

Interindividual differences in preferred directions of perceptual and motor decisions

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Both the perceptual system and the motor system can be faced with ambiguous information and then have to choose between different alternatives. Often these alternatives involve decisions about directions, and anisotropies have been reported for different tasks. Here we measured interindividual differences and temporal stability of directional preferences in eye movement, motion perception, and thumb movement tasks. In all tasks, stimuli were created such that observers had to decide between two opposite directions in each trial and preferences were measured at 12 axes around the circle. There were clear directional preferences in all utilized tasks. The strongest effects were present in tasks that involved motion, like the smooth pursuit eye movement, apparent motion, and structure-from-motion tasks. The weakest effects were present in the saccadic eye movement task. Observers with strong directional preferences in the eye movement tasks showed shorter latency costs for target-conflict trials compared to single-target trials, suggesting that directional preferences might be advantageous for solving the target conflict. Although there were consistent preferences across observers in most of the tasks, there was also considerable variability in preferred directions between observers. The magnitude of preferences and the preferred directions were correlated only between few tasks. While the magnitude of preferences varied substantially over time, the direction of these preferences was stable over several weeks. These results indicate that individually stable directional preferences exist in a range of perceptual and motor tasks.

Introduction

In daily life, humans can be faced with choices between highly similar alternatives and it might be important for survival to quickly reach a decision, even when there is little information that distinguishes the alternatives. For instance, if a wrong-way driver is heading towards you, you might be able to avoid a collision by steering to the left or to the

right, but only if you react quickly enough, without contemplating about the advantages and disadvantages of left and right. In a similar way, our perceptual system can be faced with ambiguous information and has to choose between different interpretations. Famous examples are binocular rivalry, where different information is displayed to the two eyes (Wheatstone, 1838; Blake, 2001), and two-dimensional (2-D) stimuli that allow different three-dimensional (3-D) interpretations, such as the Necker cube (Necker, 1832; Long & Toppino, 2004) or structure-from-motion stimuli (Wallach & O'Connell, 1953; Andersen & Bradley, 1998).

In some cases such situations involve decisions about directions, and preferences for certain directions have been reported previously. As an example for motor biases, saccadic eye movements are preferentially executed in certain directions when two equivalent stimuli are shown at opposite locations (Findlay, 1980). Depth order in transparent motion is a good example for directional biases in perception. In such a display, two groups of dots, moving in two different directions, form two different surfaces, and the visual information is ambiguous about the depth order of these surfaces. Previous studies showed that observers have preferences to see a certain motion direction in the front and that these preferences are stable for at least two weeks (Mamassian & Wallace, 2010; Schütz, 2011).

How can such directional preferences be implemented? Perceptual decision-making is often modeled in a Bayesian framework (for reviews see Mamassian, Landy, & Maloney, 2002; Kersten, Mamassian, & Yuille, 2004). Here directional preferences could be represented at two different stages. In the first stage, there could be a prior for certain directions. A prior is typically based on experience with the stimulus or the task, and directional preferences could be caused, for instance, by unequal probabilities of different directions and anisotropies in scene statistics (Mamassian & Goutcher, 2001). The prior is combined with sensory

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information, which is represented by the likelihood function. Ambiguous visual information will lead to an inconclusive likelihood function. By combining the inconclusive likelihood function with the prior distribution, the posterior distribution is disambiguated. In the next step, the posterior distribution is typically combined with a gain function, before a final decision is reached. The gain function is the second stage where directional preferences could be represented. Here a directional preference could be caused by unequal expected values for different directions, for instance, by differences in biomechanical costs (Soechting, Buneo, Herrmann, & Flanders, 1995).

Although the physiological basis will be quite different for the two possible stages, major theoretical implications apply to a bias in the prior and a bias in the gain function in the same way. Concerning the cause of the directional preferences, it is very likely that factors such as scene statistics or biomechanical costs are shared amongst the whole population. This leads to the prediction that directional preferences should be shared amongst the population as well. Concerning the consequences of directional preferences, there will be at least one advantage and one disadvantage. On the positive side, such preferences could save time and effort when the decision alternatives are otherwise indistinguishable. On the negative side, they might impair sensitivity to subtle differences in alternatives (Mamassian & Wallace, 2010) and lead to incorrect decisions.

