

RESEARCH ARTICLE

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Hand movement observation by individuals born without hands: phantom limb experience constrains visual limb perception

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Abstract Increasing evidence suggests that the visual analysis of other people's actions depends upon the observer's own body representation or schema. This raises the question of how differences in observers' body structure and schema impact their perception of human movement. We investigated the visual experiences of two persons born without arms, one with and the other without phantom sensations. These participants, plus six normally-limbed control observers, viewed depictions of upper limb movement under conditions of apparent motion. Consistent with previous results (Shiffrar M, Freyd JJ (1990) *Psychol Sci* 1:257), normally-limbed observers perceived rate-dependent paths of apparent human movement. Specifically, biologically impossible motion trajectories were reported at rapid display rates while biologically possible trajectories were reported at slow display rates. The aplasic individual with phantom experiences showed the same perceptual pattern as control participants, while the aplasic individual without phantom sensations did not. These preliminary results suggest that phantom experiences may constrain the visual analysis of the human body. These results further suggest that it may be time to move beyond the question of whether aplasic phantoms exist and instead focus on the question of why some people with limb aplasia experience phantom sensations while others do not. In this light, the current results suggest that somesthetic representations are not sufficient to define body schema. Instead, neural systems matching action observation, action execution and motor imagery likely contribute to the definition of body schema in profound ways. Additional research with aplasic individuals, having and

lacking phantom sensations, is needed to resolve this issue.

Keywords Body schema · Action observation · Limb aplasia · Congenital phantom limbs · Crossmodal processing

Introduction

Studies of phantom limbs after amputation have provided revolutionary insights into the neural plasticity of the human brain (Ramachandran and Hirstein 1998; Halligan 2002 for reviews). These studies have also revealed that the “body in the brain” (Berlucchi and Aglioti 1997) or “body schema” is a highly flexible central representation of the human body. More generally, research with amputees has reminded us that “[w]e stand to learn most from phantoms if we attend closely to patients' subjective reports” (Halligan et al. 1999, p. 587). Indeed, the quantity and quality of cortical reorganization can be critically related to detailed characteristics of an individual's phantom limb experience (Flor et al. 1998; Knecht et al. 1998).

In striking contrast to the rapid pace with which our understanding of the perceptual and neural correlates of limb amputation unfolds stands the near absence of experimental investigations of phantom limb phenomena in persons with limb aplasia. This may be due to the fact that many authors still doubt the very existence of “congenital phantoms” (Skoyles 1990; Flor et al. 1998). Indeed, the implicit assumption that phantom sensations of congenitally absent limbs cannot exist has occasionally resulted in an embarrassing failure to ask aplasic subjects about such sensations (Nico et al. 2004). Nonetheless, in the clinical literature, phantoms of congenitally absent limbs have been documented for well over a century (Valentin 1836; Poeck 1964; Burchard 1965; Grouios 1996). Relevant overview articles indicate that approximately 10% (Boonstra et al. 2000)

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to 20% (Weinstein et al. 1964; Melzack et al. 1997) of individuals born without limbs experience phantoms of their missing limbs. Apart from the high incidence of pain in post-amputation phantoms, which contrasts with a virtual absence of painful congenital phantoms (Melzack et al. 1997), the phenomenologies of the two types of phantoms are comparable. In both cases, postural and movement sensations predominate (Poeck 1969; Melzack et al. 1997) while thermal sensations are rare (Lacroix et al. 1992). Importantly, visual inspection of other peoples' bodies can trigger phantom sensations in amputees (Henderson and Smyth 1948) and people with limb aplasia (Melzack et al. 1997). For example, Melzack and colleagues (1997) reported the case of a 14-year-old boy with a missing right forearm and hand, whose phantom hand percept could be elicited by "playing with his friends and looking at their arms" (p. 1610).

