Psychology

Faculty of Social and Behavioural Sciences

Leiden University

Exploration of the association between temporal and spatial perception in healthy individuals

Master Thesis

Master's Specialization in Clinical Neuropsychology

Faculty of Social and Behavioural Sciences – Leiden University

Section: Health, Medical and Neuropsychology

Date: April 11, 2016

Student number: 1015826

Daily Supervisor: Dr. C.J.M. Van der Ham

CNP co-evaluator: Dr. E. Habers

Contents

Abstract

Navigation is a complex cognitive function involving the hippocampus, in which time cells and place cells are located. Therefore, a strong correlation between temporal and spatial perception is hypothesized. To date, relatively little work has incorporated the mutual interaction of temporal and spatial perception within the same experimental paradigm. Therefore, the present study mainly aimed at examining this relationship. Depending on the final research sample composition, we also aimed to look into the effect of gender and handedness on the tasks performance, because literature so far shows inconsistent findings with regard to these individual factors. We assessed temporal and spatial perception in 100 healthy individuals from four different angles: estimation, production, reproduction, and comparison. In the temporal tasks, time duration of 500 ms, 1000 ms, and 1500 ms were used. In the spatial tasks, lengths of 2 cm, 5 cm, and 8 cm were employed. Results from the multiple regression models revealed a low significant association between the space comparison task and the temporal ability assessment ($r = 0.263$, $p = 0.004$), and a moderate but high significant correlation between the time comparison task and the spatial ability assessment ($r = 0.395$, $p < 0.001$). Analysis on the coefficient of variation resulted in less consistency on the spatial tasks, which could be explained by the differences in task difficulty. Because of the unbalanced ratio of gender and handedness in the research sample, comparison of the groups was invalid and we did not draw conclusions for these effects. Our findings suggest that there is no behavioural evidence for the existence of a fully shared neural basis for the hippocampal time cells and place cells. Thus temporal perception and spatial perception seem to be unlinked. The outcomes of the present study substantiate previous findings of dissociation between temporal perception and spatial perception.

Key words: navigation • hippocampus • internal clock • distance • time cells • place cells • time and space • perception • estimation • production • reproduction • comparison • discrimination

1. Introduction

In our everyday life we are constantly facing situations in which we need to perceive time and space accurately. Time is, although invisible and fleeting, an essential aspect in perception, and timing is important to ensure the optimal functioning of organisms (e.g., Block & Zakay, 1997; Guo et al., 2014; Konturek, Brzozowski, & Konturek, 2011; Saini, Brown, & Dibner, 2015). The same applies to the perception of space, which provides cues about characteristics such as depth and distance that are crucial for movement and orientation to the environment (e.g., Crollen, Grade, Pesenti, & Dormal, 2013). Both temporal perception and spatial perception are found to be important in the navigation process (Jackson, Willey, & Cormack, 2013). Studies with patients suffering from brain damage or disease on brain function suggest that these neurological impairments have substantial impact on the patients' navigational functioning in daily life (Nico et al., 2008). To gain a better understanding of the deficits in the navigation performance of patients, it is necessary to first determine what 'normal navigational behaviour' is.

1.1 The role of the hippocampus in navigation

Navigation is a complex cognitive function that consists of a number of separate cognitive abilities, such as landmark identification, orientation, and calculation of heading vectors (Rodriquez, 2010). In order to do navigational computations, at least two quantities must be known. The first parameter is the position in space, and the second is the position in time (Gerathewohl, 1967). The brain network involved in navigation processes includes the hippocampus, which is a small region of the brain located in the medial temporal lobe. The hippocampus is part of the limbic system and is primarily associated with long-term memory and spatial navigation (Cameron & Glover, 2015). This is for example illustrated by Kolb and Wishaw (2009); patients with damage to the hippocampus due to progressive pathologies such as Alzheimer's disease experience impairments of the spatial and episodic memory as the first symptoms. Yew, Alladi, Shailaja, Hodges and Hornberger (2013) have also found that in Alzheimer patients the hippocampus is one of the first regions of the brain that become damaged leading to loss of memory and disorientation.

The hippocampus has been the target of intense scrutiny in the last decades. There is evidence for the existence of the so-called hippocampal time cells and place cells, which cooperate to organize the contents of memories (Eichenbaum, 2014; Howard & Eichenbaum, 2014). Time cells are defined as neuronal activities at particular moments during periods when behaviour and location are relatively constant (Kraus, Robinson, White, Eichenbaum, & Hasselmo, 2013; MacDonald, Lepage, Eden, & Eichenbaum, 2011; Rowland, & Moser, 2013).

Place cells are neurons that fire specifically when the animal is at a certain place in the local environment, i.e., the place field of the cell (Alme et al., 2014; Moser, Kropff, & Moser, 2008). Early studies proposed that the hippocampus is involved in generating a mental representation of the spatial layout of the external world, known as a cognitive map (O'Keefe & Dostrovsky, 1971). Recent studies suggest that the hippocampus is not only specialised in coding of spatial location, but also in coding for temporal features of events. There is evidence suggesting that the hippocampus forms temporal relationships in addition to spatial relationships (Bunsey & Eichenbaum 1996). Howard and Eichenbaum (2014) reviewed a computational model for temporal and spatial coding in the hippocampus. They found that the hippocampus has access to information about the location and temporal distance from stimuli that were experiences in the past, in order to construct the 'memory spaces'. The hippocampus enables the learning of relationships between different stimuli experienced in the environment, and these might be spatial (e.g., "The school is located about 500 m at the back side of the train station") or temporal (e.g., "The coffee is ready about 3 minutes after the button was pressed"). Thus, given the common neural basis for the time cells and place cells, these two types of perception might be related. A link between time and space processing has also been found by neuropsychological studies reporting the co-occurrence of temporal and spatial deficits in patients suffering from neglect (Basso, Nichelli, Frassinetti, & di Pellegrino, 1996; Dankert et al., 2007).

Previous studies have investigated different interactions between time processing, space processing and the perception of quantity, also referred as numerosity processing (Walsh, 2003). For example, Meck and Church (1983) suggested that time and numerosity processing are underpinned by a shared representational mechanism. Another recent study by Cappelletti, Freeman and Cipolloti (2009) tested whether time, space and number processing are sharing a common magnitude system and their data suggested a partly shared mechanism. Although some existing studies have shown that time processing influences space processing to some extent (e.g. Cappelletti et al., 2009; Ishihara, Keller, Rossetty, & Prinz, 2008; Vallesi, Binns, & Shallice, 2008), to date, relatively little work investigate the mutual interaction of temporal and spatial perception within the same experimental paradigm. Therefore, the raising question is: Is there a common neural basis in the ability to perceive time and space, or are these abilities dissociated? In addition, it is typically found that people vary a lot in their ability to perceive time intervals and distances, but what individual differences actually play a role in temporal and spatial perception? The present study was mainly conducted to directly examine the correlation between the perception of time interval duration and perception of space. The additional aim of the current study was to look into the role of different individual factors, such as gender and handedness, in perceiving these aspects. Nevertheless, this second question could only be discussed as long as it was possible with the final research sample composition.

1.2   Assessment of temporal and spatial abilities

Timing ability in humans is studied by different models that investigate experienced and remembered duration; this includes internal-clock models, attentional models, memory models, and behavioural models (Allman, Teki, Griffiths, & Meck, 2014). The concept of a physiological internal clock-like system underlying temporal information processing has been a central feature in many researches on timing and temporal perception in humans (Allman et al., 2014; Rammsayer, 2001; Van Rijn, Gu, & Meck, 2014). Traditionally, authors distinguish four main methods to assess temporal abilities in laboratory settings: (1) *time estimation task*, which is often assessed by asking subjects to estimate the presented time passage in some standard units of time, such as seconds or minutes (e.g., Bschor et al., 2004; Kitamura & Kumar, 1983; Sucala, Scheckner, & David, 2011); (2) *time production task*, where the experimenter specifies a time interval in temporal units and subjects are told to press a button as long as the given time interval had passed (e.g., Grondin, 2010; Tysk, 1984); (3) *time reproduction task*, where subjects reproduces a previous presented time interval (e.g., Mahlberg, Kienast, Bschor, & Adli, 2008); and (4) *time comparison task*, where two time intervals of almost equal length are sequentially presented and the subjects identify which of the two was displayed longer, or judge whether the second stimulus was presented shorter or longer compared to the previous one (e.g., Mioni, Mattalia & Stablum, 2013). The time estimation task is the most frequently investigated type of subjective temporal perception in literature, possibly because of its complexity and importance in terms of environmental adaptation (Block & Zakay, 1997). Both time estimation and production tasks are suitable approaches in examining individual differences on the speed rate of the internal clock (Meck, 1996; Rammsayer, 2001), but time estimation methods are less accurate because subjects tend to round off the time duration leading to more production of variability (Clausen, 1950; Craik & Hay, 1999; Montare, 1985; Montare, 1988).