While directional preferences have been observed in several different tasks, it has not been investigated specifically whether these preferences are shared among tasks or whether they are independent of one another. This is an important question because it potentially distinguishes between different architectures of decision-making (Gottlieb, Balan, Oristaglio, & Schneider, 2009; Cisek, 2012). In the extreme case, decisions could be reached in the specific modules that are responsible for the planned motor response. As a result, directional preferences should be independent for different tasks. In the other extreme case, there could be a central decision stage, which is shared for different motor systems. As a result, there should be shared directional preferences for different tasks.

In this study we investigated whether such directional preferences exist for different perceptual and motor tasks, and if this is the case, whether these preferences are aligned for the different tasks. The used tasks were selected to cover different effectors (eye movements and finger movements), different motor programs within the same effector (saccadic and smooth pursuit eye movements), and perceptual tasks (structure-from-motion and apparent motion).

Methods

Design

We performed six experiments to measure directional preferences for four motor tasks (saccadic and smooth pursuit eye movements and movements of the left and right thumb) and two perceptual tasks (structure-from-motion and apparent motion; Figure 1). The tasks were designed such that all data could be analyzed in the same way and easily be compared. In each experiment visual stimuli were arranged such that directional preferences were measured along 12 axes with a separation of 15° (Figure 2A). Each axis was presented 10 times, except in the thumb movement experiments, where each axis was only presented five times. In the eye movement and thumb movement tasks, single-target trials were interspersed to measure baseline response latency. The single targets could appear at one of 24 possible directions, each presented only once. All experiments were performed in one session of about 1 hr, in a random order. To estimate the stability of directional preferences, some of the observers repeated the experiments after about 1, 4, and 12 weeks.

Subjects

Thirty naive observers participated in these experiments (14 male and 16 female, age 23.7 ± 2.8 years, all of them right-handed). Observers were students of the Justus-Liebig-University Giessen and received either monetary compensation or partial course credit for participation. Experiments were in accordance with the principles of the Declaration of Helsinki and approved by the local ethics committee LEK FB06 at the University Giessen (proposal number 2009-0008). Twenty-eight, 21, and 18 observers repeated the experiment one, two, or three times, respectively, about 1, 4, and 12 weeks after the first measurement. One observer had to be excluded because she/he did not show any directional preferences.

Equipment

Observers were seated in a dark room facing a 21-in. Sony GDM-F520 CRT (Sony, Tokyo, Japan) monitor driven by an Nvidia Quadro NVS 290 (NVIDIA, Santa Clara, CA) graphics board with a refresh rate of 100 Hz. At a viewing distance of 47 cm, the active screen area subtended 45 degrees of visual angle (dva) in the horizontal direction, and 36 dva vertical on the subject's retina. With a spatial resolution of $1280 \times$

