



Experience with an amputee modulates one's own sensorimotor response during action observation

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ABSTRACT

Observing actions performed by others engages one's own sensorimotor regions, typically with greater activity for actions within one's own motor abilities or for which one has prior experience. However, it is unclear how experience modulates the neural response during the observation of impossible actions, beyond one's own abilities. Using fMRI, we scanned typically-developed participants as they observed actions performed by a novel biological effector (the residual limb of a woman born without arms) and a familiar biological effector (a hand). Participants initially demonstrated greater activity in the bilateral inferior and superior parietal cortices when observing actions made by the residual limb compared to the hand, with more empathic participants activating the right inferior parietal lobule, corresponding to the posterior component of the action observation network, more strongly. Activity in the parietal regions may indicate matching the kinematics of a novel effector to one's own existing sensorimotor system, a process that may be more active in more empathic individuals. Participants then received extended visual exposure to each effector, after which they showed little difference between activation in response to residual limb compared to hand actions, only in the right superior parietal lobule. This suggests that visual experience may attenuate the difference between how residual limb and hand actions are represented using one's own body representations, allowing us to flexibly map physically different others onto our own body representations.

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Introduction

When observing actions performed by another person, regions of one's own sensorimotor system become active, engaging specific cortical motor representations that correspond to the observed body parts (Buccino et al., 2001; Fadiga et al., 1995). This 'motor resonance' between observed actions and one's own motor representation occurs in a network of regions in the inferior frontal gyrus, ventral premotor cortex and inferior parietal lobule collectively referred to as the action observation network (AON; Caspers et al., 2010; Rizzolatti and Craighero, 2004). This network in humans may be related to mirror neurons, which were discovered in macaque monkeys as neurons that fired both when the monkey performed and observed actions (Gallese et al., 1996; Rizzolatti et al., 1996). Evidence suggests that our own motor experiences affect how we activate this network, with increased

activity when observing individuals more similar to ourselves (Buccino et al., 2004; Molnar-Szakacs et al., 2007) or actions with which we are more familiar (Calvo-Merino et al., 2005; Cross et al., 2006). Thus, we may utilize our own motor representations to help understand other's actions (Keysers and Gazzola, 2007). How then do we understand actions made with a body that differs from our own?

Recent studies demonstrate that we may also engage motor regions when observing actions beyond our own abilities (Aziz-Zadeh et al., 2011; Liew et al., 2011). However, these studies used actions or effectors that were visually familiar to the observer, and prior studies have shown that visual experience, even without motor practice, can still allow one to incorporate novel actions into one's own motor repertoire. For instance, individuals demonstrate increased sensorimotor activity when observing actions they have either performed or seen before (Cross et al., 2009). Even motor imagery training of phantom limbs in amputees led to changes in perceived ownership and kinematic qualities of the phantom limb, suggesting that even imagined training of a non-existent limb can affect sensorimotor representations for that limb (Moseley and Brugger, 2009). However, what remains to be explored is how we process actions made by individuals with novel body parts that we do not have and have not seen or imagined before, and the role of experience in modulating these responses. These questions hold important implications not only for the scientific community

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but also for our increasingly diverse society. In 2007, over 1.7 million individuals in the United States alone had limb differences such as amputations (Center, 2011), and many more have other uncommon physical differences. Such individuals cite perceived social stigma as a major barrier to participating in their communities, affecting their quality of life (Frank, 2000; Murray, 2009). Given that the average typically developed individual has limited exposure to individuals with physical differences, can experience change how we represent bodies unlike our own?

To answer these questions, we used functional magnetic resonance imaging (fMRI) to scan participants who had no prior experience interacting with or observing with individuals with amputations (Novices) as they observed a woman with bilateral above-elbow arm amputations perform actions with her residual upper limb, which extend several inches past her shoulder, and a typically developed woman perform the same actions with her hand as a control. During the scanning session, individuals passively observed actions made by both effectors, then received extended visual exposure to each, and then were re-scanned during action observation. We hypothesized that after visual exposure to the novel effector (e.g., residual limb), individuals would demonstrate activation in the same regions they engaged when observing a familiar effector (e.g., hand), resulting in no difference between residual limb and hand actions in the post-experience scan.