In contrast to temporal perception, study of distance or spatial perception in experimental settings is voluminous. However, assessment of spatial abilities can be performed using the same measures like in the temporal ability assessment. This is advantageous for the current study, because the same measures allow comparison of the performances on the temporal and spatial tasks. The four methods in spatial abilities assessment are: (1) *length estimation task*, where subjects estimate the length of a straight line path (e.g., Poirel et al., 2015); (2) *length production task*, where subjects produce, for example, a rectangle in a given length (e.g., Crollen, Grade, Pesenti, & Dormal, 2013); (3) *length reproduction task*, where subjects are requested to reproduce a distance they had seen (e.g., Sciutti, Burr, Saracco, Sandini, & Gori, 2014); and (4)

length discrimination task, which can be applied to measure the perceptual precisions of length judgments (e.g., Sciutti et al., 2014).

1.3   Individual factors in temporal and spatial abilities

In some cognitive abilities, there are well-documented differences between individuals and one of these is gender (Ankney, 1995; Hausmann, Slabbekoorn, Van Goozen, Cohen-Kettenis, & Güntürkün, 2000; Kimura, 1992). Generally, women perform relatively better on tasks involving fine motor skills and perceptual speed, whereas men score higher on tasks involving visual-spatial working memory and spatiotemporal responding (Halpern, 1997). Several studies indicate that gender differences in spatial and temporal abilities do exist (Hausmann et al., 2000; Philips & Silverman, 1997; Rammsayer & Lustnauer, 1989; Voyer, Voyer, & Bryden, 1995). For example, it has been observed that, on average, men outperform women on the Mental Rotation Test (Hausmann et al., 2000) and achieved better results in time durations discrimination (Rammsayer & Lustnauer, 1989) and estimation (Schiff and Oldak, 1990). Furthermore, women provide relatively longer and more variable time estimations than men (e.g., Block, Hancock, & Zakay, 2000). However, not all researchers have found these patterns (e.g., Swift & McGeoch, 1925) and because of the inconsistent findings in literature, the additional aim of the current study was to examine the effect of gender on tasks performance.

Another factor that may influence temporal and spatial perception is handedness. Handedness demonstrates contralateral control, which means that left brain portions interact with right body portions and vice versa (Whitehead & Banihani, 2014). Recent work demonstrates that temporal judgments are lateralized to different hemispheres of the brain, and that the right hemisphere particularly appears to be responsible for spatial-temporal integration (e.g., Westfall, Jasper, & Zelmanova, 2010). This is for example illustrated by Funnell, Corballis and Gazzaniga (2003), who found in their experiment with a split-brain patient that right-hemisphere based performance was superior in terms of accuracy to that of the left hemisphere, suggesting that the right hemisphere plays an important role in making temporal judgments. If there is cerebral asymmetry in temporal perception, namely if the right hemisphere is more competent regarding temporal perception, then accuracy in judging duration should be higher for the contralateral hand, which is the left hand. Burnett, Lane and Dratt (1982) examined the relationship between preferred handedness and spatial ability in undergraduate students. They found that, subjects whose handedness scores were mixed or slightly right-handed score higher on the task than strong-handers, i.e., subjects who were either extremely left-handed or extremely right-handed. Thus, their results suggest that decreased hemispheric specialization is associated with increased spatial ability. However, in their study, spatial ability was assessed using a spatial visualization task in which subjects were asked to identify the orientation of a stimulus after it has been rotated. It is unclear whether using other spatial tasks would produce

the same result. For this reason, investigation of the relationship between handedness and spatial ability assessed from other angles could be interesting.

1.4   The aim of the present study

Returning to the aim of the present study, we investigated whether the time cells and place cells share or not a common neural basis, by assessing the temporal and spatial ability in healthy individuals and examining the individual differences in perceiving time and space. An experimental setting with an adjusted method of Mioni et al. (2013) was used in the temporal ability assessment. Measurements in this assessment included estimation, production, reproduction and comparison tasks. To compare the results from the temporal tasks and the spatial tasks, an experimental setting including the four measurements (i.e., estimation, production, reproduction, and comparison) was designed for the spatial ability assessment.

Given the possibility that common neural basis may be shared between time cells and place cells, we hypothesized that temporal perception and spatial perception are highly related. Thus, participants who had high percentage of correct responses on the individual temporal tasks would also have high percentage of correct responses on the spatial ability assessment, and vice versa (i.e. participants with high percentage of correct responses on the individual spatial tasks would show more correct responses during the temporal ability assessment). However, there is behavioural evidence that the ability to perceive time and space is dissociated (e.g., Cappelletti et al., 2009; Van der Ham, Van Zandvoort, & Postma, 2010), thus our alternative hypothesis was that temporal perception and spatial perception are unrelated. If this was the case, we expected no correlation between the individual temporal and spatial tasks with the spatial and temporal assessment, respectively.

Regarding the individual differences in perceiving time and space; men generally outperform women in both temporal and spatial tasks, thus we hypothesized that this would also be the case in this study. We used the Edinburgh Handedness Inventory to determine participants' strength of handedness (Oldfield, 1971). Given that temporal perception appears to depend upon access to right-hemisphere processing and decreased hemispheric specialization is correlated with increased spatial ability, we predicted that left-handers would be more accurate in their perception of time and that mixed-handers (i.e., 'ambidextrous') would show more accuracy in spatial perception than strong-handers (i.e., 'left-handed' or 'right-handed').

At last, the coefficient of variation (CV) was derived from the tasks and analysed in order to evaluate the performance variability in all participants. Considering that the use of strategies in judging time intervals longer than 1200 ms is found to be effective (Grondin, 2010; Grondin, Ouellet, & Roussel, 2004; Grondin, Meilleur-Wells, & Lachance, 1999), we hypothesized that time duration of 500 ms and 1000 ms as targets would show higher variability than 1500 ms as

target. And because strategies can be applied to the temporal tasks, we predicted that the data of the temporal tasks would show higher consistency compared to the data of the spatial tasks.

2. Materials & Methods

2.1 Participants

A total of 102 subjects between 18–30 years old were recruited through the Leiden University Research Participation website, paper printed advertisements around campus, and the friends and family method. Inclusion criteria were being healthy and mastery of the Dutch language, and having normal or corrected-to-normal vision. Individuals with auditory or visual impairment were excluded from participation. The first experimental performance was considered as the pilot, thus the obtained data from were not used in the analysis. During assessment of the inclusion and exclusion criteria on the laboratory, one subject appeared to have autism, anxiety disorder, and major depressive disorder. This subject did complete the experiment, but since the inclusion criterion 'being healthy' was not met, the data of this participant were also excluded from analysis. Thus, as shown in Table 1, the final research sample for data analyses consisted of 100 healthy subjects (22 males, mean age of 20.14 ± 2.75 years). The study was approved by the Ethics Committee (Commissie Ethiek Psychologie) of the Faculty of Social and Behavioural Sciences of the Leiden University. Informed consent was obtained from all participants.

Table 1 | Descriptive data. Demographic characteristics of 100 healthy individuals.

Gender (male/female), frequency	22/78
Age in years [a]	20.14 (2.75)
Handedness [b] **(left/ambidextrous/right), frequency**	7/17/76
Education level [c]**, frequency**	6.0 (0.0)
1 = Less than six years of primary education	0
2 = Finished six years of primary education	0
3 = Six years primary education and less than two years of low level secondary education	0
4 = Four years of low level secondary education	0
5 = Four years of average level secondary education	0
6 = Five years of high level secondary education	84
7 = University degree	16

[a] Presented as mean (standard deviation).
[b] Measured through the Edinburgh Handedness Inventory (Oldfield, 1971).
[c] Expressed as median (interquartile ranges). The education levels are according to Verhage (1964), ranging from 1 to 7 and indicating the highest completed education. Dutch translations of the levels: 1 = minder dan lagere school; 2 = lagere school voltooid; 3 = lagere school voltooid en verdere vervolgopleiding minder dan 2 jaar.; 4 = lager dan MULO/MAVO-niveau, b.v. LTS, LEAO, LHNO; 5 = MULO/MAVO/MEAO-diploma; 6 = HAVO/VWO/HEAO/HBS/HBP-diploma; 7 = universiteit-diploma.

2.2 Stimuli & Apparatus

The white round 'smiley face' (**Figure 1A**) from Mioni et al. (2013) was applied to the current study, with permission from the authors. The original size has a diameter of 4.3 cm and this was used in the temporal tasks. For the spatial tasks, new round 'smiley faces' with other diameter sizes were created using the aspect ratio in pixels of the screen size, which could be calculated by the following formula: [stimuli size in cm] x 35.5 = [stimuli size in px]. Therefore, to make round 'smiley faces' with diameter of 2 cm, 5 cm, and 8 cm, length of 71 px, 178 px, and 284 px were used, respectively. This ratio calculation was also applied in creating a 4.3 x 4.3 cm white squared 'smiley face' (i.e., 154 x 154 px) for the time comparison task, the standard stimuli of 2 cm (71 px), 5 cm (178 px), and 8 cm (284 px) for the space comparison task, and in creating the comparison stimuli with are +/- 10% respective to the standard: 1.8 cm (64 px), 2.2 cm (78 px), 4.5 cm (160 px), 5.5 cm (195 px), 7.2 cm (256 px), and 8.8 cm (312 px). **Figure 1B** illustrates a squared 'smiley face' used in the present study.