These cross-modal interactions between the visual observation of other people's bodies and the observer's own body schema form the topic of the present report. Some authors (see especially Melzack 1990) have taken the very existence of phantom sensations of limbs that have never physically developed as unshakable evidence for innate components of body schema. The ultimate utility of such conclusions may depend upon how one defines the term "body schema". Growing evidence from behavioral (Reed and Farah 1995; Sebanz et al. 2003) and neuroimaging (Grèzes and Decety 2001) studies suggests that representations of one's own bodily actions share a common neural substrate with visual representations of the actions performed by other people. Such findings suggest that the "body schema" may be best understood as a multimodal representation of one's own body that contains input from somatosensory, proprioceptive, and vestibular systems as well as *visual information about human body dynamics*.

Here we investigate the perceptual, specifically visual, experiences of two people with bilateral congenital absence of arms during the presentation of other peoples' upper limb movements. The rareness of bilateral arm aplasia, especially when accompanied with phantom sensations, precluded investigation of a larger group of subjects. We used a paradigm introduced by Shiffrar and Freyd (1990) in which observers watch pairs of photographs depicting a human model performing simple actions. The two photographs differ only in the position of one limb segment relative to a joint, and their rapid alternation gives rise to an apparent motion percept. As long as the two photographs are flashed in rapid succession, normal observers invariably perceive the displaced limb traversing the shortest possible path of visual apparent motion. Execution of a limb movement along this seen trajectory is, however, not anatomically possible, as it would violate natural joint constraints. However, as the presentation rate slows, observers increasingly perceive paths of apparent limb movement that follow natural human limb trajectories (Shiffrar and

Freyd 1990, 1993). Apparently, stored kinesthetic knowledge about possible movements constrains the visual perception of human movement provided ample processing time is provided for cross-modal sensorimotor–visual interaction. In line with this interpretation, neuroimaging data have revealed motor and parietal cortex involvement at slow, but not rapid, presentation rates (Stevens et al. 2000). This psychophysical paradigm seemed ideally suited to quantitatively investigating interactions between phantom limb *sensation* and limb movement *observation*.

Two persons with limb aplasia were tested. While both are highly comparable in physical appearance and intelligence, they differ crucially in their experiences of their missing limbs. One participant reports vivid phantom sensations of missing arms and hands (Brugger et al. 2000), while the other has never experienced any phantom sensations whatsoever. If the experience of phantom limbs by individuals born without those limbs reflects visually-based modifications of the body schema, and if visual perception of other people's actions depends upon the observer's own body schema, then one would expect to find that the two participants in the current study differ in their visual perceptions of other people's actions. Specifically, one would predict that the individual who experiences phantoms of congenitally-missing arms would exhibit normal, rate-dependent percepts of apparent arm movement, while the individual who does not experience arm phantoms would not.

Materials and methods

Participants

Participant one, AZ, is a 46-year-old woman born without legs and with two short upper arms without elbow joints. Since her early youth, AZ has experienced phantom sensations of her missing body parts that include both voluntary and involuntary movements of her phantom arms. Her phantom reflex movements occasionally follow anatomically impossible trajectories. These occur, for instance, when reaching for a handrail in a tramcar that abruptly stops. In this case, her phantom hand is experienced "at the place of action", that is, where her upper arm stump actually touches the handrail. Intentionally induced hand and arm movements are always experienced as part of the anatomically possible repertoire of intact upper limbs. In a previous study, voluntary movement of AZ's phantom fingers activated premotor and parietal cortex, with the greatest activation in the contralateral hemisphere (Brugger et al. 2000). As for interactions between feeling and seeing a limb, we note that it has occurred to AZ that contemplation of her mirror image abolishes her phantom sensations. AZ's vision is normal. She holds a university degree and works as a consultant for handicapped individuals. The etiology of her limb deficiencies is unknown.

Participant two, CL, is a 43-year-old man born with shortened legs and absent arms (no shoulder articulations). In daily life, he uses his right foot for writing, eating, pointing, and gesturing. CL has not suffered any visual or cognitive impairments in the course of the thalidomide-related embryopathy. The skilful use of his right foot enabled him to have a successful career as a journalist. Importantly, CL has never experienced any phantom sensations of his missing limbs.

