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WHAT'S LEFT OF THE MIRROR ILLUSION WHEN THE MIRROR CAN NO LONGER BE SEEN? BILATERAL INTEGRATION OF PROPRIOCEPTIVE AFFERENTS!

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Abstract—Recent data suggest that manipulating the muscle afferents of one arm affects both ipsilateral and contralateral perceptual estimates. Here, we used the mirror paradigm to study the bimanual integration of kinesthetic muscle afferents. The reflection of a moving hand in a mirror positioned in the sagittal plane creates an illusion of symmetrical bimanual movement. Although vision clearly has a role in kinesthesia, its role in the mirror illusion might have been overestimated. Conversely, the role of bimanual integration of muscle afferents might have been underestimated. We hypothesized that muscle-proprioceptive afferents of the passively displaced arm (the image of which was reflected in the mirror) are involved in this illusion. We evoked in 19 healthy adult participants the mirror illusion by displacing passively their left arm, the image of which was reflected in the mirror. Once participants experienced the illusion that their hidden right arm was moving, we then either occluded their view of the mirror (using occlusive glasses) and/or prevent the passive left arm displacement. Participants' illusion characteristics (duration and kinematic) under these conditions were compared with classical mirror illusion (without visual occlusion). We found that as long as the arm was still moving, the kinesthetic illusion decayed slowly after visual occlusion. These findings suggest that the mirror illusion results from the combination of visuo-proprioceptive signals from the two arms and is not purely visual in origin. Our findings also support the more general concept whereby proprioceptive afferents are integrated bilaterally for the purpose of kinesthesia during bimanual tasks.

Key words: mirror paradigm, proprioception, sensory integration, kinesthesia.

INTRODUCTION

Perception of body movement (also referred to as kinesthesia) is based on several types of sensory feedback. The feedback may originate from muscle spindles (Matthews, 1972; Roll and Vedel, 1982) and cutaneous receptors (Grill and Hallett, 1995; Breugnot et al., 2006; Blanchard et al., 2011) but can also be conveyed by the visual system (Tardy-Gervet et al., 1984; Blanchard et al., 2013; Kaneko et al., 2015; Chancel et al., 2016a). The muscle spindles (containing stretch receptors that indicate changes in muscle length) seem to be particularly important for kinesthesia (Teasdale et al., 1993; Day and Cole, 2002; for a review, see Proske and Gandevia, 2012). Interestingly, several studies have shown that perceptual estimates of a limb position and/or movement are altered by manipulating the muscle afferents from the contralateral limb. For example, Izumizaki et al. (2010) and Hakuta et al. (2014) used tendon vibration to stimulate muscle afferents of either the flexor or extensor muscles of one arm, causing changes in the perceived position of the contralateral arm. These results therefore argue in favor of the bilateral integration of muscle afferents in the kinesthetic perception of a given limb.

In humans, bimanual sensory integration probably stems from the high frequency of bimanual movements performed in daily life. During bimanual activity, the central nervous system (CNS) has to simultaneously represent (and thus control) the positions and movements of both arms, and must make them interact for appropriate bimanual motor execution. On that purpose, it sounds appropriate for the CNS to take advantage of such bimanual integration. Accordingly, Brun et al. (2015) and Brun and Guerraz (2015) showed that manipulating muscle proprioception of one arm can significantly modulate the kinematics of the involuntary movement of the contralateral arm. In these experiments, participants were required to perform a strong, steady, isometric muscle contraction for several seconds with their right arm. Soon after this continuous contraction stopped, an involuntary movement (often referred to as the Kohnstamm phenomenon) occurred as a post-effect due to an involuntary sustained activity in the previously contracted muscle (Salmon, 1914; Kohnstamm, 1915; Craske and Craske, 1985; Ghafouri et al., 1998; Ivanenko et al., 2005; Duclos et al., 2007; Parkinson et al., 2009; Ghosh et al., 2014). In fact, Brun et al.

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(2015) and Brun and Guerraz (2015) showed that the velocity of this post-contraction involuntary movement is correlated with the movement velocity of the other arm (when passively imposed by a motorized manipulandum). Moreover, this velocity matching between the two arms disappears when the muscle-proprioceptive inputs arising from the passively displaced arm are masked by the co-vibration of the antagonist biceps and triceps muscles (Brun and Guerraz, 2015). The latter authors concluded that this interlimb coupling was predominantly regulated by muscle proprioceptive afferents.

