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Back-to-front: Improved tactile discrimination performance in the space you cannot see

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Abstract

We investigated any differences in people's ability to reconstruct the appropriate spatiotemporal ordering of multiple tactile stimuli, when presented in frontal space (a region where visual inputs tend to dominate) versus in the space behind the back (a region of space that we rarely see) in professional piano players and in non-musicians. Even though tactile temporal order judgments were much better in the musicians overall, both groups showed a much reduced crossed-hands deficit when their hands were crossed behind their backs rather than at the front. These results suggest that because of differences in the availability of visual input, the spatiotemporal representation of non-visual stimuli in front versus rear space is different.

Keywords: Tactile temporal order judgment; Human; Professional piano players; Learning

Our brains typically localize sensory events – including touches and sounds – according to an externally defined coordinate system, which is dominated by vision [3,6,10,18,22]. The remapping of tactile stimuli from body-centered coordinates – in which they are coded initially – into external coordinates is fast and relatively effortless when the body is in its "typical" posture (i.e., with the left hand on the left of the body and vice versa for the right hand) (e.g., see [1,13]). However, when more unusual body postures are adopted, such as crossing the hands, remapping takes more time and can result in substantial deficits in the perception of tactile stimuli, at least under conditions of bimanual and/or bimodal stimulation [15]. For example, several studies have highlighted impaired temporal order judgment (TOJ) performance regarding which of two tactile stimuli – delivered in rapid succession, one to either hand – was presented first when the hands are crossed as compared to when they are uncrossed [5,27,29]. A similar deficit has been observed when the fingers of the two hands are interleaved [30].

Recently, Röder et al. [25] reported that congenitally blind individuals do not show any such impairment in tactile TOJs as a result of crossing their hands, thus raising the following intriguing question: would crossing the hands behind the back – i.e., in a region of space where we normally have no, or very limited, visual input – result in a similar amelioration of the crossed-hands tactile TOJ deficit in normal sighted individuals? Put another way, is the multisensory spatial information concerning sensory events coded in a similar manner throughout peripersonal space [24], or might there instead be a difference between front and rear space (i.e., the space behind our backs), as a result of the existence of a detailed visual representations of the former but only occasional and very limited visual representation of the later [4,7,8,11,16 (p. 275),17]?

To address this question, we compared the effect of crossing the hands on tactile TOJ performance when the hands were placed in front of participants versus when they were placed

Abbreviations: TOJ, temporal order judgment; JND, just noticeable difference

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behind their backs. We tested two groups of participants, non-musicians as well as professional piano players, in order to uncover how extensive practice in playing piano – leading to altered tactile perception in pianists [14,23] – will affect TOJ performance in front and rear space in the latter group.

Eighteen non-musicians (mean age, 22 years; range, 19–39 years, 3 left handed) with normal or corrected-to normal vision and 15 pianists, 9 students at the Liszt F. Academy of Music as well as 6 recent graduates (mean age, 23 years; range, 18–26 years; 9 females, 2 left-handed) took part in the experiments. The pianists began piano playing at an average age of 8 years, and practiced for an average of 3 h per day. The experiment was performed in accordance with the ethical standards laid down in the Declaration of Helsinki. All participants gave their informed consent.

Participants (with their eyes closed) were presented with pairs of suprathreshold vibrotactile stimuli (30 ms duration), one to the second finger of either hand, and were required to make unspeeded TOJs regarding which finger was stimulated first. We used bone-conducting hearing aids (Oticon) as vibrotactile stimulators [27]. Participants responded by pressing the left footpedal if their left hand appeared to have been stimulated first and the right footpedal if their right hand appeared to have been stimulated first. A small block of foam was placed between the participant's arms in the crossed-hands posture in order to reduce any contact between them. The right arm was always crossed over the top of the left arm. The spatial separation between the vibrotactile stimulators (placed 20 cm in front or behind the back of the participants and 15 cm to either side of the midline) was kept constant throughout the experiment. We performed a pilot study to determine whether tactile temporal resolution differs when the task is performed with palms facing downward as compared to when they face upward. Since, the pilot experiments revealed that TOJs did not differ in the two conditions, in the main experiments – both in the uncrossed and crossed-hand conditions – the task was performed with the palms facing downward when the hands were placed in the front and with palms facing upward when hands were placed at the rear, i.e., with palm orientation that was more convenient and closer to a 'natural' posture (Fig. 1). White noise was presented through headphones to mask any sounds made by the operation of the tactile stimulators.

