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Horizontal spatial representations of time: Evidence for the STEARC effect

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ABSTRACT

It is well known that stimuli such as numerals (small vs large) and auditory pitches (low vs high) have spatial characteristics, and that responses to such stimuli are biased by the mental representation of their magnitude. Walsh (2003) has argued that any spatially and action-coded magnitude will yield a relationship between magnitude and space. Here we investigated the spatial representation of 'time' using speeded responses to the onset timing (early vs late) of a probe stimulus following periodic auditory clicks. Participants pressed one of the two response keys depending on whether the timing of a given probe was earlier or later than expected based on the preceding clicks. The results showed that left-side responses to early onset timing were faster than those to late onset timing, whereas right-side responses to late onsets were faster than those to early onsets when the response keys were aligned horizontally. Such a time–response congruity effect was not observed with the vertical alignment of responses. These results suggest that time is represented from left to right along the horizontal axis in space. The existence of a 'mental time line' in space and the spatial–temporal association of response codes (STEARC) effect are discussed.

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1. Introduction

Recent findings have shown that cognitive representations of stimuli such as numerals (from 1 to 9), auditory pitch (from low to high), letters of the alphabet (from A to Z), and months of the year (from January to December) have spatial characteristics, and that these characteristics influence the speed of manual responses (e.g., Fischer, 2003; Gevers et al., 2003; Rusconi et al., 2006). With respect to numerals, for example, smaller

numbers (e.g., 1 and 2) facilitate left-side responses compared to right-side responses, whereas larger numbers (e.g., 8 and 9) favor right-side responses [which was called the *spatial-numerical association of response codes* (SNARC) effect] (Dehaene et al., 1993; Fischer, 2003; Fischer et al., 2003; Gevers et al., 2006; Ishihara et al., 2006; Ito and Hatta, 2004). This suggests the existence of a 'mental number line,' i.e., a cognitive representation of the magnitude of numbers, and such a representation interacts with motor preparation in space. Similar to this space–number

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association, auditory pitch can be mediated by spatial information processing (Keller and Koch, 2006; Rusconi et al., 2006), where left-side (or lower) responses are faster than right-side (or upper) responses for lower pitches and vice versa for higher pitches [which was called the *spatial-musical association of response codes* (SMARC) effect]. In this regard, auditory pitch can be thought of in terms of magnitude information, yielding a relationship between pitch and space that is similar to the number-space association.

Studies using repetitive transcranial magnetic stimulation (rTMS) have revealed that the left inferior parietal lobule (IPL) plays an important role in number representation (Göbel et al., 2001, 2006; Sandrini et al., 2004). On the other hand, the right IPL is considered to be important for the representation of time (Basso et al., 1996; Harrington and Haaland, 1999; Rao et al., 2001). Rao et al. (2001), using event-related fMRI, demonstrated that early cortical activation in the right IPL (and also in the basal ganglia) is associated with the encoding of time intervals. Impairment of the right IPL (and/or the lateral temporal lobule) often causes unilateral neglect (Doricchi and Tomaiuolo, 2003; Driver and Mattingley, 1998; Karnath et al., 2001; Mattingley et al., 1998). Basso et al. (1996) investigated subjective stimulus duration in a patient with left visuospatial neglect. In a time interval comparison task (with visual stimuli displayed in the right hemifield), the patient overestimated stimulus durations at the neglected location; specifically, stimuli appearing on the left of the display were judged to be longer in duration than those on the right of the display. Such temporal overestimation in the neglected field was also found in an interval production task. Hillstrom et al. (2004) showed that a similar patient required more time to identify two successive visual targets when the second target appeared in the neglected left hemifield. It is evident that unilateral neglect patients with right parietal lesions show deficits in sensorimotor and cognitive spatial functions (Farne et al., 2003; Rode et al., 2003, 2001; Rossetti et al., 1998). In fact, the parietal cortex has been recognized as the heart of on-line action processing in space (Grea et al., 2002; Pisella et al., 2000; Rossetti et al., 2005). Therefore, the IPL can be considered to be responsible for processing space, time, and quantity information during sensorimotor transformations.

Recently, Walsh (2003a) argued that the IPL caters to the common need for space, time, and quantity information to be used in sensorimotor transformations, suggesting that the IPL is a generalized magnitude system for action. This is a notion that is supported by the results of studies employing patients, TMS, and fMRI (e.g., Farne et al., 2003 for spatial representation; Göbel et al., 2006 for numerical representation; Rao et al., 2001 for temporal representation). Information such as numerosity, amount, and duration may be represented symbolically (i.e., as a *'mental magnitude'*) irrespective of whether information is countable or uncountable (Gallistel and Gelman, 2000; Walsh, 2003a, 2003b). Such non-verbal representations undergo a fundamental qualitative and quantitative transformation during development as soon as children learn to relate them to language (Nieder, 2005). If such mental representations of magnitude interact generally with spatial processing in action, as is observed in the SNARC and SMARC effects, it can be assumed that temporal information processing would be also mediated by spatial representations during the preparation of motor

responses (Walsh, 2003a). This raises the question whether there is a space-time association that is analogous to the already established space-number association.