However, bimanual integration of muscle afferents has received little attention to date, even though it is probably active in many experimental paradigms that seek to determine the sensory contributions to kinesthesia. The mirror paradigm is one such setting. It has been shown that the reflection of a moving hand in a mirror positioned in the sagittal plane can produce the illusion of symmetrical bimanual movement (Holmes et al., 2004; Dohle et al., 2008; Ramachandran and Altschuler, 2009; Guerraz et al., 2012; Metral et al., 2015). Classically, the mirror illusion is thought to be of visual origin. Furthermore, the mirror illusion is widely used in the clinic for motor rehabilitation and pain treatment in amputees. Although vision clearly has a role in kinesthesia (Tardy-Gervet et al., 1984; Blanchard et al., 2013; Kilteni et al., 2015), its role in the kinesthetic mirror illusion might well have been overestimated. Conversely, the role of bimanual integration of muscle afferents might have been underestimated. In line with this hypothesis, Chancel et al. (2016b) showed that the velocity of the kinesthetic mirror illusion (i.e. the perceived velocity of the movement illusion of the other arm) is slowed down when a proprioceptive mask is applied to the passively displaced arm (the image of which was reflected in the mirror). These observations suggest that the mirror illusion results from the integration of congruent signals (i.e. both proprioceptive signals from the contralateral moving arm and visual signals from the moving arm's reflection in the mirror) and thus is not purely visual in origin (Chancel et al., 2016b). The primary objective of the present study was to further investigate the involvement of the contralateral muscle proprioception in the mirror illusion. To test this hypothesis, we evoked the mirror illusion and then occluded the view of the passively displaced arm and/or prevent the passive displacement. Participants' illusion characteristics (duration and kinematic) under these conditions were compared with classical mirror illusion (without visual occlusion). We hypothesized that if bimanual proprioceptive signals were indeed involved in the kinesthetic mirror illusion, the latter might carry on despite visual occlusion.

EXPERIMENTAL PROCEDURES

Participants

As reported in previous studies (Guerraz et al., 2012; Metral et al., 2015; Chancel et al., 2016a,b), some individuals do not experience the mirror illusion and so we screened the participants in a preliminary test. Twenty-two healthy, right-handed adult participants took part in this preliminary test (18 females and 4 males; mean ± SD age: 21.1 ± 2.1 years). Nineteen of them experienced the mirror illusion, and were therefore included in the experiment. None of the participants had a history of visual, proprioceptive or neuromuscular disorders. All the participants provided their written, informed consent prior to initiation of the experiment. The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and was approved by the local ethics review board (University Savoie Mont Blanc, Chambéry, France).

Material

Participants wore visual occlusion spectacles (PLATO – Portable Liquid Crystal Apparatus for Tachistoscopic Occlusion, Translucent Technologies, Inc., Toronto, Canada) that allowed the experimenter to accurately control the timing of vision availability. The spectacles' lenses incorporate liquid crystal cells that can change rapidly (in around 3 ms) from a transparent state ("shutter open") to a translucent, light-scattering state ("shutter closed") that prevents the subject from perceiving visual information. In the "shutter closed" state, the subject's eye nevertheless remains illuminated. Specific software (PLATO Driving Circuit, Translucent Technologies, Inc.) enables the lens for each eye to be controlled independently. The left lens remained closed throughout the present experiment. The right lens was opened or closed, depending on the experimental conditions (Fig. 1).

The participant sat in front of a large, custom-built box. A mirror measuring 65 × 65 cm was positioned vertically in the middle of the box, with the reflective surface facing the participant's left arm and oriented parallel to his/her midsagittal axis. The participant's forearms were positioned on each side of the mirror and were supported by two manipulanda. The distances between the manipulanda and the mirror were adjusted so that the mirror image of the left arm coincided with the position of the right arm. Each manipulandum consisted of a wooden arm (on which the participant positioned his/her forearm) and a handgrip at the end of the wooden arm. The right manipulandum was fixed, whereas the left manipulandum was fitted with a low-noise synchronous DC motor (220V, Crouzet Automatismes SAS, Valence, France) and could flex or extend (via a remote control) the participant's left forearm from the initial starting position (Fig. 1). The manipulandum's angular speed was 3.8 °/s. The participant's left forearm was adjusted on the manipulandum so that the motorized device's axis of rotation coincided with the elbow joint.

The displacements of the left manipulandum were recorded with an electromagnetic motion capture system (Fastrak™, Polhemus, Colchester, VT, USA). A sensor was positioned on the device, so as to continuously record the manipulandum (sampling frequency: 40 Hz).