The experiment was run on a Dell computer with Windows 7 operating system. Visual stimuli were displayed in black-on-white projection and were presented at the centre of a 22-inch (47.3 x 29.5 cm) Philips Brilliance LCD monitor with screen resolution of 1680 x 1050 pixels. During the space comparison task, the standard stimuli were shown 25% to the left and the comparison stimuli 25% to the right of the screen centre, with a mask in between. The mask consisted of a 45 x 15 cm (1598 x 533 px) horizontal rectangle, in which each pixel were set white or black. Throughout the experiment, participants were seated at approximately 50 cm from the computer screen. The visual angle ranges from 2.0 to 10.0 degrees.

Figure 1 | **Stimuli in the assessment of temporal and spatial perception. (A)** White coloured round 'smiley face' from Mioni et al. (2013), used with permission from the authors. In the current study, this stimulus with the original size of 4.3 cm in diameter was used during the temporal tasks. For the space estimation and space reproduction task, diameters of 2 cm, 5 cm and 8 cm were applied. **(B)** White coloured squared 'smiley face'. In the present study, this stimulus with side length of 4.3 cm was used in the time comparison task. During the space comparison task, side lengths of 1.8 cm, 2 cm, 2.2, 4.5 cm, 5 cm, 5.5 cm, 7.2 cm, 8 cm, and 8.8 cm were applied.

2.3   Instruments

An adapted method from Mioni et al. (2013) with increased number of trials was applied to the time production, time reproduction, and time comparison task in the present study. In the

following paragraphs; the standard 'target stimulus' indicates a white round 'smiley face'. In the comparison tasks, the 'comparison stimulus' was a white squared 'smiley face'.

Temporal ability assessment

Time estimation task

A target stimulus was presented on the computer screen for 500 ms, 1000 ms, or 1500 ms, and participants were asked to estimate the time duration of the target in milliseconds (**Figure 2A**). Each of the duration was randomly presented ten times, resulting in a total of 3 x 10 = 30 trials. The practice phase preceding the task consisted of 3 trials.

Time production task

Participants were asked to produce time intervals of 500 ms, 1000 ms, and 1500 ms. The target stimulus appeared as long as the spacebar was pressed and participants were instructed to release the spacebar when they thought they had reached the requested time duration (**Figure 2B**). Each of the duration was randomly presented ten times, resulting in a total of 3 x 10 = 30 trials. Prior to the task, there was a practise phase of 6 trials to let the participants get used to the operation of the spacebar.

Time reproduction task

A target stimulus was presented at the computer screen for time duration of 500 ms, 1000 ms, or 1500 ms and participants were asked to reproduce the time interval of the previously presented stimulus. They were instructed to press the spacebar as long as the previous stimulus was shown on the screen, and to release the spacebar when they thought they had reached the required time duration (**Figure 2C**). Each of the duration was randomly presented ten times, resulting in a total of 3 x 10 = 30 trials. The practise phase prior to the task consisted of 6 trials.

Time comparison task

Participants were presented with a standard stimulus, followed by a comparison stimulus, which appeared either shorter or longer than the standard stimulus. Then they were asked to judge these two different durations and decide whether the second presented stimulus was shorter or longer than the first (**Figure 2D**). In cases of uncertainty, participants should make a guess. The standard stimuli were displayed for duration of 500 ms, 1000 ms or 1500 ms. The comparison stimuli were +/- 25% respective to the standard, resulting in standard-short (500 – 375 ms, 1000 – 750 ms, and 1500 – 1125 ms) or standard-long (500 – 625 ms, 1000 – 1250 ms, and 1500 – 1875 ms). Participants were instructed to use two distinct keys on the keyboard to respond if the squared 'smiley face' was shorter or longer than the round 'smiley face'; <K> (referred to the Dutch word 'korter' = shorter) and <L> (referred to the Dutch word 'langer' =

longer). Each standard-comparison pair was randomly presented 10 times in a fixed order (i.e., first standard stimulus, then comparison stimulus), resulting in a total of 6 x 10 = 60 pairs of stimuli. The practice phase prior to the task consisted of 6 trials.
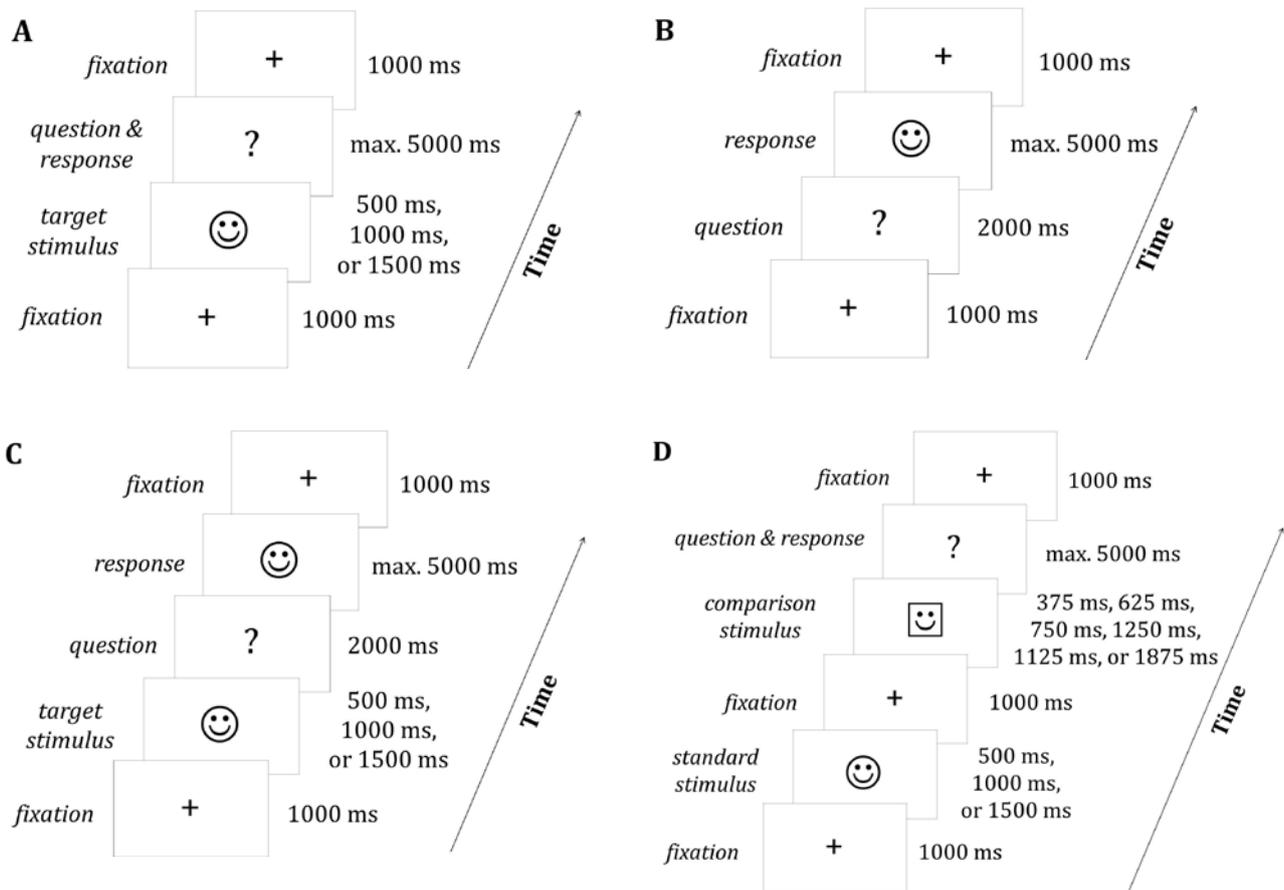

Figure 2 | Timing within a trial in each of the four temporal tasks. (A) Time estimation task, **(B)** Time production task, **(C)** Time reproduction task, and **(D)** Time comparison task.

Spatial ability assessment

Space estimation task

Instructions were analogous to the time estimation task, but here participants were asked to estimate the diameter of the target stimulus which was 2 cm, 5 cm, or 8 cm (**Figure 3A**). They were allowed to provide values with one decimal digit.

Space production task

Instructions were analogous to the time production task, but here participants were asked by a sentence that appeared on the screen to draw lines with length of 2 cm, 5 cm, or 8 cm on an answer paper (**Figure 3B**). In this task there was no practice phase.

Space reproduction task

Instructions were analogous to the time reproduction task, but in this task a target stimulus with diameter of 2 cm, 5 cm or 8 cm was presented on the screen and participants were asked to reproduce the diameter using paper and pencil (**Figure 3C**). In this task there was no practice phase.