Walsh's framework invites the hypothesis that the cognitive representation of time (e.g., early vs late) may interact with spatial representations. This is the main hypothesis that is tested in the present study. If there is a congruent/incongruent association between time and space, as is the case for numerical magnitude and space, then this association should facilitate responses in the congruent situation relative to the incongruent situation. When we use music/video players in everyday life, we navigate to points at which we wish to listen/watch by pressing control buttons that are arranged according to conventions that suggest such a space-time association. These buttons are usually marked 'rewind (\ll)', 'play ($>$)', and 'fast-forward (\gg)', where each arrow presumably indicates the 'direction' in which time is perceived to flow. Thus, this may be taken to suggest the existence of a *'mental time line'* in which the representation of time is aligned spatially from left to right. Similar to what is seen in the SNARC and SMARC effects, the congruity between spatial and temporal information along the *'mental time line'* may facilitate manual responses, which may yield a *spatial-temporal association of response codes* (STEARC) effect. Based on this hypothesis, two experiments were conducted in order to clarify the role of spatial-temporal associations in the sensorimotor transformation of stimulus information into response codes. **Experiment 1** tested the STEARC effect using horizontally arrayed left/right responses and **Experiment 2** used vertically arrayed bottom/top responses. For the vertical dimension, we were interested in whether 'early' events would be categorized in the lower portion and 'late' in the upper portion of the vertical axis (as in the vertical SNARC and SMARC effects).

2. Experiment 1: horizontally arrayed responses

2.1. Methods

2.1.1. Participants

Twenty-seven young adults (16 males, 11 females, mean age = 24.4 years, S.D. = 3.4 years) participated in this experiment. None reported any hearing problems or physical dysfunction. All participants were native speakers of German, and none had learnt languages using right-to-left or top-to-bottom orthographies. Seventeen participants were right-handed and 10 participants were left-handed according to the Edinburgh Inventory (Oldfield, 1971). They were informed of the experimental procedures in advance and consented to take part in the experiment, which was approved by the local ethics committee. The participants remained naïve about the purpose of the experiment and the hypothesis being tested. All were paid in return for participation.

2.1.2. Apparatus and stimuli

Auditory click sounds were used as stimuli. A personal computer system (MEGWARE Computer, Power Line P4) with 'Presentation' software (Neurobehavioral Systems) was used to generate auditory stimuli and to record participants' responses.

Auditory stimuli were presented to participants at a comfortable listening level through headphones (AKG, K271 Studio) connected to the computer. The click sound consisted of a 1000 Hz sinusoidal waveform with 20 msec duration. Reaction times (RTs) were measured using a response box (whose top surface measured 30 cm × 40 cm) equipped with two response buttons separated by 22 cm. The box lay on a table in front of the participant in such a way that the buttons were aligned horizontally (left/right). The distance from the midline of participant's trunk to the center of the box was 22 cm.

2.1.3. Procedure

The participants, who were tested individually, were seated wearing headphones at a table in a quiet experimental room. Before starting experimental sessions, participants performed several practice trials until they were familiar with the task. Participants performed all the tasks with their eyes closed. In each experimental trial (apart from catch trials; see below), participants listened to eight sequentially presented auditory clicks. The inter-onset interval (IOI) separating clicks was 500 msec (for the first seven clicks). The timing of the last click (i.e., the 8th click, serving as a probe) was experimentally manipulated in such a way that it was Early or Late by 43% of the IOI (−215 msec or +215 msec, respectively) (Fig. 1). The onset timing of the probe was chosen based on the results of a pilot study conducted to determine the values at which participants could easily tell whether the probes appeared earlier or later than the expected critical timing. The expected critical IOI for the probe click (i.e., 0% deviation in onset timing of the probe) was not used. Participants were instructed to listen to the entire click sequence in each trial and to indicate whether the timing of the probe click was earlier or later than the expected critical IOI by pressing one of the two response buttons as quickly and accurately as possible following the presentation of the probe. No-go trials (with no 8th click) were included as catch trials in order to force participants to attend to the entire critical IOI before initiating responses to late probes (in a modified technique inspired by Grosjean and Mordkoff, 2001). The importance of avoiding false alarms on no-go trials was stressed. The waiting interval was 4 sec. An alert sound (resembling a police

siren) was presented if participants responded during this interval on a no-go trial. Throughout each trial the left index finger was placed on the left button and the right index finger on the right button. The left response was assigned to 'early' probes and the right response to 'late' probes in the congruent condition, whereas this stimulus–response (S–R) mapping was reversed in the incongruent condition. Incorrect responses (i.e., 'early' with the right and 'late' with the left in the congruent condition and vice versa in the incongruent condition) were considered as misses and were excluded from the analyses. Once the participant responded, the next trial began following a fixed 2 sec inter-trial interval. Within the experiment, each participant completed a total of 200 trials with 40 repetitions for the probe onset timings (Early 43% and Late 43%) and 20 repetitions for the no-go (catch trial) in each of the two S–R conditions (congruent and incongruent). There were two blocks of 50 trials per condition. The presentation order of trials was randomized. The order of S–R conditions was counterbalanced across participants (congruent → incongruent → congruent → incongruent → incongruent → congruent → incongruent → congruent). Participants rested for 5 min after each set of 50 trials. The percentage of failed trials comprised 1% misses and 0% false alarms.

