruent compared to incongruent trials. Importantly, cue location does not predict target location, thus

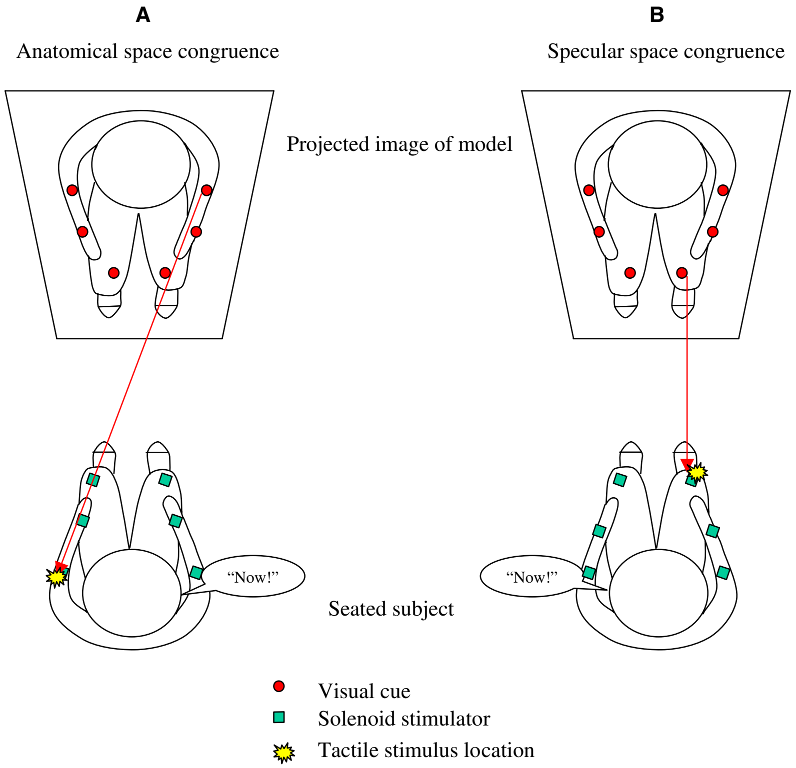

Fig. 1. A schematic of the experimental layout for body conditions in Experiments 1 and 2. Examples of anatomical space (A) and specular space (B) congruence are shown.

any effect will reflect a basic psychological association mechanism, rather than a learned expectation.

Cueing studies have previously examined the effect of viewing body parts on tactile perception. For instance, Tipper (1998) found that when subjects were presented with a tactile stimulus on their occluded hand, tactile detection was facilitated if they viewed a real-time image of the same hand projected on a screen in front of them, compared to viewing a projection of their non-stimulated hand (see also Tipper, 2001). Maravita, Spence, Sergent, and Driver (2002) used a similar experimental design to the present study, but rather than cueing, they were interested in whether visual events interfered with the processing of tactile events. They asked subjects to make tactile location judgments on their hands while viewing visual events near to another person's hands. They found that subjects had improved performance when visual and tactile events were spatially congruent compared to incongruent. Both the Tipper and Maravita studies are analogous to the present study but they differ in important ways. For instance, Tipper's subjects only viewed their own body parts not those of another person (although this condition was included in the Maravita study). Maravita et al. presented visual and tactile events very close together in time

(30 ms) so that the visual event interfered with the tactile event, rather than one cueing another. Visual events were also presented close to the hands but not on them. Furthermore, both studies only presented body parts in isolation. IBR studied here involves viewing the whole body, and differs from previous work in that subjects presumably represent a spatial map of the whole body, thereby creating a more realistic social situation.

2. Experiment 1

Experiment 1 was designed to establish basic cueing effects for body locations. Visual cues on the model's knee, arm, and wrist were followed 200 ms later by a tap from a solenoid (mechanical tapping device) at each corresponding location on the subject. Following previous work that has examined different types of spatial imitation (e.g., Bekkering, Wohlschlager, & Gattis, 2000), we considered spatial congruence in two ways. A cue and target could either be congruent in *anatomical* space, or in *specular* space. The former refers to the cue and target being in the same anatomical location (e.g., the model's left arm and the subject's left arm, see Fig. 1A). The latter refers to the cue and target being in the same specular location (e.g., the model's left knee and the subject's right knee, see Fig. 1B). Here, specular cueing but not anatomical cueing could involve a supramodal representation of space, used for both visual events on the model and tactile events on one's own body.