Space comparison task

Instructions were analogous to the time comparison task, but here participants were presented with a standard stimulus left on the screen, followed by a comparison stimulus right on the screen, which was either smaller or larger than the standard stimulus. Participants were asked to judge these two different sizes and decide whether the side length of the right presented stimulus was shorter or longer than the diameter of the left (**Figure 3D**). The standard stimuli were displayed with diameters of 2 cm, 5 cm or 8 cm. The sizes of the comparison stimuli were +/- 10% respective to the standard, resulting in standard-small (2 – 1.8 cm, 5 – 4.5 cm, and 8 – 7.2 cm) or standard-large (2 – 2.2 cm, 5 – 5.5 cm, and 8 – 8.8 cm).
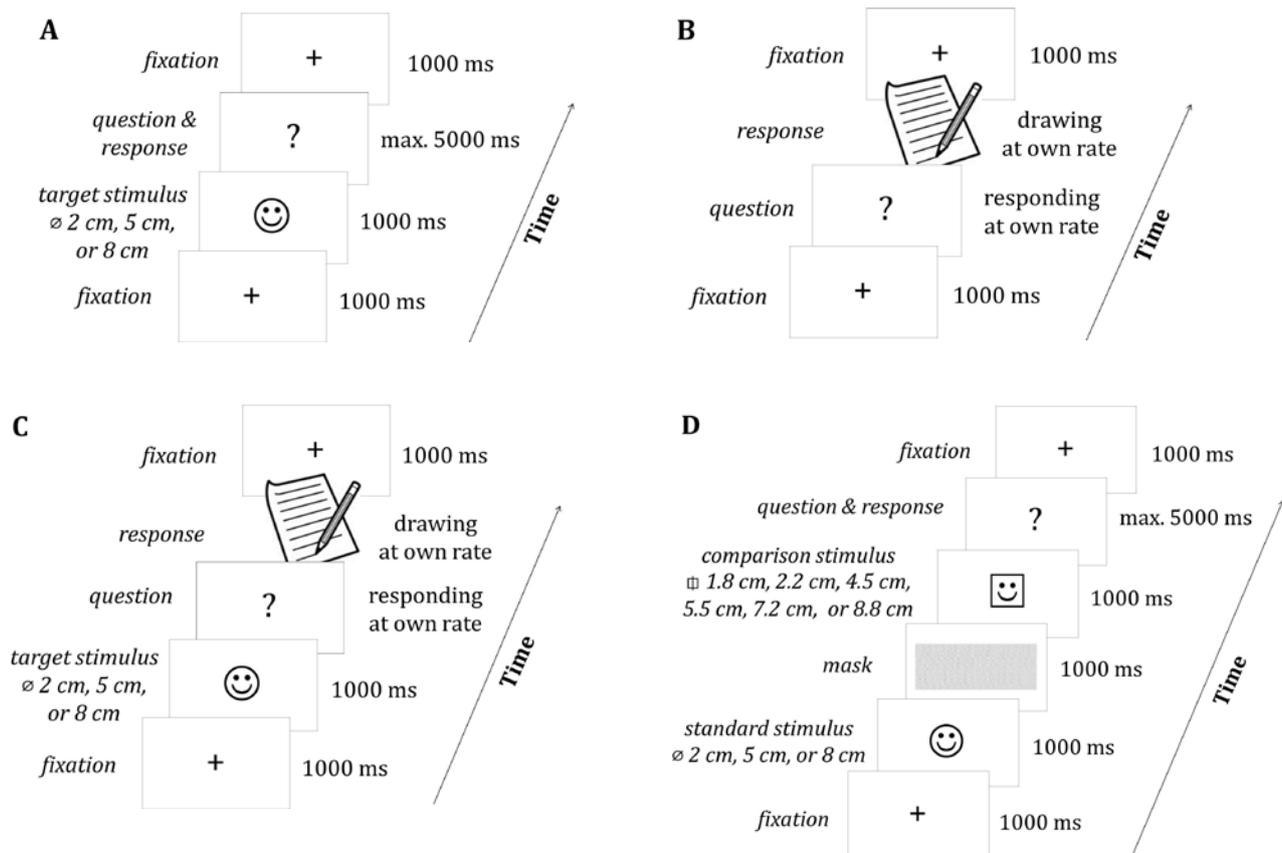

Figure 3 | **Timing within a trial in each of the four spatial tasks. (A)** Space estimation task, **(B)** Space production task, **(C)** Space reproduction task, and **(D)** Space comparison task.

A Dutch translated version of the Edinburgh Handedness Inventory was used to determine hand preference in the participants (Oldfield, 1971).

2.4 Procedure

Participants were scheduled or they could register themselves for a specific time slot online. Upon their arrival to the laboratory, they were asked to read the instructions of the experiment on an instruction sheet, followed by signing the informed consent. The inclusion and exclusion criteria for participation were assessed, and the participants were asked to remove their watches and to turn off their mobile phones during the experiment. Thereafter, participants completed a short demographic survey on the computer at their own rate.

The experimental part consisted of three sessions, which were conducted counterbalanced. Investigation of the individual differences in the perception of time and space was done by a session that lasts approximately 40 minutes. In this session, participants were asked to perform the four measurements (estimation, production, reproduction, and comparison) in a fixed order for both time and space modality. During each task of the experiment there was no provision of feedback. To avoid serial order carryover effects, half of the participants started with the temporal tasks followed by the spatial tasks (*Version A*), and half of the participants completed the measures in the opposite order (*Version B*). Another session of 25 minutes examined the spatial and temporal order memory in navigation and in a third session of 15 minutes, participants filled out some questionnaires and they performed the Bergen left-right discrimination test. In this thesis, the focus will be solely on the examination of the individual differences in the perception of time and space.

During the debriefing, participants were informed about the purpose of the research and they were given an opportunity to ask questions. They were asked not to pass the information on to third parties as that knowledge could impact the data collection and subsequent results. At last, since the present study was part of a larger study, participants were also informed about another experiment and they were invited to participate in that experiment as well.

All instructions in the experiment were written in Dutch. The participants were tested individually in a small, quiet laboratory in the Department of Psychology at the Leiden University. Delivery of stimulus and recording of response was controlled using E-Prime® version 2.0.

2.5 Measures

To identify outliers, raw scores from the estimation, production and reproduction tasks were first converted to Z-scores. Any data value with a Z-score less than -3 or greater than +3 was considered as an outlier. A final data set of raw scores without outliers was then obtained. These scores were converted into standardized scores in order to make both temporal and spatial assessments having the same value unit. The averaged Z-score of each of the three individual tasks (i.e., time duration of 500 ms, 1000 ms, and 1500 ms in the temporal tasks, and diameter of 2 cm, 5 cm, and 8 cm in the spatial tasks) were added up to construct a unit-weighted composite of Z-scores for the concerned task. Thus, these calculations resulted in total six Z-score composites; three representing the estimation, production and reproduction task in the temporal ability assessment, and three for the same tasks in the spatial ability assessment. With regard to the comparison tasks; since it concerned binary data (i.e. correct or incorrect), analysis of correct responses was performed and the obtained proportions were then standardized according the Z-formula, as mentioned above. In this case, the averaged Z-score from each of the six individual tasks (i.e. standard-comparison pairs) were added up to form a Z-score composite. This resulted in two Z-score composites; one for the time comparison task and one for the space comparison task.

2.6 Design

The study design was a 4 x 2 within-subjects design. The within-subjects factors were task (estimation, production, reproduction, comparison) and modality (time, space). There were two between-subjects factors and these included gender (male versus female), and handedness (left-handed, ambidextrous, right-handed).

2.7 Statistical analysis

All statistical analyses were performed using SPSS software for windows version 21.0 (Type III Sum of Squares) with a two-tailed alpha set at 0.05, and confidence intervals at 95%. Firstly, descriptive statistics were carried out to analyse the demographic characteristics of the sample. Mean and standard deviations or median and interquartile ranges are given for each variable, depending on the distribution of the data. At second, assumptions were checked in order to insure that the data collected was appropriate for the type of analyses we wanted to conduct.

The General Linear Model – Repeated Measures (GLM-RM) approach using the standardized data was applied to examine the performance pattern of the participants on the four different tasks within the modality time and the modality space, with gender and handedness as between-subject factors. A multiple regression analysis was conducted to

investigate whether participants' performance at the temporal ability assessment could be predicted by their performance on the individual spatial tasks, and to examine whether the performance at the spatial ability assessment could be predicted by their performance on the individual temporal tasks.

The CV was derived from the tasks by the formula: $c_v = \sigma\ /\ \mu$, in which, c_v is the coefficient of variation, σ is the standard deviation, and μ is mean judgment. The CV gave an indication of the variability in temporal and spatial judgment for each participant, and it evaluated whether the performance of the same target was consistent in each participant (Mioni et al., 2013). CV values were analysed by separate mixed-model analysis of variance (ANOVA) that was conducted for each dependent variable with gender (male vs. female) as the between factor and stimulus duration (500 ms, 1000 ms, 1500 ms) or stimulus diameter/side length (2 cm, 5 cm, 8 cm) as the within factor.

3. Results

Table 2 presents the behavioural data of all participants on the estimation, production, reproduction and comparison tasks in the temporal and spatial ability assessment.

Table 2 | Behavioural data. Average performance on the temporal and spatial ability assessments.