There were 10 possible stimulus onset asynchronies (SOAs) between the stimuli (in the uncrossed condition: −200, −90, −55, −30, −15, 15, 30, 55, 90, or 200 ms and in the crossed condition: −300, −180, −110, −60, −15, 15, 60, 110, 180, or 300 ms; where negative values indicate that the left hand was stimulated first) presented according to the method of constant stimuli. At the beginning of the experiment, observers completed 4 blocks of 30 practice trials. The practice blocks were followed by 8 blocks of 200 experimental trials, with the posture (uncrossed versus crossed) and the space (front versus rear) alternated between successive blocks of trials, and the order of presentation counterbalanced across observers.

The mean percentages of right first responses were calculated for each participant, SOA, and posture. The data were modelled by a Weibull psychometric function, using the psignifit toolbox (ver. 2.5.6) for Matlab (http://bootstrap-software.org/psignifit/). We calculated just noticeable differences (JNDs; the smallest interval needed to indicate temporal order reliably) by subtracting the SOA needed to achieve 75% performance from that needed to achieve 25% performance and dividing by two [27].

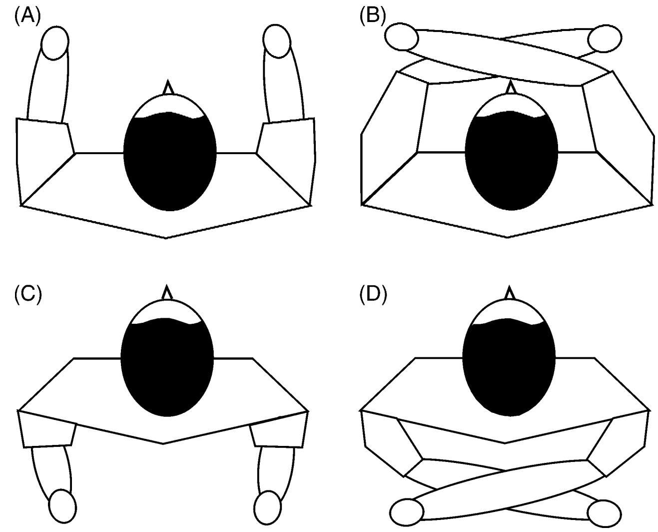

Fig. 1. A schematic illustration of hand postures (uncrossed and crossed) when they were placed in the front (A, B) and at the rear space (C, D).

In accordance with previous results [27,29] – based on their TOJ performance with crossed-hands at short intervals – participants (both non-musicians and pianists) fell into two groups: (1) veridical-TOJ group, including those who reported the veridical temporal order (10 out of 18 non-musicians; and 8 out of 15 pianists) and (2) reversed-TOJ group, including those who reliably reported a reversed subjective temporal order at shorter SOAs (<300 ms). Given that it is still unclear what causes this reversal of TOJ performance in certain individuals we focused our analyses on the data from the veridical-TOJ group (non-musicians: Fig. 2A and B; pianists: Fig. 2C and D). Data from the reversed-TOJ group, who showed the same pattern of results, can be found in the Supplementary Material.

Crossing the hands led to a significant decrement in performance in both front and rear space in the non-musicians (see Fig. 3; the main effect of hand posture: $F(1,9) = 21.3, p < 0.001$). Importantly, there was also a significant main effect of space (front/rear; ($F(1,9) = 8.4, p < 0.02$), as well as a significant interaction between hand position and posture; $F(1,9) = 5.6, p < 0.05$, attributable to the reduced decrement in performance observed when the hands were crossed behind the back as compared to when they were crossed in front of the participants.

We also tested whether professional piano players (i.e., individuals who had had extensive practice in playing the piano with the hands positioned in front) showed a similar pattern of results. In general, the piano players exhibited better temporal resolution than the non-musicians in all conditions (see Fig. 3; $F(1,16) = 9.1, p < 0.008$). Just as for the non-musicians, there were significant main effects of hand posture ($F(1,3) = 9.2, p < 0.02$) and space ($F(1,7) = 10.2, p < 0.02$), as well as a significant interaction between hand position and posture ($F(1,7) = 8.9$,