2.1. Method

2.1.1. Participants

Sixteen paid volunteers (9 female) aged between 18 and 39 years participated (mean age = 27.5 years). In this and the subsequent experiments, subjects were right-handed, and had normal or corrected to normal vision and touch (by self report).

2.1.2. Stimuli

Six digital stimuli were made of a seated adult male model, one for each visual cue location (left arm, right arm, left wrist, right wrist, left knee, right knee). Visual cues were delivered via ultra-bright white light-emitting diodes (LEDs) attached to the model at the six body locations. A fixation cross was applied to each stimulus, located on the model's sternum. Each stimulus was shown for 4 s, the intertrial interval was 500 ms (see Fig. 1 for a schematic of the experimental layout).

Tactile stimulation was delivered via a 2-mm thick metal rod propelled by 12-V solenoids. Six solenoids were attached to the subject's body (right and left knee, wrist, arm). Eye movements were monitored online by the experimenter using a mirror positioned so that the subject's eyes could be viewed throughout each experimental block. To ensure against auditory location cues from the solenoids, subjects listened to white noise (60 db) over headphones during each stimulus. Vocal responses were recorded via a microphone.

2.1.3. Procedure

Each subject performed six blocks of 42 trials. On each trial the seated subject viewed the model in a stimulus file projected on a white wall at a distance of 150 cm, subtending an angle of 4°. Subjects were instructed to look at the fixation cross throughout. This was continually verified by the experimenter using a mirror. Two hundred milliseconds after the cue, the tactile target was delivered via the solenoid (100 ms duration) at one of the six randomised locations on the subject's body. The subjects' task was to make a speeded vocal response ("Now!") when the target was detected. The target was omitted on catch trials (15%). Neutral cue (all six LEDs flash), and no cue trials (subjects view model but no LEDs flash) were also included (10%).

2.2. Results and discussion

Fig. 2 illustrates the mean of median RTs for specular and anatomical spatial congruence. Two within-subjects ANOVA were carried out. No main effect of specular congruence was found [$F(1,15) < 1$]. However, a main effect of anatomical spatial congruence was found, with subjects 14 ms faster when cue and target were in the same anatomical body position (296 ms) compared to when they were not (310 ms) [$F(1,15) = 19.78, p < 0.01$].

These data were also analysed in terms of laterality and verticality. In specular space no main effects were found [$F(1,15) < 1$]. However, in anatomical space a main effect of laterality was found, with subjects 9 ms faster when cue and target stimuli were on the same anatomical side of the body (left or right) (302 ms) compared to the opposite sides of the body (311 ms) [$F(1,15) = 16.11, p < 0.01$]. A small main effect was also found for verticality, with subjects 6 ms faster when cue and target stimuli were in the same vertical position on the body (top or bottom) (307 ms) compared to when they were not (313 ms) [$F(1,15) = 5.89, p < 0.05$].

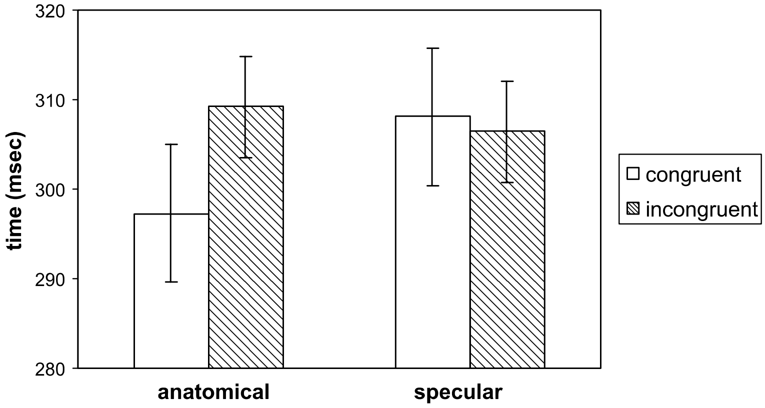

Fig. 2. The congruent and incongruent mean of median RTs for anatomical and specular spatial congruence in Experiment 1, SRT.