							Z-score [b]
Standard	**500 ms**		**1000 ms**		**1500 ms**		
TE	427.53 (207.07)		927.74 (360.18)		1485.84 (517.29)		-0.41 (0.57)
TP	565.35 (274.15)		961.17 (414.27)		1261.55 (520.82)		-0.21 (0.57)
TR	469.75 (159.23)		794.67 (169.23)		1142.85 (244.17)		-0.50 (0.55)
Comparison	375 ms	625 ms	750 ms	1250 ms	1125 ms	1875 ms	
TC [a]	0.82 (0.23)	0.56 (0.22)	0.74 (0.23)	0.83 (0.15)	0.62 (0.23)	0.91 (0.13)	-1.50 (0.69)
Standard	**2.0 cm**		**5.0 cm**		**8.0 cm**		
SE	1.96 (0.69)		4.80 (1.60)		8.19 (3.15)		0.08 (0.56)
SP	2.38 (0.67)		4.59 (0.85)		6.77 (1.67)		-0.86 (0.51)
SR	2.19 (0.44)		3.91 (0.64)		5.68 (1.08)		-2.75 (0.53)
Comparison	1.8 cm	2.2 cm	4.5 cm	5.5 cm	7.2 cm	8.8 cm	
SC [a]	0.71 (0.24)	0.72 (0.23)	0.52 (0.24)	0.80 (0.19)	0.45 (0.24)	0.91 (0.14)	-0.08 (0.64)

NOTE: Data are presented as mean (standard deviation). Abbreviations: TE = time estimation, TP = time production, TR = time reproduction, TC = time comparison, SE = space estimation, SP = space production, SR = space reproduction, SC = space comparison.
[a] Values were calculated using the proportion of correct responses.
[b] Composite *Z*-scores used in the GLM-RM analysis. Data presented as the sum of the *Z*-scores from the individual tasks (standard deviation).

3.1 Relationship between modality and tasks performance

First of all, correlation and multiple regression analyses were conducted to examine the relationship between the temporal ability assessment and the individual spatial tasks, and between the spatial ability assessment and the individual temporal tasks. **Table 3** summarizes

the descriptive statistics and regression analysis results. Evaluation of standardized residuals and normal probability plots revealed no residual outliers, and assumptions of linearity and homogeneity of variance were met. The smallest variable tolerance value was 0.71, which was above the threshold of 0.10 indicating no significant multicollinearity.

As presented in **Table 3**, the scores on the space comparison task is positively and significantly correlated with the criterion ($r(98) = 0.263$, $p = 0.004$), indicating that those with higher percentage of correct responses on this variable tend to have higher percentage of correct responses during the temporal ability assessment. Furthermore, the relationship between the scores on the time comparison task and the criterion is a positive and highly significant ($r(98) = 0.395$, $p < 0.001$), indicating that participants with more correct responses on the time comparison task tend to have more correct responses on the spatial ability assessment.

The multiple regression model with the individual spatial tasks as predictors produced $R^2 = 0.132$, $F(4,95) = 3.60$, $p = 0.009$. The space comparison scale had significant positive regression weight ($\beta = 0.258$, $p = 0.009$), indicating participants with higher percentage of correct responses on this scale were expected to have higher percentage of correct responses on the temporal ability assessment, after controlling for the other variables in the model. Space estimation, production and reproduction did not contribute to the multiple regression model. With respect to the individual temporal tasks as predictors, the multiple regression model revealed $R^2 = 0.166$, $F(4,95) = 4.73$, $p = 0.002$. The time comparison scale showed significant positive regression weight ($\beta = 0.386$, $p < 0.001$), which indicates that participants with higher percentage of correct responses on this scale were expected to have higher percentage of correct responses on the spatial ability assessment, after controlling for the other variables in the model. Time estimation, production and reproduction did not contribute to the regression model.

Table 3 | Summary statistics. Correlations and results from the regression analysis.

Variable	Mean	SD	Correlation with Temporal ability assessment	Multiple regression weights B	β
Temporal ability assessment	-0.22	0.21			
Space estimation	-0.28	0.97	0.031	0.220	0.106
Space production	-0.56	0.92	0.204	0.408	0.173
Space reproduction	-1.17	1.03	0.209	0.252	0.121
Space comparison	0.02	1.00	0.263*	0.480	0.258*
Variable	**Mean**	**SD**	**Correlation with Spatial ability assessment**	**Multiple regression weights B**	**β**
Spatial ability assessment	-0,49	0.52			
Time estimation	-0.19	0.97	0.048	0.196	0.098
Time production	-0.21	0.97	0.074	0.141	0.068
Time reproduction	-0.48	1.03	0.091	0.097	0.045
Time comparison	0.05	1.00	0.395**	0.632	0.386**

3.2 Performance pattern on the temporal and spatial tasks

At second, GLM-RM analyses using composite Z-scores were applied to examine the effect of gender and handedness on the tasks performance, and to examine the performance pattern on the four different tasks within the modalities time and space, with gender and handedness as between-subject factors. Each composite Z-score indicates how many standard deviations it is from the mean ($Z = 0$), which is presented in **Table 2** for each task. The score can be positive or negative, indicating whether it is above or below the group mean.

No significant effect of handedness was observed ($F(2,94) = 2,88$, $p = 0.061$, $\eta_p^2 = 0.06$), but there was a significant main effect of gender ($F(1,94) = 4,98$, $p = 0.028$, $\eta_p^2 = 0.05$), suggesting that males were less accurate than females on the tasks (-1.29 versus -0.26, respectively). Furthermore, the gender × task interaction effect was significant ($F(3,92) = 2,73$, $p = 0.048$, $\eta_p^2 = 0.08$). Both male and female participants showed larger deviation on the reproduction task (-2.33 and -0.93, respectively). The handedness × task interaction effect was also significant ($F(6,184) = 2,63$, $p = 0.018$, $\eta_p^2 = 0.08$). Left-handers and right-handers revealed more deviation on the reproduction task than mixed-handers (-3.54 and -0.81 versus -0.54, respectively), whereas mixed-handers deviated more on the production task than left-handers and right-handers (-0.96 versus -0.51 and -0.13, respectively). At last, a significant interaction effect of task × modality was found ($F(3,92) = 3,84$, $p = 0.012$, $\eta_p^2 = 0.11$).
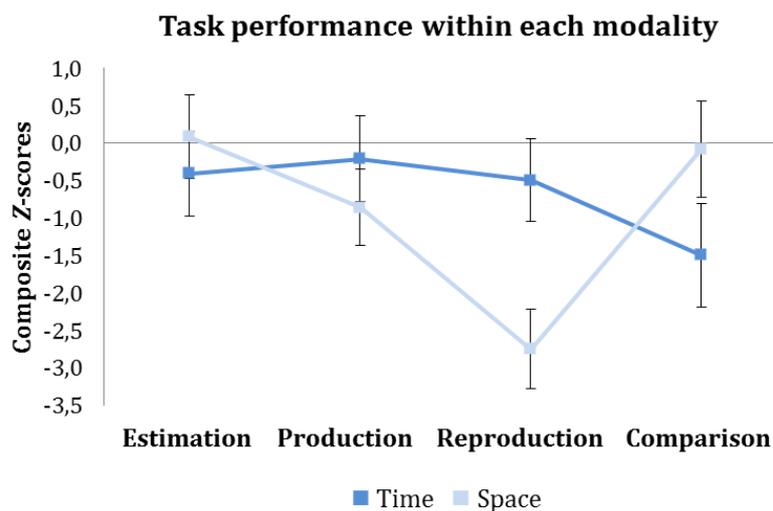

Figure 4 | **General performance pattern on the four different tasks within the modalities time and space.** Analysed on composite Z-scores. The error bars indicate standard errors.

As illustrated in **Figure 4**, within tasks there was a large difference between performance on the reproduction tasks, followed by the difference between the comparison tasks, production

tasks and estimation tasks (2.25, 1.42, 0.65 and 0.49, respectively). Within modality, largest deviations were found on the time comparison task with reference to the time reproduction, time estimation and time production task (1.50, 0.50, 0.40 and 0.21, respectively). Participants deviated more on the space reproduction task with reference to the space production, space estimation and space comparison task (2.75, 0.86, 0.08 and 0.08, respectively).