We also tested six normally-limbed control observers (“intact observers”) who were carefully matched by age and education to AZ and CL, respectively. All eight subjects gave written informed consent to participate in the experiment, which was performed in accordance with the Declaration of Helsinki.

Stimuli and procedure

The stimulus set was similar to that used by Shiffrar and Freyd (1990). Six stimulus pairs, each consisting of two black and white photographs, were used. The picture pairs depicted the start and end positions of the following arm and hand actions: (1) a man rotating his right hand about his wrist (Fig. 1A); (2) the same for a woman’s left hand; (3) the front view of a man rotating his left forearm about his elbow such that his hand is seen at the 11-o’clock and 8-o’clock positions; (4) the same for a woman’s right forearm; (5) the side view of a man rotating his left arm backwards about his shoulder

with the hands shown at the 2-o’clock and 4-o’clock positions, and; (6) the same for a woman’s right arm.

Stimuli were presented in the center of a computer screen (software *MacProbe*; Hunt 1994) and subtended approximately 15° of visual angle both horizontally and vertically from the participants’ viewing position. On each trial, the two photographs of each stimulus pair were presented for 90 ms each and separated by one of four inter-stimulus intervals (ISIs): 135, 435, 735, and 1,035 ms. These ISIs were selected because they yielded the most consistent apparent motion percepts in pilot studies with healthy volunteers. Each stimulus pair was presented four times, once with each ISI. For each participant, the sequences of stimulus pairs and ISIs were pseudo-randomized across trials. Each trial consisted of 12 cycles of alternation between the two photographs. Immediately following each trial, the participants indicated their perceived path of apparent motion on a response sheet (Fig. 1B). As in Shiffrar and Freyd (1990, 1993), two possible paths of apparent motion were depicted on the response sheet. The short, physically impossible path was always labeled “A”. The longer, physically possible path was labeled “B”. Although two additional response options included the possibility of seeing “both A and B” paths and “neither A nor B” paths, participants were encouraged to primarily decide between options A and B.

Results

For each of the eight volunteers, the percentages of trials during which they reported perceiving the short, impossible “A” path of apparent motion and the long, possible “B” path of apparent motion were determined at each ISI. The proportion of short to long paths is displayed in Fig. 2. The six intact observers perceived the short, anatomically impossible paths of apparent limb motion at the 135 and 435 ms ISIs. Conversely, at the longer 735 and 1,035 ms ISIs, these same participants were more likely to perceive the longer, anatomically possible paths of apparent limb rotation. Consistent with previous results (Shiffrar and Freyd 1990), all six intact observers produced this same pattern of apparent motion perceptions. We calculated the slope of the linear regression line for each of these subjects. The boundaries of the respective 95% confidence interval were -0.219 and -0.132 .

The two participants with limb aplasia, however, reported divergent patterns of apparent motion perception. AZ’s perceived paths of apparent motion depended upon ISI in the same manner as path perception depended upon ISI for intact observers. AZ perceived the short, anatomically impossible paths of apparent limb motion at the 135 ms ISI and longer, anatomically possible paths at 1,035 ISI. At the 735 ISI AZ favored neither the anatomically possible nor the anatomically impossible path. The slope of her linear regression was