These results provide evidence for a visual–tactile association mechanism representing perceptual body events interpersonally. In particular, a reliable effect was found when the visual cue and tactile target were in the same *anatomical* position on the model's and subject's bodies, and not when these were in corresponding specular spatial locations. This finding suggests that the transformation of visual information from the model's body to the corresponding anatomical location on the subject's body occurs in a somatotopic rather than a visual/spatial frame of reference. This frame of reference may reflect a special spatial representation of touch. Consistent with this, in a tactile cueing study, Röder, Spence, and Rösler (2002) found that attention to tactile stimuli on the hand occurred in a somatotopic rather than allocentric frame of reference.

The wrist stimuli in this experiment allowed us to use planned comparisons to assess whether the remapping of visual events from the model's body to corresponding locations on the subject's body used a retinotopic visual or somatotopic/anatomical frame of reference. If IBR occurs in anatomical space, a visual cue on the model's wrist should facilitate RTs to a tactile event on the subject's contralateral arm more than one on their contralateral knee, because wrist and arm are closer in anatomical space than wrist and knee. However, if the transformation were related to retinotopic visual space, then we would expect equivalent RTs because the arm and knee are approximately equidistant from the wrist in the retinotopic projection of a seated model. We used planned comparison pairwise t-tests to compare the conditions. Subjects were fastest for the wrist–wrist combination (285 ms), followed by the wrist–arm combination (301 ms) and the wrist–knee combination (314 ms), and indeed a significant difference was found for the critical comparison between wrist–arm and wrist–knee (13 ms, $t = 2.4$, $p < 0.05$). Hence, we can conclude that the transformation of interpersonal sensory information occurs in anatomical space rather than retinotopic space.

One limitation of the SRT experiment is that it is not possible to determine whether any effect is due to a change in perception or a change in response criterion. Therefore, in the following experiment, we attempted to exclude the possibility of a criterion-shift by using a choice reaction time (CRT) paradigm. We also included non-body stimuli to demonstrate the body-specific nature of the effect.

3. Experiment 2

Experiment 2 was designed to demonstrate body-specificity for IBR. Visual cues on the model's knee and arm were followed 500 ms later by a tap from one of the two solenoids arranged distal-proximally at each corresponding location on the subject. A 2×2 experimental design was used with factors of visual background on which cue flashes were superimposed (model's body or a non-body image of a house) and spatial congruence between cue and target (congruent–incongruent).

It should be noted that all anatomical congruent trials are specular incongruent, and all specular congruent trials are anatomical incongruent. However, anatomical congruence is not simply the inverse of specular congruence. For example, the trial, 'left arm cue-right knee target', is incongruent in anatomical space because cue and target occur on the same side of the external space (specular) rather than the same side of the body (anatomical), but it is also incongruent in the specular space because cue and target occur on different body parts (arm and knee). Hence, of the four targets that could follow each cue, one is anatomically congruent and specularly incongruent (e.g., right arm–right arm), one is specularly congruent and anatomically incongruent (e.g., right arm–left arm), and two are incongruent in both anatomical and specular frame of reference (e.g., right arm–right knee; right arm–left knee). Therefore, using a full factorial design here would have violated the parametric assumption that all observations are independent. Instead, we used two separate ANOVAs to test two separate hypotheses, which we regard as two alternative hypotheses about spatial organisation.

3.1. Method

3.1.1. Participants

Twelve paid volunteers (6 female) aged between 18 and 31 years participated (mean age = 23.9 years).

3.1.2. Stimuli

Eight digital stimuli were created. Four were made of a seated adult male model, one for each visual cue location (left arm, right arm, left leg, right leg). Four were made of a control non-body stimulus (a house). Visual cue locations in the control stimuli were identical to those in the body stimuli. The visual cue was a small digitally applied red coloured circle. A fixation cross was applied to each stimulus, located on the model's sternum and in the corresponding position on the house stimuli. Each stimulus was shown for 4 s, the intertrial interval was 500 ms. Four pairs of solenoids were attached to the subject's body (left arm, right arm, left leg, right leg). Solenoids of each pair were located 50 mm apart in proximal distal direction.

3.1.3. Procedure

Each subject performed eight blocks of 48 trials (four blocks of body stimuli four blocks of house stimuli) in a counterbalanced ABBABAAB design. In each stimulus presentation the visual cue (100 ms flash) occurred at one of the four randomised locations, either 1 or 2 s after the image appeared. Five hundred milliseconds after the cue, a tactile target was delivered via the solenoid (100 ms duration) at one of the pairs of four randomised locations on the subject's body. The subjects' task was to determine which of the pair of solenoids had tapped them by making a speeded vocal response ("Near!" or "Far!") within a 2400 ms response window. Subjects were instructed that taps nearest to their body centre should be given a 'near' response, with those further away in space given 'far' responses.

