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# Motor coordination uses external spatial coordinates independent of developmental vision

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## ABSTRACT

The constraints that guide bimanual movement coordination are informative about the processing principles underlying movement planning in humans. For example, symmetry relative to the body midline benefits finger and hand movements independent of hand posture. This symmetry constraint has been interpreted to indicate that movement coordination is guided by a perceptual code. Although it has been assumed implicitly that the perceptual system at the heart of this constraint is vision, this relationship has not been tested. Here, congenitally blind and sighted participants made symmetrical and non-symmetrical (that is, parallel) bimanual tapping and finger oscillation movements. For both groups, symmetrical movements were executed more correctly than parallel movements, independent of anatomical constraints like finger homology and hand posture. For the blind, the reliance on external spatial factors in movement coordination stands in stark contrast to their use of an anatomical reference frame in perceptual processing. Thus, the externally coded symmetry constraint evident in bimanual coordination can develop in the absence of the visual system, suggesting that the visual system is not critical for the establishment of an external-spatial reference frame in movement coordination.

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## 1. Introduction

To guide actions in the world, the brain faces a difficult challenge: sensory information about objects must be translated into appropriate muscle contractions that bring the effector towards them. However, the spatial coordinate systems inherent in the different senses – for example, an eye-centered reference frame for visual information falling onto the retina (Batista, Buneo, Snyder, & Andersen, 1999) – does not readily define the kinds of muscle activations and joint constellations necessary for movement towards objects (Herbort, Butz, & Pedersen, 2010). Much research has, therefore, been concerned with the question what

kind of coordinate system dominates movement planning and execution.

One field of research in which this debate has been central is the coordination between different effectors. Movements that are mirror symmetrical with respect to the body midline are executed with greater precision, and can be performed at higher speeds, than non-symmetrical movements. For example, when rhythmically flexing and extending the right and left wrists, movement performance is superior when both wrists are flexed and extended in synchrony, compared to when one wrist must be flexed while the other is extended (Cohen, 1971; Kelso, 1984; Kelso, Scholz, & Schöner, 1986). Similar principles govern other types of finger movements like tapping (Mechsner, Kerzel, Knoblich, & Prinz, 2001), finger flexion and extension (Carson & Riek, 1998; Riek, Carson, & Byblow, 1992), and finger abduction and adduction (Mechsner et al., 2001). Finger flexion and extension are

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movements that bring the finger down and up, respectively, when the hand is held palm down. Finger abduction and adduction, in contrast, are movements that bring the right index finger to the left and right, respectively, when the right hand is held palm down. In the following, we will refer to the latter as “finger oscillation” for brevity.

There has been an extensive debate about the origin of “mirror symmetry” for bimanual movement coordination. It was originally suggested that symmetry pertained to the use of homologous muscles in the two wrists, hands, or fingers, respectively (Cohen, 1971; Kelso, 1984; Riek et al., 1992). This owed to the fact that, due to the body’s symmetry, movements towards the midline require the use of homologous muscles in the two hands. Accordingly, performance advantages of symmetric movements may be due simply to synergies in the motor system during co-activation of homologous muscles. However, it was later shown that the tendency for mirror symmetry was preserved when the hands were held in opposite postures – one facing up, and the other facing down (Mechsner et al., 2001). In this situation, bimanual finger movements were still performed most successfully when the fingers of the two hands were directed towards and away from the body midline in synchrony, although this now required the concurrent use of non-homologous muscles in the two hands. Moreover, participants performed significantly worse in a condition in which the fingers had to be moved “in parallel”, that is, in the same direction in space (both fingers towards the left side in space, then both towards the right side in space). Note, that this movement requires the use of homologous muscles when the hands are positioned in opposite postures. Thus, the facilitation of coordination by symmetry seemed to depend on perceptual factors, and not on motor-related mechanisms like muscle synergies.

Further evidence for the use of perceptual codes in motor coordination comes from a tapping task (Mechsner et al., 2001). In this task, participants had to tap bimanual finger patterns. When participants tapped a mirror-symmetrical pattern (that is, tap the two middle fingers, then the two index fingers), they performed better than when they tapped a parallel pattern (that is, the left middle with the right index finger, then the left index with the right middle finger). If movement coordination were based on muscle homology, then, in this latter case, participants should tap best whenever two homologous fingers are tapped together. To test this hypothesis, tapping patterns were modified such that participants used the right middle and ring fingers, rather than the right index and middle fingers. Note, that in this case two homologous fingers (the two middle fingers) tap together in a parallel rather than in a symmetrical tapping pattern. However, again, participants preferred the spatially mirror-symmetrical tapping pattern, further supporting the conclusion that movement coordination is governed by “perceptual” rather than by anatomical factors (Mechsner et al., 2001). Others have referred to non-anatomical influences on movement coordination as effects of “mutual movement direction”, which results in “extrinsic”, as opposed to egocentric, muscle-based coordinative constraints (Swinnen et al., 1998). Here, we refer to space-based coordination principles as

being based on an external spatial reference frame, and contrast this term with an anatomical, muscle-based coding scheme.

An advantage of certain spatial coordination patterns has been demonstrated for non-homologous limbs, too. For example, participants performed more successfully when they had to move a hand and a foot up and down in synchrony, than when they had to move the two effectors asynchronously, that is, one up and the other down (Baldissera, Cavallari, & Civaschi, 1982). This effect was independent of whether the hand was turned upward or downward. Such coordinative preferences cannot be due to muscle homology, given that they involve different kinds of limbs. Their existence has, therefore, been interpreted as evidence for movement coordination being entirely organized according to perceptual factors (Mechsner, 2004), just like the finger coordination results by Mechsner and colleagues. In contrast, others have suggested that movement coordination is subject to several different types of constraints, among them both anatomical and perceptual factors (Amazeen, DaSilva, & Amazeen, 2008; Riek & Woolley, 2005; Swinnen et al., 1998; Temprado, Swinnen, Carson, Tourment, & Laurent, 2003).

However, it remains unspecified which types of perceptual information might be at the heart of the external spatial biases that have been observed. The identification of an impact of external coordinates on coordination does not in itself reveal the cognitive functions which underlie such organizational principles as mirror symmetry, nor the perceptual systems which establish them. Intuitively, our perception of space is tightly linked with our visual sense: for example, the description of symmetry in terms of movement direction usually coincides with a visual description of the respective movements. Moreover, vision is intricately linked to movement planning and execution. For example, it is known that movements that are aimed directly at a visual target can be executed extremely fast and, possibly, bypass cortical control (Day & Lyon, 2000; Pruszynski et al., 2010). Furthermore, movements are regularly corrected online based on visual input with seemingly little effort during execution (Day & Reynolds, 2005), and movement trajectories are adjusted such that they appear visually approximately straight (Wolpert, Ghahramani, & Jordan, 1995).

External coordinates may, however, be derived from other sensory systems, such as proprioception, the vestibular system, and even audition. In the bimanual tapping paradigm, emphasizing visual symmetry or parallelism by visually marking the respective fingers did not alter the advantage of mirror-symmetrical movements independent of whether homologous or non-homologous fingers were tapped (Mechsner & Knoblich, 2004). Moreover, occluding vision of the hands did not change the tapping pattern (Mechsner et al., 2001). Yet such independence of immediate visual information does not exclude that symmetry is defined visually. This can be convincingly illustrated with a different perceptual process, namely, tactile localization. There is ample evidence that touch is recoded from skin-based (that is, anatomically-based) into external coordinates. Such recoding is demonstrable by localization impairments induced by body postures which lead to

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