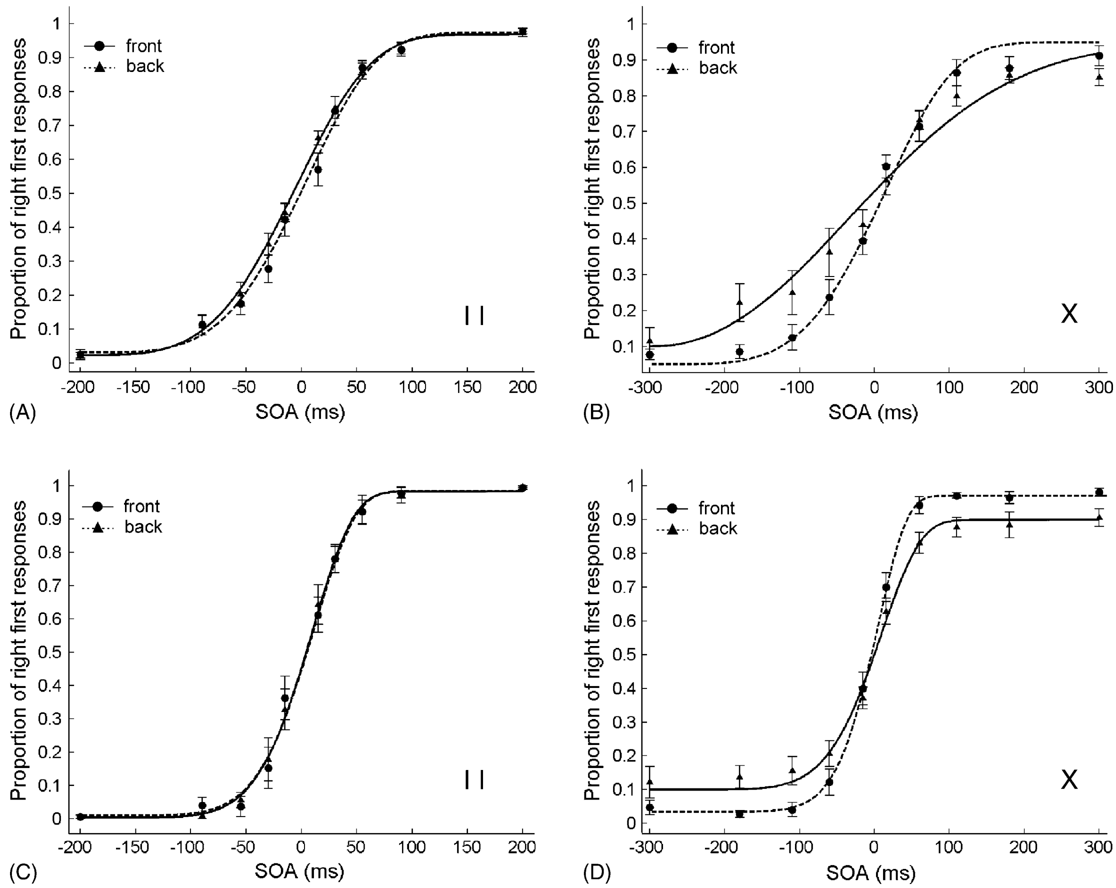

Fig. 2. Proportion of right hand first responses of the veridical-TOJ group. Weibull fits to the mean proportions of right hand first responses across individual observers are presented for the non-musicians (A—uncrossed posture; B—crossed posture) and pianists (C—uncrossed posture; D—crossed posture), both when the hands were placed in front and rear space.

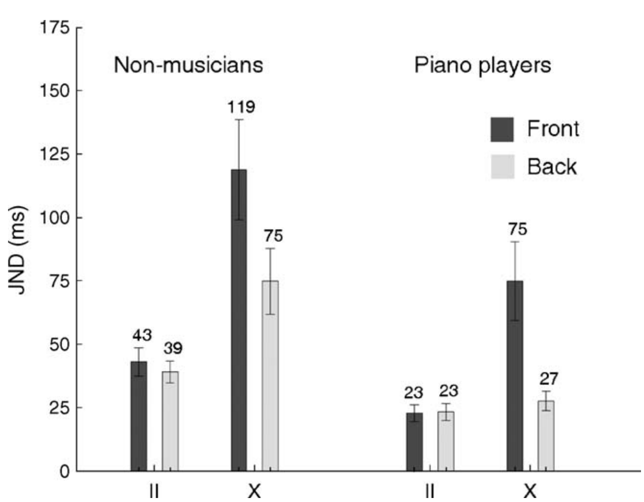

Fig. 3. TOJ performance. Average JNDs (calculated by subtracting the SOA needed to achieve 75% performance from that needed to achieve 25% performance and dividing by two) are shown for the non-musicians and pianists for all four conditions tested (II = uncrossed posture; and X = crossed posture). JNDs were determined independently for all observers based on the slope of the Weibull functions that were fitted to the individual data obtained in the four conditions (see Fig. 1 for the Weibull fit to participants' mean performance). Error bars represent the between observer S.E.M.

$p < 0.02$). Importantly, the trained pianists showed no significant hand crossing deficit when their hands were crossed behind their backs (post hoc analyses: $p = 0.712$).