3.2. Results and discussion

The two definitions of spatial congruence (anatomical and external) were analysed separately. Fig. 3A illustrates the mean of median RTs across subjects for specular

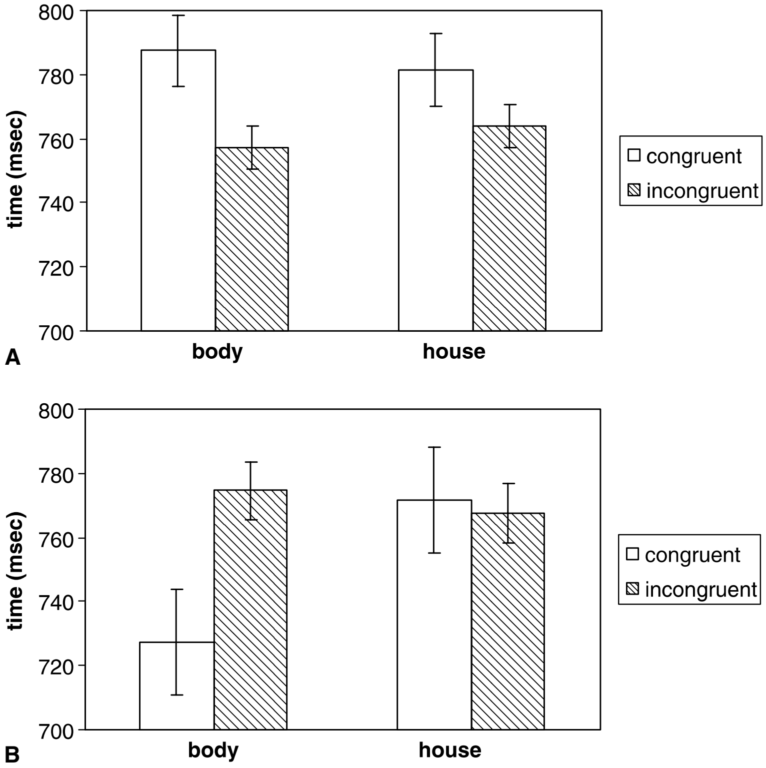

Fig. 3. The mean of median RTs for all conditions across subjects for (A) specular spatial congruence and (B) anatomical spatial congruence in Experiment 2, CRT.

spatial congruence. A within-subjects ANOVA was carried out with two factors (stimulus-type and specular spatial congruence). No main effects or interactions were found [all $F(1,11) < 1$]. For body stimuli, subjects were more likely to make errors when the cue and target were congruent (5.1%) compared to incongruent (4.8%), but this was not a significant pattern ($F(1,11) < 1$). For non-body stimuli, subjects were more likely to make errors for congruent (4.9%) compared to incongruent (4.6%), but again this was not a significant pattern ($F(1,11) < 1$).

Fig. 3B illustrates the mean of median RTs across subjects for anatomical spatial congruence. No main effects were found [all $F(1,11) < 1$], but an interaction was found between stimulus-type and anatomical spatial congruence [$F(1,11) = 4.23$, $p < 0.05$]. Simple main effects were examined for each stimulus type (body and non-body). An effect of anatomical spatial congruence for body stimuli was found, with subjects 47 ms faster when cue and target were anatomically congruent (727 ms) compared to when they were incongruent (775 ms) [$t = 2.2, p < 0.05$]. For cues on non-body stimuli, no main effect of anatomical spatial congruence was found, with subjects 4 ms slower when cue and target were anatomically congruent (772 ms) compared to when they were incongruent (768 ms) [$t = 0.92$, $p > 0.05$]. Hence, the congruency effect for body (+47 ms) was significantly larger than the congruency effect for house (−4 ms).

This critical interaction is illustrated in Fig. 3B. For body stimuli, subjects were more likely to make errors when the cue and target were incongruent (6.1%) compared to congruent (5.1%), but this was not a significant pattern ($F(1,11) < 1$). For non-body stimuli, subjects showed a similar level of errors for incongruent (4.9%) and congruent (4.8%) trials ($F(1,11) < 1$). Therefore, these results confirmed that the IBR effect for anatomical spatial congruence was not due to a speed–accuracy trade-off, i.e., subjects were faster but no less accurate when cue and target stimuli were congruent.