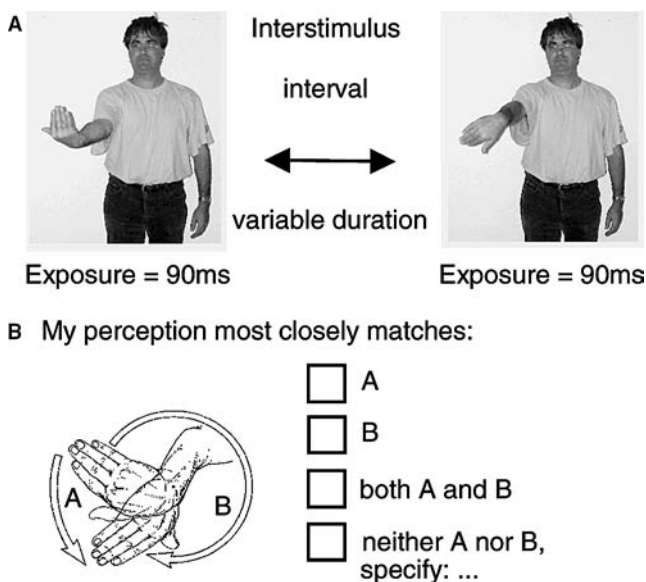
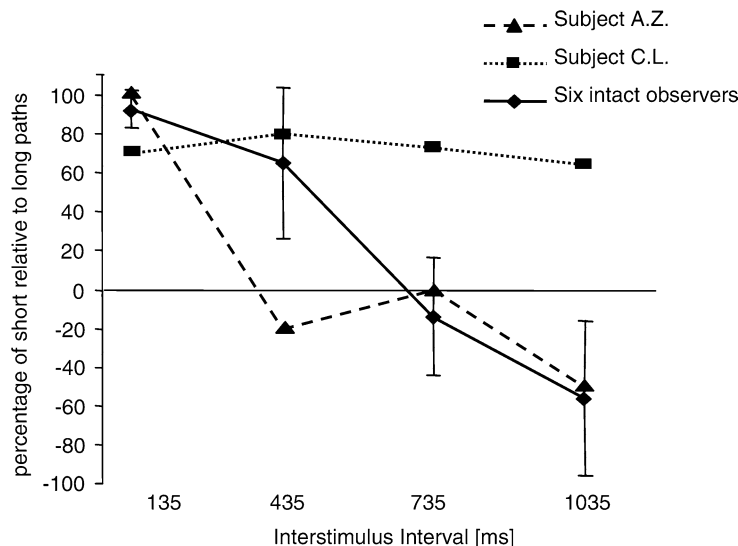


Fig. 1 **A** A sample stimulus pair that normally produces an apparent rotation of the hand rotating about the wrist at long ISIs. The *arrow* indicates that the two photographs in each pair were sequentially flashed in rapid alternation (12 cycles with an inter-stimulus interval of 135, 435, 735, or 1,035 ms). **B** Response sheet (for the sample stimulus displayed in **A**) on which observers indicated, after each trial, what option best described their percept on that trial

Fig. 2 Difference between percentage of short (A in Fig. 1B) and long (B in Fig. 1B) paths of apparent motion plotted as a function of interstimulus interval. Data are averaged over the six different stimulus pairs. *Solid line* shows data from six intact observers (mean \pm 95% confidence intervals)



-0.143 and thus lies within the intact observers' confidence interval.

Conversely, CL consistently perceived the short, anatomically impossible paths of apparent arm/hand rotation at all ISIs. The slope of his linear regression was -0.008 and thus outside the confidence interval of intact observers.

We further calculated, for each ISI, the intact observers' 95% confidence interval for the mean proportion of short to long path percepts. AZ's data lie within the boundaries formed by these control participants' responses, except at the ISI of 435 ms. In contrast, CL's data lie outside these boundaries, except at the ISI of 435 ms (Fig. 2).

The percentages of "A and B" and "Neither A nor B" responses across all ISIs were 13.5% (SD = 8.7%) for the controls and 16.7 and 12.5% for participants AZ and CL, respectively.

Discussion

Six intact observers showed the kinesthetically modulated perceptions of apparent limb motion first described in Shiffrar and Freyd (1990). While rapid display rates, or short ISIs, triggered the visual perception of short, anatomically impossible trajectories, longer ISIs allowed stored knowledge about natural joint mechanics to constrain perceived paths of apparent limb motion. This implicit biasing of what is seen by what is possible, given the biomechanical limitations of the human body, was also observed for AZ, but not for CL.