When their hands were uncrossed, TOJ performance was similar at the front and rear, in both non-musicians (post hoc analyses: $p = 0.082$) and pianists (post hoc analyses: $p = 0.971$), suggesting that simply placing the hands behind the back did not influence TOJ performance deleteriously.

The results of this study show that crossing the hands behind the back leads to a much smaller impairment in tactile TOJs as compared to when the hands are crossed in front. Our results also show that even though extensive training in pianists resulted in significantly improved temporal resolution overall, it did not eliminate the difference between the efficiency of TOJs in front and rear space, suggesting that the superior tactile temporal resolution we found in the space behind peoples' backs cannot simply be explained by incidental differences in tactile experience with crossed-hands at the rear versus in the front.

Importantly, the finding that TOJ performance in the crossed-hands posture was significantly better in the space behind participants – i.e., in the region where people have very limited access to visual information – than in the space in front of participants – a region of space that tends to be dominated by visual inputs

– are in line with recent results showing that congenitally blind individuals do not show any such impairment in tactile TOJs as a result of crossing their hands [25]. The results of electrophysiological studies in macaques (see refs. [12,28] for recent reviews) as well as neuropsychological and brain imaging studies in humans (see ref. [19] for a recent review) converge on the view that a distributed neural network – involving the superior colliculus, putamen, parietal and premotor cortical areas – is responsible for the multisensory representation of peripersonal space surrounding the hand. In these brain regions, many neurons are multimodal, responding to tactile, visual, and sometimes even auditory stimuli.

It has also been shown that in the frontal, visible part of peripersonal space tactile stimuli are typically localized according to an externally defined coordinate system, which is predominantly determined by visual inputs. In sighted individuals, crossed-hands effects are believed to reflect the longer time that may be required for the remapping of tactile stimuli into an externally defined reference frame when the external and body-centered coordinates conflict [18]. In congenitally blind individuals, however, crossing the hands has no effect on tactile temporal resolution [25], suggesting that due to the lack of any visual reference frame: (1) remapping of tactile stimuli from body-centered into externally defined coordinates is independent of hand posture; or (2) localization of tactile stimuli in space and time can take place more directly, based on the body-centered coordinates. Further studies are required to uncover exactly why crossed-hands effects are absent in congenitally blind individuals. However, it is reasonable to suppose that the underlying mechanisms are common with those leading to reduced crossed-hands effect in the space behind us – where little or no visual information is available – as found in the present study. Such a conclusion is also supported by our findings that in non-musicians, even when the hands are uncrossed, tactile temporal resolution tends to be better in rear space than that in the front (although note that this difference did not quite reach statistical significance). This is because it was also shown earlier that tactile temporal resolution in congenitally blind individuals is better than in the sighted controls both in the case of uncrossed and crossed-hand postures. If it is in fact the case that it is the lack of a visual reference frame in the representation of peripersonal space that leads to improved tactile temporal resolution in both congenitally blind individuals as well as at the rear space of sighted individuals, our results raise the following intriguing possibility: Namely, that the spatiotemporal representation of tactile stimuli in space behind the backs of sighted individuals – especially in those who are trained in tasks requiring fine spatiotemporal analyses of tactile information – might be used as a normal model for the spatial representation of tactile information in congenitally blind individuals.

Our results also have important implications with respect the learning processes leading to professional piano playing. Musician's brains constitute a useful model for studying neuroplasticity evoked by extensive long-term training [20,21,26]. Recently, it has been shown that there are structural differences in the gray matter [9] as well as in the white matter [2] between professional piano players and non-musicians. Interestingly, it has also been shown that extensive practice in playing the piano leads not only to improved motor skills but also to higher spatial tactile resolution in pianists as compared to non-musicians [23]. Here, we show for the first time that the temporal resolution of tactile stimuli is also significantly higher in professional piano players than in non-musicians. Thus, our results are in agreement with Ragert et al.'s [23] suggestion that extensive piano practice has a broad effect on somatosensory information processing and sensory perception, even beyond training-specific constraints.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neulet.2006.02.037.