The results from the second experiment provide further evidence for a visual–tactile association mechanism representing the perceptual body events interpersonally.[1] In particular, a significant effect was found when the visual cue and tactile target were in the same *anatomical* position on the model's and subject's bodies, and not when these were in corresponding specular spatial locations. Again, this finding suggests that the transformation of visual information from the model's body to the corresponding anatomical location on the subject's body occurs in a somatotopic rather than a visual/spatial frame of reference. In addition, the congruency effect was only found for bodies and not houses, providing a clear demonstration of the body-specific nature of the cueing effect.

4. General discussion

The aim of this study was to investigate whether a visual–tactile association mechanism important for representing our own bodies might also be used for representing the bodies of other people. Results from each experiment supported this hypothesis. In all experiments, we found a congruency effect for anatomical body position, i.e., subjects were faster at detecting tactile events on their body when a visual event occurred in the same anatomical location on a model's body. Importantly, the effect was shown to be body-specific by comparison with non-body stimuli (houses). There was no evidence for a similar interpersonal representation in specular space. We demonstrated that the congruity benefit in anatomical space was

---

[1] A CRT experiment without non-body stimuli was also carried out with an SOA of 200 ms, in order to assess whether the anatomical congruency effect could be interpreted as a processing *cost* of congruence in specular space, due to the attentional mechanism inhibition of return (IOR). IOR refers to a slowing of RTs to targets that appear at the same side of space compared to those on the opposite side (Posner & Cohen, 1984), and is commonly found for SOAs above approximately 350 ms. IOR is not found at SOAs less than approximately 250 ms. Instead, RTs are *facilitated* to targets that appear at the same versus a different location (Posner, Rafal, Choate, & Vaughan, 1985).

If the anatomical congruency effect of Experiment 2 had merely been due to IOR in specular space, then the effect should be absent at shorter SOAs. This was not the case in Experiment 1 (SRT), and when the SOA was reduced to 200 ms in the CRT experiment here, the anatomical congruency effect was still found: subjects were 24 ms faster when cue and target were in the same anatomical body position (744 ms) compared to when they were not (768 ms) [$F(1,11) = 11.75, p < 0.01$].

not merely due to a congruity cost in specular space reflecting cross-modal IOR, since it occurred at SOAs below the standard IOR level. Therefore, we concluded that the proposed IBR mechanism was a special, automatic mechanism for associating sensory body events.

Interestingly, the effect of anatomical congruence found throughout the present study contrasts with evidence from the developmental literature on imitation. In young children, specular imitation is a more natural behaviour than anatomical imitation (Bekkering et al., 2000; Gleissner, Meltzoff, & Bekkering, 2000), and only later do they learn to transpose the relationship between self and other (Wapner & Cirillo, 1968). However, our cueing task differs from imitation in two crucial ways. First, imitation is an *action* task, requiring the interpersonal translation of observed sensory information into an appropriate motor pattern. In contrast, our task was *sensory*, requiring observation of a non-predictive visual event followed by processing of a tactile event. The organisation of action and sensory tasks may be quite different. Goal-directed actions are represented in external spatial co-ordinates (Craighero, Fadiga, Rizzolatti, & Umilta, 1999), whereas tactile localisation involves a map of the body surface (Rapp, Hendel, & Medina, 2002). In addition, Bekkering and colleagues have recently provided evidence that imitation is goal-directed, rather than a direct visual-to-motor mapping between observed and imitated actions. Here, a motor pattern of imitation will be activated that is most strongly associated with the main goal, with the action used to achieve that goal of secondary importance (Bekkering et al., 2000; Wohlschlager, Gattis, & Bekkering, 2003). In many imitation tasks, the goal is defined by its location in an external space common to both participants, and the participants face each other in confrontation across this space (e.g., Prinz, 2002). This arrangement might favour a specular interpersonal translation rather than an anatomical one.