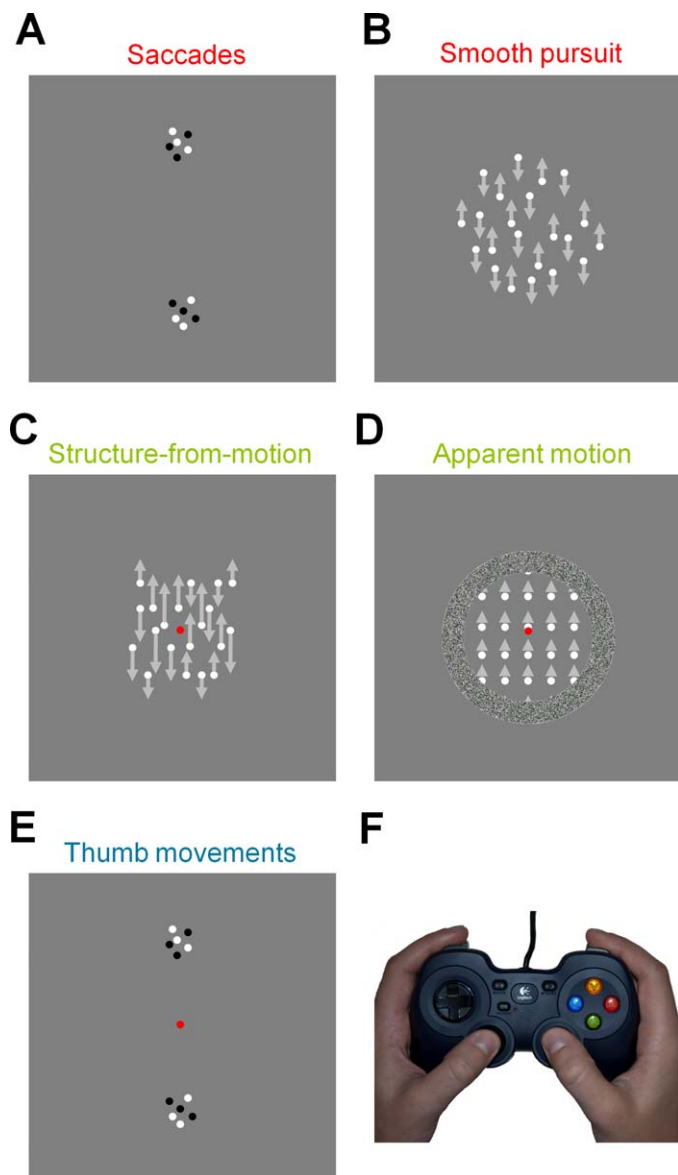


Figure 1. Illustration of experimental stimuli and tasks. All trials started with a red fixation target at the screen center (Thaler et al., 2013). Stimuli are not drawn to scale. (A) In the saccade task, observers had to saccade from central fixation to one of two peripheral dot clouds. (B) In the smooth pursuit task, observers had to pursuit one of two spatially overlapping RDKs. (C) In the structure-from-motion task, observers had to indicate the perceived rotation of an ambiguously rotating cylinder. The length of the vectors indicates the speed of the dots, according to the orthographic projection. (D) In the apparent motion task, observers had to indicate the perceived motion direction of an ambiguously moving grid of dots. (E) In the thumb movement task, observers had to move a joystick on a standard game pad in the direction of one of two peripheral dot clouds. (F) Image of an observer with the game pad.

1024 pixels, this results in 28 pixels/dva. The luminance of white, gray, and black pixels was 94, 48, and 1 cd/m^2 , respectively, and the output of the monitor was linearized. The observer's head was stabilized by a chin and a forehead rest, and the display was viewed binocularly. Eye position signals of the right eye were recorded with a video-based eye tracker (EyeLink 1000; SR Research Ltd., Kanata, Ontario, Canada) and sampled at 1000 Hz. Thumb movements were registered with the left and right analog sticks on a game pad (Logitech F310; Logitech, Morges, Switzerland) (Figure 1F) and sampled at 125 Hz. Stimulus display was controlled by the Psychtoolbox (Brainard, 1997; Pelli, 1997) and the eye tracker by the Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002).

Visual stimuli

All stimuli were presented on a homogeneous gray background. Stimuli in all tasks were composed of a number of dots with a size of 0.14×0.14 dva. In the saccade and the thumb movement tasks, two wedges at opposite directions were shown. The wedges had an inner and outer radius of 7.5 and 12.5 dva. The number of dots was varied in different trials between 20 and 25, and the dot density was varied between 1.6 and 2 dots/dva². The dots were stationary. In the smooth pursuit task, two random-dot kinematograms (RDK), each consisting of 157 dots, were shown simultaneously in a circular aperture of 10 dva radius, centered at the screen center. The dots were moving at a speed of 10 dva/s in opposite directions for the two RDKs. Individual dots had a lifetime of 200 ms and were randomly repositioned afterwards. In the structure-from-motion task, 200 dots were displayed in a square area of 10×10 dva, centered at the screen center. Dot velocity was following a sinusoidal function to generate the orthographic projection of a cylinder, rotating at a speed of 90°/s. The rotation direction of such a display is ambiguous. In the apparent motion task, a grid of dots with a spacing of 0.8 dva was displayed within a circular aperture of 8 dva radius, centered at the screen center. The aperture was surrounded by a 2-dva thick noise pattern to facilitate the appearance of an aperture and the perception of apparent motion (Williams, Elfar, Eskandar, Toth, & Assad, 2003). Every 100 ms the dots stepped halfway to the next dot by 0.4 dva. This is consistent with a motion of 4 dva/s in two possible directions.