2.1.4. Data analyses

To improve the internal validity of the study, RTs either shorter than 120 msec or longer than the mean + 3S.D. were discarded as outliers. The percentage of trials eliminated according to these criteria was 3%. A repeated-measure analysis of variance (ANOVA) with a 2 (responding position: left and right) × 2 (onset timing: early and late) design was performed on RT data. When a significant interaction was detected, simple main effects were subsequently tested. The criterion for statistical significance was set at $p < .05$. Additional analyses were conducted as specified below.

2.2. Results and discussion

The ANOVA on RT showed that there was a significant interaction between position and onset timing [$F(1, 26) = 13.29$, $p < .01$]. No significant main effects were found [position, $F(1, 26) = 0.21$, $p = .65$; onset timing, $F(1, 26) = 0.03$, $p = .86$]. The mean RTs for each onset timing in each position are shown in Fig. 2. Subsequent tests performed to unpack the interaction showed significant simple main effects of onset timing in each position [Left, $F(1, 26) = 10.42$, $p < .01$; Right, $F(1, 26) = 5.25$, $p < .05$]. RTs for early onset timing were shorter than those for late onset timing in left-side responses and vice versa in right-side responses. The analyses also revealed that there were significant simple main effects of position in each onset timing condition [Early, $F(1, 26) = 10.49$, $p < .01$; Late, $F(1, 26) = 10.34$, $p < .01$]. These effects confirmed that RTs for left-side responses were reliably shorter than those for right-side responses in early onset timing and vice versa in late onset timing. The above results demonstrate a space–time association in horizontally arrayed responses (i.e., the STEARC effect).

To examine the STEARC effect for each participant, RT differences between left response and right response for early and late onset timings were calculated at the individual level and then linear regression was applied (x : onset timings [Early

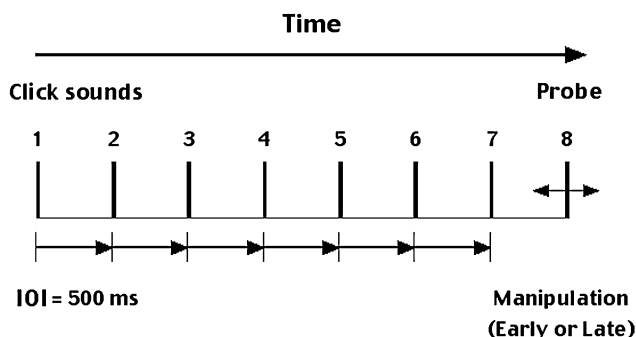


Fig. 1 – Schematic representation of the auditory stimuli. Participants were instructed to indicate whether the timing of a given probe (i.e., 8th click) was earlier or later than the expected critical IOI by pressing one of the two response buttons.

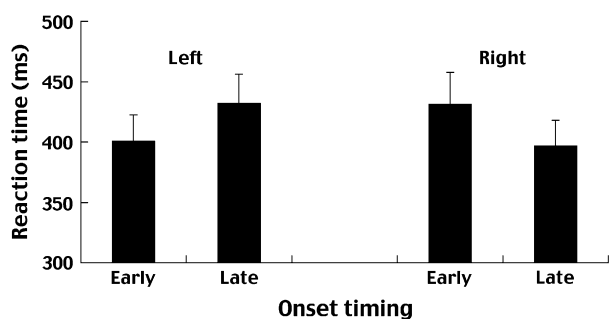


Fig. 2 – Mean RTs for each onset timing at each position. Analyses showed a significant interaction between position and onset timing. Each error bar indicates the range of one standard error.

and Late], y : RT differences [msec]. Positive slopes of the regression line indicate participants who showed the STEARC effect with ‘Early-Left’ and ‘Late-Right’ associations (i.e., left-to-right mapping), whereas negative slopes of the regression line indicate participants who showed the reversed STEARC effect with ‘Late-Left’ and ‘Early-Right’ associations (i.e., right-to-left mapping). The slope coefficients of regression lines fitted to each participant’s data are plotted as a function of the mean RT is shown in Fig. 3. Positive values represent the STEARC effect, whereas negative values represent the reversed STEARC effect. The approximate range of the RT distribution was from 200 msec to 700 msec. Only 5 out of 27 participants (including four right-handed and one left-handed individuals) showed a reversed STEARC effect. To substantiate this observation, the slope coefficients of 27 participants (i.e., indices of both the strength of space–time associations and the directional preference of associations for individual participants) were analyzed by Wilcoxon’s rank sum test. Positive values were categorized as the STEARC effect and negative values were categorized as the reversed STEARC effect. The analysis revealed that there was a significant difference between two sets of data ($z = -3.40$, one-tailed test, $p < .01$). This demonstrates that the effect of space–time association in the horizontal dimension differs according to participants’ preferential spatial mappings of time. As is shown in Fig. 3, the majority showed the STEARC effect with a left-to-right mapping. This experiment confirmed that the properties of time