Interpersonal representations are well established in the domains of action and affect. However, few studies have directly investigated a purely *sensory* mirror system, such as IBR. Such a system would match perceptual events across bodies for sensory stimuli, in the absence of observed or executed motor action. We now consider the similarities between IBR and these other interpersonal matching systems. Mirror neurons in the monkey premotor cortex are active both when the animal performs a grasping action, and when it observes a conspecific performing the same action (Gallese, Fadiga, Fogassi, & Rizzolati, 1996). A similar system may exist in humans (Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Hari et al., 1998). Recent evidence based on the mirror system hypothesis has suggested that the human brain may also match *perceptual* events via a sensory mirror system. Consistent with this, Keysers et al. (2004) showed that secondary somatosensory cortex (SII) was activated both when subjects were touched, and when they watched movies of other people being touched. However, while this study found that the activity was touch-specific, it was not body-specific. That is, SII activity was found both when subjects observed other people being touched and when they observed inanimate objects being touched. Nevertheless, the present results provide the first behavioural evidence to support Keysers et al.'s suggestion of a shared interpersonal tactile representation, originally based on neuroimaging evidence.

Patient studies of emotional responses are moreover consistent with a further *affective* mirror system. Hutchinson et al. (1999) examined whether neurons in the anterior cingulate cortex of locally anaesthetised patients responded to painful stimuli. They were found to respond both when the patient's hand was stimulated, and when the patient watched pinpricks being applied to an experimenter's hand. Furthermore, a patient with subcortical brain injury (to the insula and putamen) was unable to subjectively experience the emotion of disgust, and was also unable to detect disgust in other people (e.g., facial expressions, non-verbal emotional sounds) (Calder, Keane, Manes, Antoun, & Young, 2000). Consistent with this, Wicker et al. (2003) showed that the anterior insula area was activated both when subjects experienced the emotion of disgust and when they observed disgusted facial expressions of other people.

These studies demonstrate that the human mind makes emotional as well as sensorimotor links between people, however, we suggest that purely sensory events linked to a passive body can also be associated interpersonally. Accordingly, evidence for a common network of activity both when subjects received painful stimuli and when they observed others experiencing the same pain has been found (Singer et al., 2004). However, this latter study showed that understanding someone else's pain involved affective (anterior insula and cingulate cortex) but *not* sensory areas (SI, SII, posterior insula) underlying pain. The authors argued that there is a decoupled representation of painful bodily stimuli for the self and other. That is, a representation of the sensory consequence (e.g., location, intensity) may be an important part of the subjective experience of pain, but is decoupled from a representation of the subjective consequence of the stimulus (e.g., how painful or unpleasant it was) for other people. This is in contrast with the evidence presented here where the sensory components are key to the association between self and other. We believe that our results provide the first behavioural evidence in normal subjects for interpersonal body representation based on a somatotopic spatial map, at the purely sensory level. Thus, now there is evidence for interpersonal mirror systems that function at three different levels—motor (e.g., Gallese et al., 1996), emotional (e.g., Singer et al., 2004), and sensory (the present study and Keysers et al., 2004). Future research could usefully investigate the relationship between these systems. They can clearly be dissociated, but are they hierarchically arranged, with one system being more fundamental than the others?

5. Conclusion

We conclude that IBR is an automatic sensory mechanism for visual–tactile association that underlies understanding of others' perceptual states. Both spatial and temporal features distinguish IBR from general spatial attention. This sensory association of events on two different bodies via a single location on an interpersonal body representation may be a basic precursor to empathy and theory of mind. In particular, the spatial specificity of body representation may reflect a first step towards the human ability to track the specific, detailed contents of other minds. In a social environment, we understand the percepts of others by employing the same mechanism used to perceive our own body, and this mechanism involves an interpersonal somatotopic map.

Acknowledgment

This work was supported by Economic and Social Research Council grant R000239946 awarded to P.H.

References

Astafiev, S., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience, 7*, 542–548.

Bekkering, H., Wohlschlager, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experiment Psychology A, 53*, 153–164.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature, 391*, 756.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatopic manner: an fMRI study. *European Journal of Neuroscience, 13*, 400–404.

Calder, A. J., Keane, J., Manes, F., Antoun, N., & Young, A. W. (2000). Impaired recognition and experience of disgust following brain injury. *Nature Neuroscience, 3*, 1077–1078.

Craighero, L., Fadiga, L., Rizzolatti, G., & Umilta, C. (1999). Action for perception: a motor-visual attentional effect. *Journal of Experimental Psychology: Human Perception and Performance, 25*, 1673–1692.

DeRenzi, E., & Scott, G. (1970). Autotopagnosia: fiction or reality? Report of a case. *Archives of Neurology Chicago, 23*, 221–227.