3.3   Performance variability and consistency

Finally, the CV was calculated and analysed by separate mixed-models ANOVA to determine the performance variability and consistency in each participant during the temporal and spatial ability assessment (**Figure 5**).
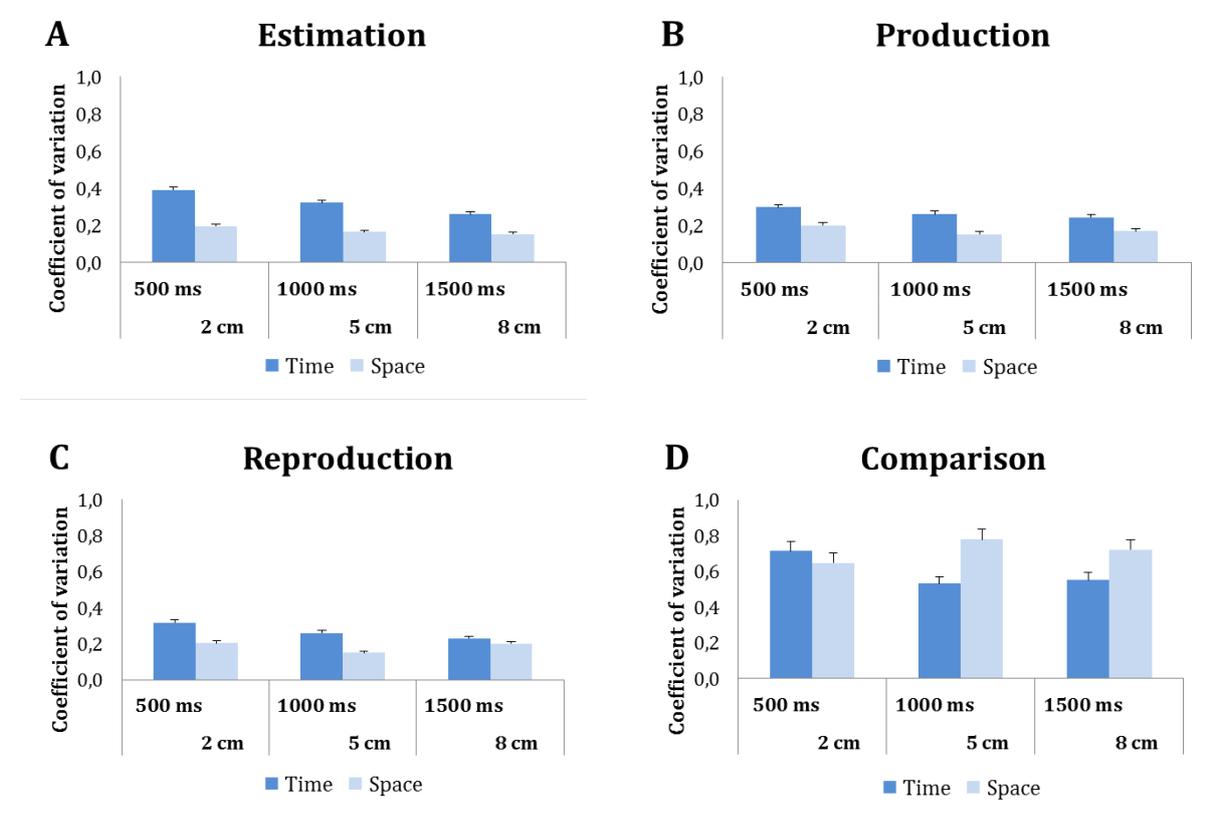
Figure 5 | **Consistency of performance in temporal ability and spatial ability assessment.** Analysed on coefficient of variation in the **(A)** Estimation, **(B)** Production, **(C)** Reproduction, and **(D)** Comparison tasks. The error bars indicate standard errors.

Analysis of CV on the estimation tasks revealed significant main effect of duration ($F(2,97)$ = 16,34, $p < 0.001$, $\eta_p^2 = 0.25$), but no significant main effect for length ($F(2,97) = 2,88$, $p = 0.061$, $\eta_p^2 = 0.06$). Estimation of 500 ms determined more variability than estimating longer durations such as 1000 ms or 1500 ms (0.41, 0.33 and 0.27, respectively) (**Figure 5A**). Analysis of CV on

the production tasks showed significant main effect of duration ($F(2,97) = 3,97$, $p = 0.022$, $\eta_p^2 = 0.08$) and significant main effect of length ($F(2,97) = 16,18$, $p < 0.001$, $\eta_p^2 = 0.25$). Production of 500 ms determined more variability than producing 1000 ms or 1500 ms (0.30, 0.27 and 0.25, respectively) and participants were more variable when producing 2 cm than longer distances such as 5 cm or 8 cm (0.21, 0.15 and 0.17, respectively) (**Figure 5B**). Analysis of CV on the reproduction tasks revealed significant main effect of duration ($F(2,97) = 6,52$, $p = 0.002$, $\eta_p^2 = 0.12$) and significant main effect of length ($F(2,97) = 25,69$, $p < 0.001$, $\eta_p^2 = 0.35$). Reproduction of 500 ms determined more variability than reproducing 1000 ms or 1500 ms (0.32, 0.26 and 0.24, respectively) and participants were more variable when reproducing 2 cm than longer distances such as 5 cm or 8 cm (0.22, 0.15 and 0.19, respectively) (**Figure 5C**). Analysis of CV on the time comparison task showed significant main effect of duration ($F(5,94) = 30,45$, $p < 0.001$, $\eta_p^2 = 0.62$) and significant main effect of length ($F(5,94) = 28,61$, $p < 0.001$, $\eta_p^2 = 0.60$). Participants were more variable when comparing 500 ms duration than 1000 ms or 1500 ms (0.71, 0.54 and 0.60, respectively) and they were more variable when comparing 5 cm than 2 cm or 8 cm (0.77, 0.67 and 0.67, respectively) (**Figure 5D**).

4. Discussion

The main purpose of the current study was to investigate whether there is behavioural evidence for the existence of a common neural basis for the hippocampal time cells and place cells. So far, relatively little work has incorporated the mutual interaction of temporal and spatial perception within the same experimental paradigm. This study was therefore conducted to directly examine this correlation. Temporal and spatial ability in healthy subjects were assessed using an adjusted method of Mioni et al. (2013) with a partly new experimental design. Results revealed a low significant association between the space comparison task and the temporal ability assessment, and a moderate but high significant correlation between the time comparison task and the spatial ability assessment. The additional aim of the study was to examine the individual differences in perceiving time and space; this included gender and participants' strength of handedness, which was measured through the Edinburgh Handedness Inventory (Oldfield, 1971). Our results showed that male participants were generally less accurate than female participants on the different tasks. No effect of handedness on temporal and spatial perception was found. In the following paragraphs, we discuss our findings in further detail.

Starting with the relationship between temporal and spatial perception; results from the correlation and multiple regression analyses showed that the comparison task exclusively is a predictor of participant's performance on the temporal or spatial ability assessment, and that estimation, production and reproduction task do not seem to be involved. A possible reason for

this finding is that comparing stimuli to each other is a task that requires higher order cognitive skills including the working memory (Ivry & Spencer, 2004; Lewis & Miall, 2003a; Lewis & Miall, 2003b). Our findings indicate that there is cooperation of the time cells and place cells in the hippocampus in organizing memories. However, the correlation between the space comparison task and temporal ability assessment is low, and the correlation between the time comparison task and spatial ability assessment is moderate. Thus, our hypothesis that there is a strong association between temporal and spatial perception is not supported, and in fact, our findings are in line with previous studies, which stated that temporal perception and spatial perception are unlinked (e.g., Cappelletti et al., 2009; Casasanto & Boroditsky, 2008; Van der Ham et al., 2010). It could be that the different measurements, which were applied to assess the temporal and spatial function, simply have differential neuronal correlates, causing the dissociation of the ability to perceive time and the ability to perceive space. Another possibility is that the dissociation is caused by the constant environment during the experiment (i.e., participants were tested in a small laboratory during the whole experiment). Several theoretical conceptions have proposed that the distance travelled is the main function of hippocampal networks (e.g., O'Keefe & Burgess, 2005). For example, a previous study with animals reported that temporal tuning only occurs when the animal is moving (Kraus et al., 2013), suggesting that hippocampal neurons were strongly influenced by both time and distance. Thus, although there is evidence that the time cells and place cells cooperate closely (Eichenbaum, 2014; Howard & Eichenbaum, 2014), a certain hippocampal neuronal firing pattern may be required, which is associated with the elapsed time or distance travelled.

The additional purpose of the current study was to look into the effect of gender and handedness on the tasks performance, because up to now, literature shows inconsistent findings with regard to these individual factors. We hypothesized that men would outperform women on the tasks and that left-handers would be more accurate in temporal perception while mixed-handers would show more accuracy in spatial perception than strong-handers. Our results showed that males generally deviated more from the target value on the different tasks than females and there was no effect of handedness observed on the temporal and spatial perception. As mentioned earlier, we could only discuss the role of gender and handedness in perceiving time and space, as long as it was possible with the composition of the final research sample. It should be noted that in the current study the ratio of males and females was unbalanced, as well as the different categories of handedness (mixed-handers and strong-handers). Thus, comparison of the groups may be invalid and therefore, we will not discuss the role of gender and handedness in further detail. It is nonetheless worth discussing participants' general responses in order to understand their performance pattern on each time and space estimation, production, reproduction and comparison task. By doing this, we can, where that is possible, see

if our results are consistent with previous findings and to evaluate critically the strengths and weaknesses of our experimental design.