Materials and methods

Participants

Nineteen healthy, typically-developed participants (9 females, 10 males; mean \pm SD = 24.8 \pm 4.8 years) who had minimal to no prior experience with individuals with amputations as assessed by a self-report questionnaire were recruited for this study. In specific, participants were asked to state how much contact they have had with individuals with amputations, if any, and to specify the amount (daily, weekly, monthly, yearly or less) and type of contact (friend, family member, acquaintance, or other). Individuals who had less than yearly contact with an acquaintance or stranger were included in the study. Due to technical difficulties, data from three novice participants was incomplete and excluded from the study, resulting in 16 novice participants total. Amount of experience for all participants was briefly quantified during the initial screening and further elaborated upon with an extensive behavioral questionnaire after the fMRI scanning procedure. Detailed questions were not asked prior to the fMRI experiment to avoid biasing participants to the goal of the study. All participants were right-handed, had normal or corrected-to-normal vision, and were safe for fMRI. Written informed consent was obtained from all participants before inclusion in the study. This study was approved by the University of Southern California Institutional Review Board and was performed in accordance with the 1964 Declaration of Helsinki.

Stimuli

Action observation runs

Stimuli consisted of 2-second video clips of goal-oriented, goal-matched actions performed by an individual with physical differences using her upper residual limb and typically developed women using their hands (see Fig. 1 for the experimental scanning paradigm and action observation example run). Hand action observation (HAO) and residual limb action observation (RLAO) clips both contained the same set of actions (e.g., flip book page, squeeze binder clip, press down book crease, flick rubber ball), performed by the right hand or right residual limb respectively. These actions were chosen because they were goal-oriented and possible for both the actress with hands and the actress with residual limbs to perform using only one effector. Control stimuli consisted of still images of the hand (hand still; HS) or upper residual limb (residual limb still; RLS) and were also presented for 2 s.

Catch trials consisted of a red frame outlining an image of a hand, presented for 2 s, indicating that participants should press the button boxes they were given. Participants were informed that the button-press stimuli were to ensure they paid careful attention to the stimuli throughout each run. A fixation cross was presented during rest trials with a randomly varied duration between 2 and 8 s.

Visual exposure runs

To provide participants with increased visual exposure to both hand and residual limb actions, visual exposure stimuli consisted of 16-second blocks of short 4-second video clips of different actions of each effector, cropped to provide more of the body and context for each of the actions. Hand visual exposure observations included actions such as a hand and arm twisting off a bottle cap and threading a needle through a piece of fabric, while residual limb visual exposure actions included using the residual limb to push objects and using the residual limb plus mouth to manipulate a pencil. These videos were intended to provide subjects with visual experience of each effector in a more natural, realistic setting and to provide the most context for the unique kinematics of each effector. Thus, actions during this run differed slightly between typically developed and congenital amputee actresses in order to highlight the kinematic range of each effector. fMRI data was collected during this run but excluded from the current analysis as it falls beyond the scope of the current investigation.

AON localizer run

In order to identify neural regions that were active both during action observation and during action execution, participants performed one AON localizer run at the end of the scanning session. This entailed observing 3-second videos of hands picking up objects (e.g., keys, a mug), still images of a hand next to an object, rest trials with a fixation cross, and action execution trials. Action execution trials were cued by a red box flashing briefly for 500 ms before a static image of a hand was presented for the remaining 2500 ms. This cued participants to perform a basic hand action (see below) for the duration of the clip.

Task design and procedure

Participants were provided short training runs outside of the scanner, prior to the scanning session (for a complete schematic of the experimental paradigm, see Fig. S1). For action observation runs, participants were asked to watch the actions performed on the screen and pay attention to the movements and actions that they saw. They were further informed that at the end of each run, they might be asked "What was the last action you saw?" During the action observation training, they were shown 4 clips each of hand actions and residual limb actions to familiarize them with the format of stimulus presentation and the effectors they would be seeing in the scanner, and to train them to respond to the catch trials. An additional motive of these clips was to lessen any initial emotional or attentional effects the unfamiliar effector may evoke. Action observation runs consisted of 16 trials of each condition, plus a randomly varied rest period between 2 and 8 s. The trial order of the design was then optimized using a genetic algorithm (Wager and Nichols, 2003). The total run time was 5 min and 36 seconds (168 TRs), for each of 4 runs. For the analyses, the first two action observation runs (PRE) and the second two action observation runs (POST) were averaged for a total of 32 trials per condition in each analysis.

After two action observation runs (PRE), there was a visual exposure run, during which participants observed longer video clips (16 s each) consisting of several actions, followed by longer rest trials with a fixation cross (12 s). Following this run, participants observed another two action observation runs (POST).

For the AON localizer run, participants were asked to watch the actions performed on the screen and pay attention to the movements

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