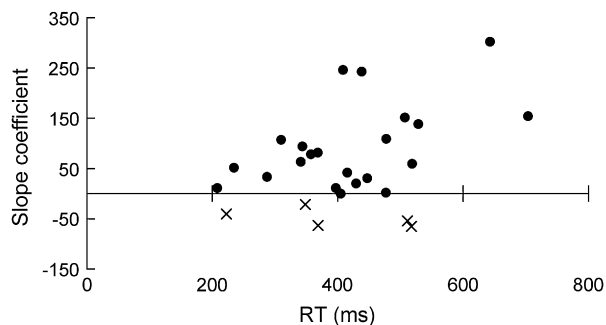


Fig. 3 – Slope coefficients for each participant as a function of RT. Filled circles represent participants who showed the STEARC effect, whereas crosses represent the reversed STEARC effect.

information such as ‘early’ and ‘late’ effectively modulate motor preparation in space.

3. Experiment 2: vertically arrayed responses

A strong space–time association was observed in horizontally arrayed left/right responses, where left-side responses to early onset timing were faster than those to late onset timing whereas right-side responses to late onsets were faster than those to early onsets. This experiment was designed to investigate whether a corresponding space–time association holds in the vertical dimension (as in the vertical SNARC and SMARC effects). Based on the SNARC/SMARC mappings as well as the up-right/down-left advantage (Adam et al., 1998; Proctor and Cho, 2001), ‘early’ events (which have small quantities of time information) were categorized as low and ‘late’ events (which have large quantities of time information) as high on the vertical axis in the congruent condition, and vice versa in the incongruent condition.

3.1. Methods

3.1.1. Participants

Thirty young adults (15 males, 15 females, mean age = 24.6 years, S.D. = 2.3 years) participated in this experiment. None of them had participated in Experiment 1. All participants were right-handed. All participants were native speakers of German, and none had learnt languages using right-to-left orthographies. One participant had learnt Japanese, which has a top-to-bottom orthography, for three years.

3.1.2. Apparatus and stimuli

Apparatus and stimuli were the same as those used in Experiment 1, except that the response box was placed perpendicularly to the midline of participant’s trunk by rotating the box 90° on the table top in such a way that the buttons were now aligned vertically. This arrangement (actually near/far in the transverse plane) can be thought of as being equivalent to the true vertical (bottom/top in the coronal plane) alignment of response buttons (see e.g., Ito and Hatta, 2004; Rusconi et al., 2006; Vu et al., 2000). The distance from the midline of the participant’s trunk to the center of the box was 22 cm.

3.1.3. Procedure

The general procedure was the same as that in Experiment 1, except the following points. The left index finger was placed on the bottom button and the right index finger on the top button. The bottom response was assigned to the ‘early’ probe and the top response to the ‘late’ probe in the congruent condition, whereas this S–R mapping was reversed in the incongruent condition. The percentage of failed trials comprised 1% misses and 1% false alarms.

3.1.4. Data analyses

The data analyses were conducted in a similar fashion to those in Experiment 1. The percentage of trials eliminated as outliers was 3%.

3.2. Results and discussion

The ANOVA on RT showed that there was neither a significant interaction nor significant main effects [position \times onset timing, $F(1, 29) = 0.15, p = .70$; position, $F(1, 29) = 2.65, p = .11$; onset timing, $F(1, 29) = 0.75, p = .39$]. The mean RTs for each onset timing in each position are shown in Fig. 4. These results indicate that there was no reliable space–time association in the vertical dimension. The RT difference between bottom and top responses was close to zero for the early and late onset timings, suggesting the absence of a space–time association in vertically arrayed responses.

As in Experiment 1, RT differences were calculated at the individual level and then linear regression was applied (x : onset timings [Early and Late], y : RT differences [msec]). The slope coefficients of regression lines fitted to each participant's data are plotted as a function of mean RT in Fig. 5. Positive values represent the STEARC effect (time mapped from bottom to top), whereas negative values represent the reversed STEARC effect (time mapped from top to bottom). The range of the RT distribution (approx. 200–700 msec) was similar to that observed in Experiment 1. Almost half (16) of the participants showed the reversed STEARC effect. To substantiate this observation, the slope coefficients of 30 participants (i.e., the effect of space–time association for individual participants) were analyzed by Wilcoxon's rank sum test. Positive values were categorized as the STEARC effect and negative values were categorized as the reversed STEARC effect. The result showed that there was a significant difference between two sets of data ($z = 4.64$, one-tailed test, $p < .01$). This demonstrates that the effect of space–time association in the vertical dimension differs according to participants' preferential spatial mappings of time. As shown in Fig. 5, the balanced distribution of slope coefficients prevented any consistent space–time association from being revealed among participants as a group. This experiment confirmed that there is no reliable vertical spatial representation of time. This suggests that there is ambiguity concerning the direction in which time is perceived to flow along the vertical dimension. Such ambiguity apparently led to conflicting space–time mappings canceling one another out in the context of vertically oriented responses.