When we look at the performance pattern of all participants, an increased deviation in the time estimation task was found as there was a decrease in time duration. This result can be explained by the fact that benefits can be expected from counting numbers explicitly in judging time duration that lasts longer than 1000 ms. For instance, is has been demonstrated that the use of strategies are ineffective for periods shorter than approximately 1200 ms (Grondin, 2010; Grondin et al., 2004; Grondin et al., 1999). Production of 1000 ms revealed the least deviation compared to the production of 500 or 1500 ms. As the feedback of the participants after the experiments provided, they applied the strategy vocal counting when they were asked to produce a duration of 1000 ms (e.g., counting '*een-en-twintig*' in Dutch). However, it was harder to use any strategy in producing 500 or 1500 ms. Furthermore, the participants in our study overproduced 500 ms and underproduced 1000 and 1500 ms durations, with the magnitude of underproduction increasing as the time duration increased. This pattern of overproducing 500 ms and the reversal underproduction of 1500 ms is described by the Vierordt's Law, which states that there is a 'central tendency' to overproduce short time intervals and to underproduce long time intervals (Lejeune & Wearden, 2009). Results from the time reproduction task showed less deviation as there was an increase in time duration. A possible reason for this finding is that perceiving short time intervals such as 500 ms is assumed to be 'automatic', which means it is independent of neural systems associated with attention and working memory (Ivry & Spencer, 2004; Lewis & Miall, 2003a; Lewis & Miall, 2003b). Cognitively controlled timing seems to have effect for time intervals longer than 1000 ms. Comparing 500 ms showed the highest number of errors with reference to 1000 ms and 1500 ms. This result was also found in the performance of the control group in the study by Mioni et al. (2013). Generally, the time comparison and time reproduction task in our study showed largest deviation from the target duration than time estimation and time production task. This finding is supported by the fact that, as explained earlier, in comparing and reproducing time duration higher order of cognitive functions (e.g., attention, working memory, and executive function) are needed to keep active the reference duration in order to subsequently compare it with the comparison duration or to reproduce it (Craik & Hay, 1999; Grondin, 2010; Mioni et al., 2013). Of course, our results do not imply that the participants are dealing with cognitive dysfunctions, but it is possible that a response bias was present among participants (e.g., as they became fatigued or loss of attention and concentration).

With regard to the deviations on the spatial ability assessment, it is more difficult to compare the present findings with previous results, because of the minimal research literature on distance and spatial perception. However, it remains possible to evaluate the tasks within the

spatial ability assessment by comparing the tasks to each other. It is remarkable that the participants deviated more from the target diameter as the diameter increased. The average proportion of correct responses was also lower in comparing 5 cm and 8 cm than in comparing 2 cm. Within the spatial ability assessment, participants deviated most when they were asked to reproduce lengths. Participants detailed a number of different strategies that they used in order to perform the spatial tasks. Apparently, short distances were better to estimate and recall as they could judge by visualizing a ruler. When the diameter increased, it was harder to apply this method, because the target stimuli were presented fast and participants were not able to count the centimetres. The space production task showed the second largest deviation. The thing to notice is that the drawing time within the space production and reproduction tasks was without constraints and perhaps participants spent too much time on analysing the diameters which leads to more doubts and less production of accuracy. For instance, it is found that there is a visual guidance system that controls actions over short extent of space, whereas explicit awareness is responsible for longer distances (Proffitt, 2006).

Comparing the four individual tasks between the modality time and the modality space, the general performance pattern illustrated the largest difference in performance between the reproduction tasks, followed by the difference in performance between the comparison tasks, production tasks and estimation tasks, respectively. Space reproduction task seemed to be more difficult than the time reproduction task, while space comparison task appeared to be easier than the time comparison task. Although we were not able to completely rule out differences in task difficulty, we tried in our method to avoid this by equating parameters such as using identical experimental stimuli and instructions.

In order to evaluate the performance variability in all participants, we calculated the CV from the tasks. We predicted that time duration of 1500 ms as target would show less variability compared to shorter durations, because in that case strategies could be applied which was harder when the target was 500 ms or 1000 ms (Grondin, 2010; Grondin et al., 2004; Grondin et al., 1999). This hypothesis is supported by the current findings; maintaining a stable representation of duration seems possible when strategies can be used to help participants in providing their answer. Furthermore, we hypothesized that there would be less variability in performance on the temporal tasks than in performance on the spatial tasks. Analyses on the CV values revealed results that are similar to the pattern of the control group found in Mioni et al. (2013). Strikingly, performance on all spatial tasks generally showed less variability compared to performance on the temporal tasks and this was not expected. It might be suggested that the spatial tasks used in the current study were generally less difficult than the temporal tasks, so that was easier for the participants to maintain a stable performance during each task. However,

as described earlier, differences in task difficulty were avoided as far as possible by using an equal experimental setup for both temporal and spatial assessment.

In conclusion, the present study directly explored the relationship between the ability to perceive time and the ability to perceive space. Evidence from this study supports the idea that there is no fully shared neural basis underpinning temporal perception and spatial perception. Because of the great amount of trials for each target time duration and length, results from this study allow us to understand the performance pattern, and moreover, to evaluate the performance variability on the different tasks. These are important aspects, because the current study used a partly new experimental design to compare different temporal and spatial measurements. By evaluating the performance pattern and variability we can criticize whether our method was valid for appropriate comparison in investigating the relationship between temporal and spatial perception. Thus, for future studies on this association, it is suggested to keep the present findings in mind in order to develop an optimal method to examine the temporal and spatial ability in subjects. To further look into the issue of temporal and spatial perception, it would also be interesting to see how our experimental findings would apply to real world situations, such as estimating the time duration to a destination or judging the distance when navigating from one point to another. Thus a recommendation for future research is to include both short and long time intervals and distances as targets in order to better evaluate the effect of temporal and spatial perception in daily life.

5. Acknowledgements

References

Ahmad, I. A. (1996). A Class of Mann-Whitney-Wilcoxon Type Statistics. *The American Statistician*, *50*(4), 324-327.

Allman, M. J., Teki, S., Griffiths, T. D., & Meck, W. H. (2014). Properties of the internal clock: first-and second-order principles of subjective time. *Annual Review of Psychology*, *65*, 743-771.

Alme, C. B., Miao, C., Jezek, K., Treves, A., Moser, E. I., & Moser, M. B. (2014). Place cells in the hippocampus: Eleven maps for eleven rooms. *Proceedings of the National Academy of Sciences*, *111*(52), 18428-18435.

Ankney, C. D. (1995). Gender differences in brain size and mental abilities: Comments on R. Lynn and D. Kimura. *Personality and Individual Differences*, *18*(3), 423-424.

Basso, G., Nichelli, P., Frassinetti, F., & di Pellegrino, G. (1996). Time perception in a neglected space. *Neuroreport*, *7*(13), 2111-2114.

Block, R. A., Hancock, P. A., & Zakay, D. (2000). Gender differences in duration judgments: A meta-analytic review. *Memory & Cognition*, *28*(8), 1333-1346.

Block, R. A., & Zakay, D. (1997). Prospective and retrospective duration judgments: A meta-analytic review. *Psychonomic Bulletin & Review*, *4*(2), 184-197.

Brooks, J. L. (2012). Counterbalancing for serial order carryover effects in experimental condition orders. *Psychological Methods*, *17*(4), 600.

Brown, S. W., & Stubbs, D. A. (1992). Attention and interference in prospective and retrospective timing. *Perception London*, *21*, 545-545.

Bschor, T., Ising, M., Bauer, M., Lewitzka, U., Skerstupeit, M., Müller-Oerlinghausen, B., & Baethge, C. (2004). Time experience and time judgment in major depression, mania and healthy subjects. A controlled study of 93 subjects. *Acta Psychiatrica Scandinavica*, *109*(3), 222-229.

Bunsey, M., & Eichenbaum, H. (1996). Conservation of hippocampal memory function in rats and humans. *Nature*, *379*(6562), 255-257.

Burnett, S. A., Lane, D. M., & Dratt, L. M. (1982). Spatial ability and handedness. *Intelligence*, *6*(1), 57-68.

Cameron, H. A., & Glover, L. R. (2015). Adult Neurogenesis: Beyond Learning and Memory. *Annual Review of Psychology*, *66*, 53-81.

Cappelletti, M., Freeman, E. D., & Cipolotti, L. (2009). Dissociations and interactions between time, numerosity and space processing. *Neuropsychologia*, *47*(13), 2732-2748.

Casasanto, D., & Boroditsky, L. (2008). Time in the mind: Using space to think about time. *Cognition*, *106*(2), 579-593.

Clausen, J. (1950). An evaluation of experimental methods of time judgment. *Journal of Experimental Psychology*, *40*(6), 756.

Craik, F. I., & Hay, J. F. (1999). Aging and judgments of duration: Effects of task complexity and method of estimation. *Perception & Psychophysics*, *61*(3), 549-560.

Crollen, V., Grade, S., Pesenti, M., & Dormal, V. (2013). A common metric magnitude system for the perception and production of numerosity, length, and duration. *Frontiers in Psychology*, *4*, 449.

Danckert, J., Ferber, S., Pun, C., Broderick, C., Striemer, C., Rock, S., & Stewart, D. (2007). Neglected time: impaired temporal perception of multisecond intervals in unilateral neglect. *Journal of Cognitive Neuroscience*, *19*(10), 1706-1720.

Eichenbaum, H. (2014). Time cells in the hippocampus: a new dimension for mapping memories. *Nature Reviews Neuroscience*, *15*(11), 732-744.

Funnell, M. G., Corballis, P. M., & Gazzaniga, M. S. (2003). Temporal discrimination in the split brain. *Brain and Cognition*, *53*(2), 218-222.