Downing, P. E., Jiang, Y. H., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science, 293*, 2470–2473.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology, 73*, 2608–2611.

Gallese, V. (2001). The 'shared-manifold' hypothesis—from mirror neurons to empathy. *Journal of Consciousness Studies, 8*, 33–50.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolati, G. (1996). Action recognition in the premotor cortex. *Brain, 119*, 593–609.

Gleissner, B., Meltzoff, A. N., & Bekkering, H. (2000). Children's coding of human action: cognitive factors influencing imitation in 3-year-olds. *Developmental Science, 3*, 405–414.

Haggard, P., Newman, C., Blundell, J., & Allison, N. M. (2000). The perceived position of the hand in space. *Perception and Psychophysics, 62*, 363–377.

Hari, R., Forss, N., Avikainen, S., Kirveskari, S., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences USA, 95*, 15061–15065.

Hutchinson, W. D., Davis, K. D., Lozano, A. M., Tasker, R. R., & Dostrovsky, J. O. (1999). Pain-related neurons in the human cingulate cortex. *Nature Neuroscience, 2*, 403–405.

Keysers, C., Wicker, B., Gazzola, V., Anton, J.-L., Fogassi, L., & Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron, 42*, 335–346.

Kinsbourne, M., & Warrington, E. K. (1962). A study of finger agnosia. *Brain, 85*, 47–66.

Maravita, A., Spence, C., Sergent, C., & Driver, J. (2002). Seeing your own touched hands in a mirror modulates cross-modal interactions. *Psychological Science, 13*, 350–355.

Ogden, J. A. (1985). Autotopagnosia: occurrence in a patient without nominal aphasia and with an intact ability to point to parts of animals and objects. *Brain, 108*, 1009–1022.

Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance, X* (pp. 531–556). Hillsdale, NJ: Erlbaum.

Posner, M. I., Rafal, I. D., Choate, L. S., & Vaughan, J. (1985). Inhibition of return: neural basis and function. *Cognitive Neuropsychology, 2*, 211–228.

Prinz, W. (2002). Experimental approaches to imitation. In A. Meltzoff & W. Prinz (Eds.), *The imitative mind: Development, evolution, and brain bases* (pp. 143–162). Cambridge: Cambridge University Press.

Rapp, B., Hendel, S. K., & Medina, J. (2002). Remodeling of somatosensory hand representations following cerebral lesions in humans. *Neuroreport, 13*, 207–211.

Reed, C. L., & Farah, M. J. (1995). The psychological reality of the body schema: a test with normal participants. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 334–343.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169–192.

Röder, B., Spence, C., & Rösler, F. (2002). Assessing the effect of posture change on tactile inhibition-of-return. *Experimental Brain Research, 143*, 453–462.

Sathian, K., Zangaladze, A., Hoffman, J. M., & Grafton, S. T. (1997). Feeling with the mind's eye. *Neuroreport, 8*, 3877–3881.

Semenza, C. (1988). Impairment in localisation of body parts following brain damage. *Cortex, 24*, 443–449.

Semenza, C., & Goodglass, H. (1985). Localisation of body parts in brain injured subjects. *Neuropsychologia, 23*, 161–175.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R., & Frith, C. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science, 303*, 1157–1162.

Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing: evidence from a case of autotopagnosia. *Brain, 114*, 629–642.

Tessari, A., & Rumiati, R. I. (2002). Motor distal component and pragmatic representation of objects. *Cognitive Brain Research, 14*, 218–227.

Tipper, S. P. (1998). Vision influences tactile perception without proprioceptive orienting. *Neuroreport, 9*, 1741–1744.

Tipper, S. P. (2001). Vision influences tactile perception at body sites that cannot be viewed directly. *Experimental Brain Research, 139*, 160–167.

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion re-visited: visuo-tactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance, 31*, 80–91.

Wapner, S., & Cirillo, L. (1968). Imitation of a model's hand movements: age changes in transposition of left-right relations. *Child Development, 39*, 887–894.

Wicker, B., Keysers, C., Pially, J., Royet, J. P., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. *Neuron, 40*, 655–664.

Wohlschlager, A., Gattis, M., & Bekkering, H. (2003). Action generation and action perception in imitation an instance of the ideomotor principle. *Philosophical Transactions of the Royal Society London B, 358*, 501–515.