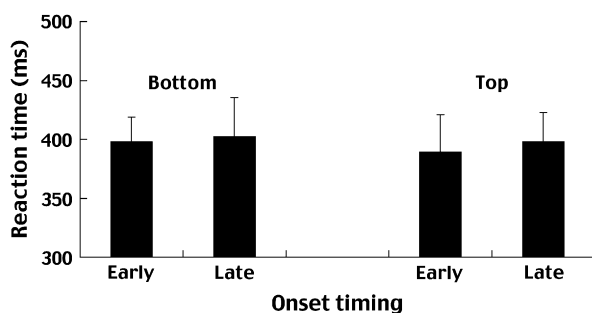


Fig. 4 – Mean RTs for each onset timing at each position. Analyses showed neither a significant interaction nor significant main effects. Each error bar indicates the range of one standard error.

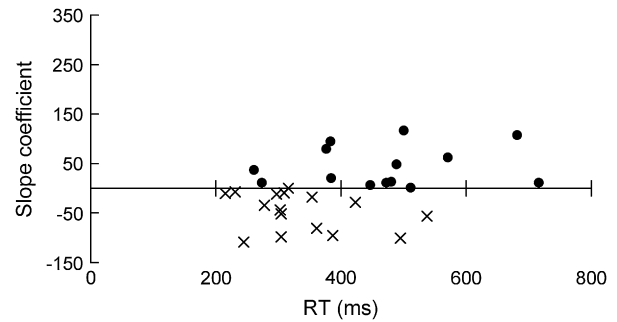


Fig. 5 – Slope coefficients for each participant as a function of RT. Filled circles represent participants who showed the STEARC effect, whereas crosses represent the reversed STEARC effect.

4. Analyses of 'horizontal' versus 'vertical' slope coefficients and RTs

In order to compare the space–time association between the horizontal and vertical arrayed responses directly, slope coefficients calculated in Experiments 1 and 2 were fed into a one-way ANOVA. Slope coefficients indicate both the strength of space–time associations (i.e., larger values indicate stronger associations and smaller values indicate weaker associations) and the directional preference of associations (i.e., positive values, left [bottom] to right [top] mapping; negative values, right [top] to left [bottom] mapping). Thus such a comparison allows us to test whether there are quantitative and qualitative differences between the horizontal and vertical arrays. The mean slope coefficient was 66.24 (S.E. = 15.09) for the horizontal array and -4.36 (S.E. = 14.32) for the vertical array. This analysis yielded a significant difference between the horizontal and vertical arrays [$F(1, 55) = 11.52, p < .01$], indicating that the characteristics of the space–time association were different for the different response dimensions. The horizontally arrayed responses elicited a strong STEARC effect with a left-to-right preference whereas the vertically arrayed responses elicited unreliable effects.

Mean RT was 415.19 (S.E. = 23.73) for the horizontal array and 396.90 (S.E. = 22.51) for the vertical array. An ANOVA performed on these RT data revealed that this difference was not significant [$F(1, 55) = 0.31, p = .58$], which indicates that participants' mean RTs did not differ reliably across experiments.

To substantiate these observations further, a multivariate analysis of variance (MANOVA) was performed on slope coefficients and RTs. This analysis detected a significant difference between the horizontal and vertical arrays [Pillai's trace, $F(2, 54) = 5.94, p < .01$], confirming that a more reliable space–time association was present on the horizontal dimension than on the vertical dimension.

5. General discussion

The present study was designed to investigate whether evidence for the mapping of information about time onto spatial coordinates can be found in both horizontally and vertically

arrayed responses. The results were consistent with the existence of a ‘mental time line’ that interacts with action (i.e., the STEARC effect) only on the horizontal dimension. Here there was a facilitatory effect in the congruent condition, where left-side responses were faster than right-side responses for earlier onset timings of click sounds and vice versa for later onset timings (Fig. 2). This suggests the existence of a space–time association that impacts upon the sensorimotor transformation process that mediates stimulus perception and response preparation. Importantly, our results revealed no space–time association in the vertical dimension (Fig. 4).

The question concerning why the space–time association appeared to differ for the horizontally and vertically arrayed responses is puzzling. It should be noted that the stimuli, experimental conditions, and procedures used in the present study were exactly the same across two experiments, except for the orientation of response positions (horizontal vs vertical). Additionally, the lack of a space–time association in the vertical array cannot be ascribed to slow responding, which would indicate that participants had difficulties in making judgments (go/no-go) about how to respond. Indeed, the number of failed responses (misses and false alarms) was very small and there was no significant overall RT difference between Experiments 1 and 2, implying that participants experienced no difficulties with the tasks. Therefore, the horizontal prevalence suggests that the ‘mental time line’ is tightly mapped onto the horizontal axis only, as reflected in some conventions that apply in daily life (e.g., the directions of control buttons on music/video players).