On first consideration, the current results may appear surprising since AZ was born without hands and forearms and therefore has never executed any movements with these body parts. Since her early youth, however, she has experienced vivid phantom sensations of all missing body parts, including individual fingers. Importantly, while AZ does not report the experience of pain or temperature in her phantoms, she does report

highly vivid postural and movement sensations in them (Brugger et al. 2000). Our previous quantification of AZ's phantom movement sensations also involved a limb laterality task based on Parsons (1994). In this task, observers report whether a visually depicted hand or foot comes from the right or left side of the body. Intact observers showed longer reaction times whenever stimuli differed by larger physical rotations from their own corresponding body parts. AZ's data showed the same pattern; namely, longer reaction times for stimuli requiring a 180° rotation of her phantoms. These findings, together with those of the present experiment, strongly suggest that years of phantom movement experience may impose similar constraints on the visual analysis of human body stimuli as do years of sensorimotor experience with physically intact limbs. In addition, the current results indicate that, just like observers with intact bodies, AZ's visual processing is influenced by kinesthetic body schema information.

The causality underlying this potential crossmodal interaction between phantom limb sensation and the visual analysis of body motion is unclear. One could argue that AZ's visual perception of human movement is constrained by innate information about kinesthetic properties of the human body (Melzack 1990; Melzack et al. 1997). Alternatively, the proprioceptive or kinesthetic components of the body schema per se need not be innate. It is conceivable that somatic phantom sensations in people with congenital limb aplasia arise from activations of a system matching action observation and action execution (Grèzes and Decety 2001; Rizzolatti et al. 2001; Stevens et al. 2000). Anecdotal clinical observation (Melzack et al. 1997) is in fact compatible with the view that limb movement observation may be a prerequisite for the development of limb movement sensations. On the other hand, long-term limb observation alone cannot dictate the presence or absence of phantom sensations. If it did, then all sighted persons with limb aplasia would report such sensations. Thus, what remains to be understood is why only a minority of

people with limb aplasia experience congenital phantoms.

The finding that CL's visual perception of apparent limb movements is timing-independent emphasizes the importance of each individual's history of phantom sensations (recall that CL has never experienced phantoms of his congenitally absent limbs). Interestingly, CL's timing-independent perception of apparent limb rotations in the current task concurs with his absence of a regular reaction time pattern in limb laterality tasks (Funk 2001). However, these results do not help us to identify the factors that determine whether or not a person with limb aplasia will develop congenital phantoms. We are currently studying the functional neuroanatomy of AZ's and CL's action observation systems to find out whether the neural circuits known to be involved in normally-limbed individuals (Buccino et al. 2001) are differently engaged in aplasic persons. It is conceivable that limb observation triggers limb sensation only in those aplasic persons whose neural circuitry allows for a rich integration of motor representations and their visual counterparts. Recent work on premotor cortex contributions to feelings of ownership for a visually observed limb may be relevant here (Ehrsson et al. 2004).

In summary, our preliminary data show that phantom sensations of congenitally absent limbs can influence the visual perception of other peoples' bodies in much the same way as does a lifelong use of physically developed limbs. These results should be corroborated in a larger sample of persons with limb aplasia, and leave several pressing questions to be addressed. First, are the performance differences described in the present study reflected in activation differences, primarily of the motor and parietal cortex, during limb movement observation (Stevens et al. 2000)? Second, is the presence/absence of intact biological motion processing accompanied by *structural* changes in areas of the motor cortex? Such changes have been reported in some (Gowers 1879; Stoeckel et al. 2005), but not other (Hamzei et al. 2001) individuals with congenital limb deficiencies. Lastly, how does the congenital absence of a *single arm* constrain participants' perceptions of hand movement? This question is interesting independent of participants' histories of phantom sensations (see Funk and Brugger 2002; Nico et al. 2004), and is especially important with respect to traditional theories concerning the origins of congenital phantoms (Valentin 1836; Burchard 1965; Grouios 1996). These theories suggest that, in unilateral amelia, phantom sensations of a missing arm could arise from sensorimotor representations of its existing counterpart.

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