Gerathewohl, S. (1967). Orientation and navigation in space-time. *Annals of the New York Academy of Sciences*, *138*(2), 504-514.

Grondin, S. (2010). Timing and time perception: a review of recent behavioural and neuroscience findings and theoretical directions. *Attention, Perception, & Psychophysics*, *72*(3), 561-582.

Grondin, S., Meilleur-Wells, G., & Lachance, R. (1999). When to start explicit counting in a time-intervals discrimination task: A critical point in the timing process of humans. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(4), 993.

Grondin, S., Ouellet, B., & Roussel, M. E. (2004). Benefits and limits of explicit counting for discriminating temporal intervals. *Canadian Journal of Experimental Psychology, 58*(1), 1.

Guo, J. H., Qu, W. M., Chen, S. G., Chen, X. P., Lv, K., Huang, Z. L., & Wu, Y. L. (2014). Keeping the right time in space: importance of circadian clock and sleep for physiology and performance of astronauts. *Military Medical Research*, *1*(1), 23.

Halpern, D. F. (1997). Gender differences in intelligence: Implications for education. *American Psychologist*, *52*(10), 1091.

Hausmann, M., Slabbekoorn, D., Van Goozen, S. H., Cohen-Kettenis, P. T., & Güntürkün, O. (2000). Gender hormones affect spatial abilities during the menstrual cycle. *Behavioral neuroscience*, *114*(6), 1245.

Howard, M. W., & Eichenbaum, H. (2014). Time and space in the hippocampus. *Brain Research*. 345-354.

Ishihara, M., Keller, P. E., Rossetti, Y., & Prinz, W. (2008). Horizontal spatial representations of time: evidence for the STEARC effect. *Cortex*, *44*(4), 454-461.

Ivry, R. B., & Spencer, R. M. (2004). The neural representation of time. *Current opinion in neurobiology*, *14*(2), 225-232.

Jackson, R. E., Willey, C. R., & Cormack, L. K. (2013). Learning and Exposure Affect Environmental Perception Less than Evolutionary Navigation Costs. *PloS one*, *8*(4).

Kimura, D. (1992). Gender differences in the brain. *Scientific American*, *267*(3), 118-125.

Kitamura, T., & Kumar, R. (1983). Time estimation and time production in depressive patients. *Acta Psychiatrica Scandinavica*, *68*(1), 15-21.

Kolb, B., & Whishaw, I. Q. (2009). *Fundamentals of Human Neuropsychology*. NY: Macmillan.

Konturek, P. C., Brzozowski, T., & Konturek, S. J. (2011). Gut clock: implication of circadian rhythms in the gastrointestinal tract. *Journal of Physiology and Pharmacology*, *62*(2), 139-150.

Kraus, B. J., Robinson, R. J., White, J. A., Eichenbaum, H., & Hasselmo, M. E. (2013). Hippocampal "time cells": time versus path integration. *Neuron*, *78*(6), 1090-1101.

Lejeune, H., & Wearden, J. H. (2009). Vierordt's The Experimental Study of the Time Sense (1868) and its legacy. *European Journal of Cognitive Psychology*, *21*(6), 941-960.

Lewis, P. A., & Miall, R. C. (2003a). Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Current opinion in neurobiology*, *13*(2), 250-255.

Lewis, P. A., & Miall, R. C. (2003b). Brain activation patterns during measurement of sub-and supra-second intervals. *Neuropsychologia*, *41*(12), 1583-1592.

MacDonald, C. J., Lepage, K. Q., Eden, U. T., & Eichenbaum, H. (2011). Hippocampal "time cells" bridge the gap in memory for discontiguous events. *Neuron*, *71*(4), 737-749.

Mahlberg, R., Kienast, T., Bschor, T., & Adli, M. (2008). Evaluation of time memory in acutely depressed patients, manic patients, and healthy controls using a time reproduction task. *European Psychiatry*, *23*(6), 430-433.

Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes*, *9*(3), 320.

Meck, W. H. (1996). Neuropharmacology of timing and time perception. *Cognitive Brain Research*, *3*(3), 227-242.

Mioni, G., Mattalia, G., & Stablum, F. (2013). Time perception in severe traumatic brain injury patients: a study comparing different methodologies. *Brain and Cognition*, *81*(3), 305-312.

Montare, A. (1985). Learning effects of knowledge of results upon time estimation. *Perceptual and Motor Skills*, *60*(3), 871-877.

Montare, A. (1988). Further learning effects of knowledge of results upon time estimation. *Perceptual and Motor Skills*, *66*(2), 579-588.

Moser, E. I., Kropff, E., & Moser, M. B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neurosciences*, *31*, 69-89.

Nico, D., Piccardi, L., Iaria, G., Bianchini, F., Zompanti, L., & Guariglia, C. (2008). Landmark based navigation in brain-damaged patients with neglect. *Neuropsychologia*, *46*(7), 1898-1907.

O'Keefe, J., & Burgess, N. (2005). Dual phase and rate coding in hippocampal place cells: theoretical significance and relationship to entorhinal grid cells. *Hippocampus*, *15*(7), 853-866.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*(1), 171-175.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*(1), 97-113.

Phillips, K., & Silverman, I. (1997). Differences in the relationship of menstrual cycle phase to spatial performance on two-and three-dimensional tasks. *Hormones and Behavior*, *32*(3), 167-175.

Poirel, N., Vidal, M., Pineau, A., Lanoë, C., Leroux, G., Lubin, A., ... & Houdé, O. (2015). Evidence of different developmental trajectories for length estimation according to egocentric and allocentric viewpoints in children and adults. *Experimental Psychology, 58*(2), 131-135.

Proffitt, D. R. (2006). Distance perception. *Current Directions in Psychological Science*, *15*(3), 131-135.

Rammsayer, T. H. (2001). Ageing and temporal processing of durations within the psychological present. *European Journal of Cognitive Psychology*, *13*(4), 549-565.

Rammsayer, T., & Lustnauer, S. (1989). Gender differences in time perception. *Perceptual and Motor Skills*, *68*(1), 195-198.

Rodriguez, P. F. (2010). Human navigation that requires calculating heading vectors recruits parietal cortex in a virtual and visually sparse water maze task in fMRI. *Behavioural Neuroscience*, *124*(4), 532.

Rowland, D. C., & Moser, M. B. (2013). Time finds its place in the hippocampus. *Neuron*, *78*(6), 953-954.

Saini, C., Brown, S. A., & Dibner, C. (2015). Human peripheral clocks: applications for studying circadian phenotypes in physiology and pathophysiology. *Frontiers in Neurology*, *6*.

Schiff, W., & Oldak, R. (1990). Accuracy of judging time to arrival: effects of modality, trajectory, and gender. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(2), 303.

Sciutti, A., Burr, D., Saracco, A., Sandini, G., & Gori, M. (2014). Development of context dependency in human space perception. *Experimental Brain Research*, *232*(12), 3965-3976.

Sucala, M., Scheckner, B., & David, D. (2011). Psychological time: interval length judgments and subjective passage of time judgments. *Current Psychology Letters. Behaviour, Brain and Cognition*, *26*(2).

Swift, E. J., & McGeoch, J. A. (1925). An experimental study of the perception of filled and empty time. *Journal of Experimental Psychology*, *8*(3), 240.

Tucker-Drob, E. M. (2011). Individual differences methods for randomized experiments. *Psychological Methods*, *16*(3), 298.

Tysk, L. (1984). Time perception and affective disorders. *Perceptual and Motor Skills*, *58*(2), 455-464.

Vallesi, A., Binns, M. A., & Shallice, T. (2008). An effect of spatial–temporal association of response codes: Understanding the cognitive representations of time. *Cognition*, *107*(2), 501-527.

Van der Ham, I. J. M., Van Zandvoort, M. J. E., & Postma, A. (2010). Ruimtelijke en tijdsgebonden aspecten van navigatie in twee neurologische patiënten. *Tijdschrift voor Neuropsychologie, 5*, 33-41.

Van Rijn, H., Gu, B. M., & Meck, W. H. (2014). Dedicated clock/timing-circuit theories of time perception and timed performance. *Neurobiology of Interval Timing, 829,* 75-99.

Verhage, F. (1964). *Intelligentie en Leeftijd: Onderzoek bij Nederlanders van twaalf tot zevenenzeventig jaar.* Assen: Van Gorcum.

Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of gender differences in spatial abilities: a meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*(2), 250.

Walsh, V. (2003). A theory of magnitude: common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*(11), 483-488.

Westfall, J. E., Jasper, J. D., & Zelmanova, Y. (2010). Differences in time perception as a function of strength of handedness. *Personality and Individual Differences*, *49*(6), 629-633.

Whitehead, L., & Banihani, S. (2014). The evolution of contralateral control of the body by the brain: Is it a protective mechanism? *Laterality: Asymmetries of Body, Brain and Cognition*, *19*(3), 325-339.

Yew, B., Alladi, S., Shailaja, M., Hodges, J. R., & Hornberger, M. (2013). Lost and forgotten? Orientation versus memory in Alzheimer's disease and frontotemporal dementia. *Journal of Alzheimer's Disease*, *33*(2), 473-481.