References

[1] R. Amlôt, R. Walker, Are somatosensory saccades voluntary or reflexive? Exp. Brain Res. 168 (2006) 557–565.
[2] S.L. Bengtsson, Z. Nagy, S. Skare, L. Forsman, H. Forssberg, F. Ullen, Extensive piano practicing has regionally specific effects on white matter development, Nat. Neurosci. 8 (2005) 1148–1150.
[3] M. Botvinick, J. Cohen, Rubber hands 'feel' touch that eyes see, Nature 391 (1998) 756.
[4] D.J. Bryant, B. Tversky, N. Franklin, Internal and external spatial frameworks for representing described scenes, J. Memory Language 31 (1992) 74–98.
[5] F. Drew, Attention: experimental and critical, Am. J. Psychol. 7 (1896) 533–573.
[6] H.H. Ehrsson, C. Spence, R.E. Passingham, That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb, Science 305 (2004) 875–877.
[7] A. Farne, E. Ladavas, Auditory peripersonal space in humans, J. Cogn. Neurosci. 14 (2002) 1030–1043.
[8] N. Franklin, B. Tversky, Searching imagined environments, J. Exp. Psychol.: Gen. 119 (1990) 63–76.
[9] C. Gaser, G. Schlaug, Brain structures differ between musicians and non-musicians, J. Neurosci. 23 (2003) 9240–9250.
[10] M.S.A. Graziano, Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position, Proc. Natl. Acad. Sci. U.S.A. 96 (1999) 10418–10421.
[11] M.S. Graziano, D.F. Cooke, C.S. Taylor, Coding the location of the arm by sight, Science 290 (2000) 1782–1786.
[12] M.S.A. Graziano, C.G. Gross, C.S.R. Taylor, T. Moore, A system of multimodal areas in the primate brain, in: C. Spence, J. Driver (Eds.), Crossmodal space and crossmodal attention, Oxford University Press, Oxford, 2004, pp. 51–67.
[13] J.M. Groh, D.L. Sparks, Saccades to somatosensory targets. 1. Behavioral characteristics, J. Neurophysiol. 75 (1996) 412–427.
[14] T. Hatta, A. Ejiri, Learning effects of piano playing on tactile recognition of sequential stimuli, Neuropsychologia 27 (1989) 1345–1356.
[15] N.P. Holmes, D. Sanabria, G.A. Calvert, C. Spence, Crossing the hands impairs performance on a nonspatial multisensory discrimination task. Brain Res., in press.
[16] W. James, Principles of Psychology, vol. 2, Henry Holt, New York, 1890.

[17] N. Kitagawa, M. Zampini, C. Spence, Audiotactile interactions in near and far space, Exp. Brain Res. 166 (2005) 528–537.

[18] S. Kitazawa, Where conscious sensation takes place, Conscious. Cogn. 11 (2002) 475–477.

[19] E. Ladavas, E.A. Farnè, Neuropsychological evidence for multimodal representations of space near specific body parts, in: C. Spence, J. Driver (Eds.), Crossmodal Space and Crossmodal Attention, Oxford University Press, Oxford, 2004, pp. 69–98.

[20] T.F. Münte, E. Altenmuller, L. Jancke, The musician's brain as a model of neuroplasticity, Nat. Rev. Neurosci. 3 (2002) 473–478.

[21] C. Pantev, B. Ross, T. Fujioka, L.J. Trainor, M. Schulte, M. Schulz, Music and learning-induced cortical plasticity, Ann. N.Y. Acad. Sci. 999 (2003) 438–450.

[22] F. Pavani, C. Spence, J. Driver, Visual capture of touch: out-of-the-body experiences with rubber gloves, Psychol. Sci. 11 (2000) 353–359.

[23] P. Ragert, A. Schmidt, E. Altenmuller, H.R. Dinse, Superior tactile performance and learning in professional pianists: evidence for meta-plasticity in musicians, Eur. J. Neurosci. 9 (2004) 473–478.

[24] G. Rizzolatti, L. Fadiga, L. Fogassi, V. Gallese, The space around us, Science 277 (1997) 190–191.

[25] B. Röder, F. Rösler, C. Spence, Early vision impairs tactile perception in the blind, Curr. Biol. 14 (2004) 121–124.

[26] G. Schlaug, The brain of musicians. A model for functional and structural adaptation, Ann. N.Y. Acad. Sci. 930 (2001) 281–299.

[27] D.I. Shore, E. Spry, C. Spence, Confusing the mind by crossing the hands, Cog. Brain Res. 14 (2002) 153–163.

[28] B.E. Stein, T.R. Stanford, M.T. Wallace, J.V. Vaugham, W. Jiang, Crossmodal spatial interactions in subcortical and cortical circuits, in: C. Spence, J. Driver (Eds.), Crossmodal Space and Crossmodal Attention, Oxford University Press, Oxford, 2004, pp. 25–50.

[29] S. Yamamoto, S. Kitazawa, Reversal of subjective temporal order due to arm crossing, Nat. Neurosci. 4 (2001) 759–765.

[30] M. Zampini, C. Harris, C. Spence, Effect of posture change on tactile perception: impaired direction discrimination performance with interleaved fingers, Exp. Brain Res. 166 (2005) 498–508.