A possible explanation for the unreliable space–time association in the vertical axis may be that task-irrelevant spatial codes in general are represented from left to right as a default orientation (Gevers and Lammertyn, 2005; Nicoletti et al., 1988; Rubichi et al., 2005; Wiegand and Wascher, 2005). The null effect found in with vertically aligned responses in Experiment 2 can be thought of as reflecting the activation of such a left-to-right prevalence mechanism. In fact, similar results (i.e., horizontal prevalence) have been found in previous space–number studies (Ishihara et al., submitted for publication, 2006).

The results of the present study do not deny the possibility that there are contextual influences tied to the specific experimental conditions. The flexibility of space–number associations has been shown repeatedly (Bächtold et al., 1998; Fischer, 2006; Leuthard et al., 2005). Bächtold et al. (1998) demonstrated that, in the SNARC paradigm, the RT advantage for smaller numbers with the left-hand response (as well as the right-hand advantage for larger numbers) could be reversed, producing faster response for smaller numbers with the right hand than with the left hand and vice versa for larger numbers when participants were asked to imagine a clock face with the instruction to distinguish between “earlier than six o’clock” and “later than six o’clock”. This suggests that the mental number line representing spatial positional codes is flexible and can shift with changes in the current cognitive situation. Given such flexibility in cognitive spatial mappings, a vertical STEARC effect might be observed, for example, if prior to testing participants were instructed to imagine scenes in which the law of gravitation is clearly in operation, such as when an apple falls from a tree (traveling downwards over

time). Under such contextual influences, upper-side responses to early onset timing might be faster than those to late onset timing, whereas lower-side responses to late onsets might be faster than those to early onsets. However, in neutral situations (without any specific context) such as those in the present study, the horizontal dimension seems to serve as a default axis with time information being captured from left to right.

One may be concerned about the influence of specific task constraints used in the present study, such as left–right button responses and go/no-go judgments, on the individual response strategies. SNARC related studies have revealed individual differences in the way that numbers are associated with space (Fischer, 2006; Wood et al., 2006). Fischer (2006) proposed the idea of a strategic origin of the SNARC effect. In his framework, the SNARC effect can be thought of as the result of an individual’s strategic association of response codes (i.e., Fischer’s STARC effect). In the light of this idea, the spatial mappings [‘Early-Left’ and ‘Late-Right’ advantageous associations (i.e., left-to-right mapping)] found in the present study could be interpreted to be due to abundant experience with such mappings in daily life.

With respect to the neural correlates of the cognitive representation of time in spatial coordinates, the present study does not address the issue concerning whether temporal information interacts with spatial information directly or indirectly by first interacting with quantity information within Walsh’s (2003a) generalized magnitude system in the IPL. In either case, however, the present study suggested that temporal information interacted with spatial information in action. Neuropsychological studies and brain imaging studies have revealed that the right IPL plays an important role in the representation of time (Basso et al., 1996; Harrington and Haaland, 1999; Rao et al., 2001). Furthermore, damage to this cortical area induces severe deficits in attention and spatial functions, particularly for the left side of space, as observed in unilateral neglect patients (Farne et al., 2003; Rode et al., 2003, 2001; Rossetti et al., 1998). Therefore, the right IPL seems to play a crucial role for space–time associations during processes involving sensorimotor transformation. The horizontal prevalence found in the present study, where ‘early’ events were associated with left space and ‘late’ events with right space, may reflect spatial–temporal characteristics at some stage during such transformations.

In this regard, it is reasonable to consider the possibility that the STEARC effect is mediated by verbal codes. Language, of course, is predominantly a left hemisphere dependent function. Furthermore, it has been suggested that the left parietal cortex is responsible for action planning, while the right parietal cortex is especially involved in the on-line control of action (e.g., Haaland and Harrington, 1989a, 1989b; Hermsdörfer et al., 1999; Winstein and Pohl, 1995). Therefore, it is possible that the initial ‘early’ or ‘late’ decision made by the participant simultaneously activated a verbal code, which in turn led to the activation of an appropriate motor program (predominantly in the left hemisphere). This information may be transferred to the right parietal cortex, which has been purported to function as a bottleneck through which spatially encoded magnitudes must pass (Walsh, 2003a). Thus, the results of the present study may be due to the influence of the

right parietal spatial encoding of magnitudes on both spatial-temporal 'verbal' and spatial-temporal 'motor' information.

Finally, we would like to propose that the STEARC effect may be utilized as a clinical test for the early detection of neurological disorders associated with spatiotemporal attentional functions. As neuropsychological studies have shown, patients with neglect for the left side of space tend to overestimate the duration of visual targets presented at 'neglected' locations in the intact right hemifield (e.g., Basso et al., 1996). Furthermore, accuracy at identifying two successive visual targets varies as a function of the duration of the time interval separating the targets (i.e., a high proportion of incorrect responses is made with short intervals) when the second target appears in the neglected left hemifield (e.g., Hillstrom et al., 2004). These findings are consistent with the notion of a spatial-temporal gradient of attention. Here we suggest that spatiotemporal deficits during motor preparation would be indicated in the (horizontal) STEARC paradigm by prolonged RTs (and/or a high proportion of incorrect responses) on the neglected side of the 'mental time line' in space.

6. Conclusion

The present study showed that temporal information interacted with spatial information in action. Support for the existence of a 'mental time line' that is tightly mapped onto the horizontal axis was found. No spatial-temporal association was observed in the vertical dimension. The horizontally based mapping may be a default option in spatially and action-coded magnitude information processing. These novel findings invite further investigations of the 'mental time line' in relation to sensorimotor transformations mediating perception and action.

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REFERENCES

- Adam JJ, Boon B, Paas FGWC, and Umilta C. The up-right/down-left advantage for vertically oriented stimuli and horizontally oriented responses: a dual-strategy hypothesis. *Journal of Experimental Psychology: Human Perception and Performance*, 24: 1582-1595, 1998.
- Bächtold D, Baumüller M, and Brugger P. Stimulus-response compatibility in representational space. *Neuropsychologia*, 36: 731-735, 1998.
- Basso G, Nichelli P, Frassinetti F, and Di Pellegrino G. Time perception in a neglected space. *Neuroreport*, 7: 2111-2114, 1996.
- Dehaene S, Bossini S, and Giraux P. The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General*, 122: 371-396, 1993.
- Doricchi F and Tomaiuolo F. The anatomy of neglect without hemianopia: a key role for parietal-frontal disconnection? *Neuroreport*, 14: 2239-2243, 2003.
- Driver J and Mattingley JB. Parietal neglect and visual awareness. *Nature Neuroscience*, 1: 17-22, 1998.
- Farne A, Roy AC, Paulignan Y, Rode G, Rossetti Y, Boisson D, and Jeannerod M. Visuo-motor control of the ipsilateral hand: evidence from right brain-damaged patients. *Neuropsychologia*, 41: 739-757, 2003.
- Fischer MH. Spatial representations in number processing - evidence from a pointing task. *Visual Cognition*, 10: 493-508, 2003.
- Fischer MH. The future for SNARC could be STARK. *Cortex*, 42: 1066-1068, 2006.
- Fischer MH, Castel AD, Dodd MD, and Pratt J. Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience*, 6: 555-556, 2003.
- Gallistel CR and Gelman R. Non-verbal numerical cognition: from reals to integers. *Trends in Cognitive Sciences*, 4: 59-65, 2000.
- Gevers W and Lammertyn J. The hunt for SNARC. *Psychology Science*, 47: 10-21, 2005.
- Gevers W, Lammertyn J, Notebaert W, Verguts T, and Fias W. Automatic response activation of implicit spatial information: evidence from the SNARC effect. *Acta Psychologica*, 122: 221-233, 2006.
- Gevers W, Reynvoet B, and Fias W. The mental representation of ordinal sequences is spatially organized. *Cognition*, 87: B87-B95, 2003.
- Göbel S, Walsh V, and Rushworth MF. The mental number line and the human angular gyrus. *Neuroimage*, 14: 1278-1289, 2001.
- Göbel S, Calabria M, Farne A, and Rossetti Y. Parietal rTMS distorts the mental number line: simulating 'spatial' neglect in healthy subjects. *Neuropsychologia*, 44: 860-868, 2006.
- Grea H, Pisella L, Rossetti Y, Desmurget M, Tilikete C, Grafton S, Prablanc C, and Vighetto A. A lesion of the posterior parietal cortex disrupts on-line adjustments during aiming movements. *Neuropsychologia*, 40: 2471-2480, 2002.
- Grosjean M and Mordkoff JT. Temporal stimulus-response compatibility. *Journal of Experimental Psychology: Human Perception and Performance*, 27: 870-878, 2001.
- Haaland KY and Harrington DL. Hemispheric control of the initial and corrective components of aiming movements. *Neuropsychologia*, 27: 961-969, 1989a.
- Haaland KY and Harrington DL. The role of the hemispheres in closed loop movements. *Brain and Cognition*, 9: 158-180, 1989b.
- Harrington DL and Haaland KY. Neural underpinnings of temporal processing: a review of focal lesion, pharmacological, and functional imaging research. *Reviews in the neurosciences*, 10: 91-116, 1999.
- Hermsdörfer J, Laimgruber K, Kerkhoff G, Mai N, and Goldenberg G. Effects of unilateral brain damage on grip selection, coordination, and kinematics of ipsilesional prehension. *Experimental Brain Research*, 128: 41-51, 1999.
- Hillstrom AP, Husain M, Shapiro KL, and Rorden C. Spatiotemporal dynamics of attention in visual neglect: a case study. *Cortex*, 40: 433-440, 2004.
- Ishihara M, Farne A, Jacquin-Courtois S, Salemme R, Imanaka K, and Rossetti Y. Vertical spatial representations of numbers during motor preparation in manual pointing, submitted for publication.
- Ishihara M, Jacquin-Courtois S, Flory V, Salemme R, Imanaka K, and Rossetti Y. Interaction between space and number representations during motor preparation in manual aiming. *Neuropsychologia*, 44: 1009-1016, 2006.

- Ito Y and Hatta T. Spatial structure of quantitative representation of numbers: evidence from the SNARC effect. *Memory and Cognition*, 32: 662–673, 2004.
- Karnath HO, Ferber S, and Himmelbach M. Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature*, 411: 950–953, 2001.
- Keller PE and Koch I. Exogenous and endogenous response priming with auditory stimuli. *Advances in Cognitive Psychology*, 2: 269–276, 2006.
- Leuthard J, Bächtold D, and Brugger P. Is “left” always where the thumb is right?: stimulus–response compatibilities as a function of posture and location of the responding hand. *Cognitive and Behavioral Neurology*, 18: 173–178, 2005.
- Mattingley JB, Husain M, Rorden C, Kennard C, and Driver J. Motor role of human inferior parietal lobe revealed in unilateral neglect patients. *Nature*, 392: 179–182, 1998.
- Nicoletti R, Umilta C, Tressoldi EP, and Marzi CA. Why are left–right spatial codes easier to form than above–below ones? *Perception and Psychophysics*, 43: 287–292, 1988.
- Nieder A. Counting on neurons: the neurobiology of numerical competence. *Nature Reviews Neuroscience*, 6: 177–190, 2005.
- Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9: 97–113, 1971.
- Pisella L, Grea H, Tilikete C, Vighetto A, Desmurget M, Rode G, Boisson D, and Rossetti Y. An ‘automatic pilot’ for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience*, 3: 729–736, 2000.
- Proctor RW and Cho YS. The up–right/down–left advantage occurs for both participant- and computer-paced conditions: an empirical observation on Adam, Boon, Paas, and Umilta (1998). *Journal of Experimental Psychology: Human Perception and Performance*, 27: 466–471, 2001.
- Rao SM, Mayer AR, and Harrington DL. The evolution of brain activation during temporal processing. *Nature Neuroscience*, 4: 317–323, 2001.
- Rode G, Pisella L, Rossetti Y, Farne A, and Boisson D. Bottom-up transfer of sensory-motor plasticity to recovery of spatial cognition: visuomotor adaptation and spatial neglect. *Progress in Brain Research*, 142: 273–287, 2003.
- Rode G, Rossetti Y, and Boisson D. Prism adaptation improves representational neglect. *Neuropsychologia*, 39: 1250–1254, 2001.
- Rossetti Y, Revol P, Mcintosh R, Pisella L, Rode G, Danckert J, Tilikete C, Dijkerman HC, Boisson D, Vighetto A, Michel F, and Milner AD. Visually guided reaching: bilateral posterior parietal lesions cause a switch from fast visuomotor to slow cognitive control. *Neuropsychologia*, 43: 162–177, 2005.
- Rossetti Y, Rode G, Pisella L, Farne A, Li L, Boisson D, and Perenin MT. Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature*, 395: 166–169, 1998.
- Rubichi S, Nicoletti R, and Umilta C. Right–left prevalence with task-irrelevant spatial codes. *Psychological Research*, 69: 167–178, 2005.
- Rusconi E, Kwan B, Giordano BL, Umilta C, and Butterworth B. Spatial representation of pitch height: the SMARC effect. *Cognition*, 99: 113–129, 2006.
- Sandrini M, Rossini PM, and Miniussi C. The differential involvement of inferior parietal lobule in number comparison: a rTMS study. *Neuropsychologia*, 42: 1902–1909, 2004.
- Vu K-PL, Proctor RW, and Pick DF. Vertical versus horizontal spatial compatibility: right–left prevalence with bimanual responses. *Psychological Research*, 64: 25–40, 2000.
- Walsh V. A theory of magnitude: common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, 7: 483–488, 2003a.
- Walsh V. Time: the back-door of perception. *Trends in Cognitive Sciences*, 7: 335–338, 2003b.
- Wiegand K and Wascher E. Dynamic aspects of stimulus–response correspondence: evidence for two mechanisms involved in the SIMON effect. *Journal of Experimental Psychology: Human Perception and Performance*, 31: 453–464, 2005.
- Winstein CJ and Pohl PS. Effects of unilateral brain damage on the control of goal-directed hand movements. *Experimental Brain Research*, 105: 163–174, 1995.
- Wood G, Nuerk HC, and Willmes K. Crossed hands and the SNARC effect: a failure to replicate Dehaene, Bossini and Giraux (1993). *Cortex*, 42: 1069–1079, 2006.