Experimental procedure

Observers had to fixate a red combination of a bull's eye and cross hair (Thaler, Schütz, Goodale, &

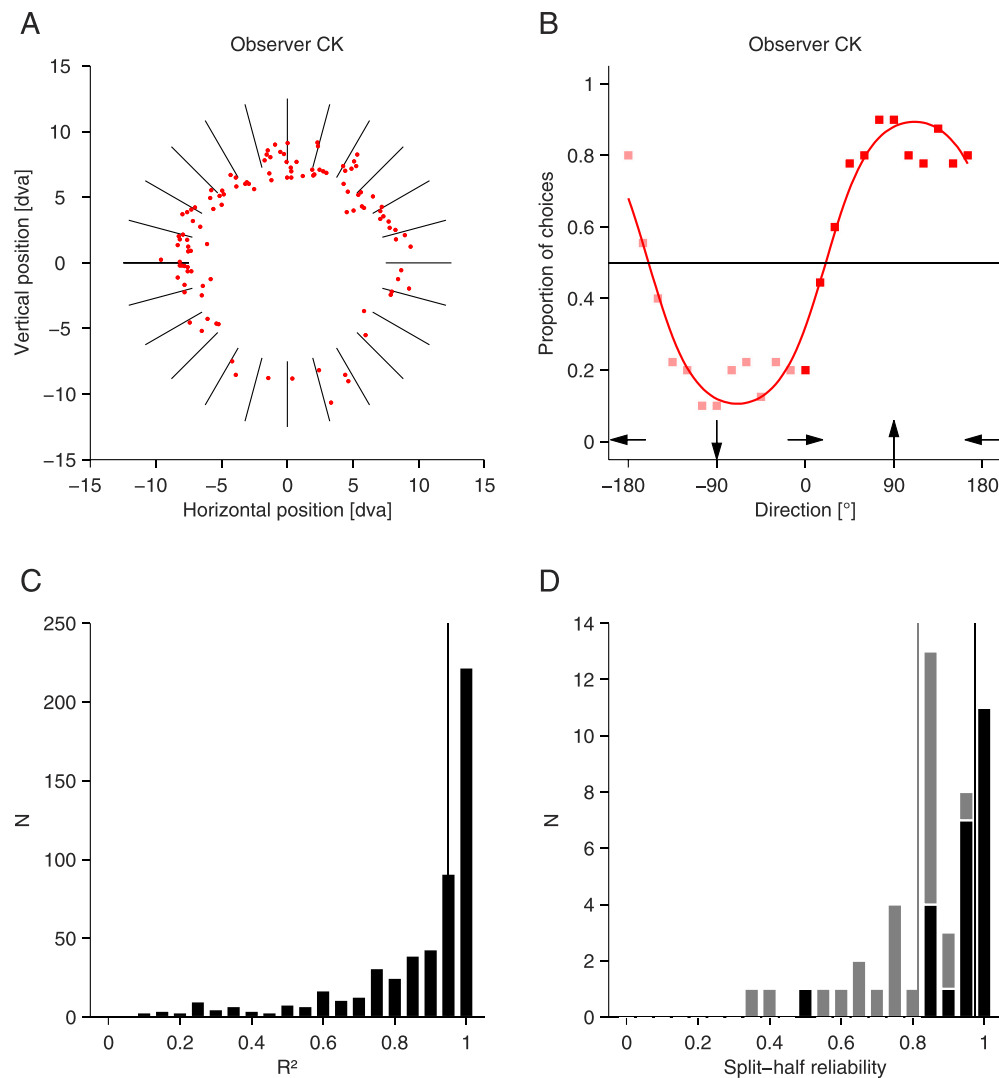


Figure 2. Analysis of directional preferences. (A) Saccade endpoints for observer CK. The black lines indicate the centers of the presented stimuli. In each trial two stimuli at opposite directions were shown. If there would be no directional preference, saccade endpoints should be distributed equally in all directions. (B) Proportion of saccade choices for observer CK based on the saccade endpoints from (A). Only the dark data points represent independent data. The light data points are calculated by subtracting the dark data points from unity. If there would be no directional preference, all data points should lie on the black horizontal line. The colored line is the fit of the model with a preferred direction of 111° , a magnitude of preferences of 0.329 and an R^2 of 0.95. (C) Distribution of R^2 of the model for all data sets. The vertical line indicates the median R^2 of 0.95. (D) Split-half reliability of the estimations of the magnitude of preferences (gray) and of the preferred direction (black). The vertical lines indicate the median reliabilities of 0.81 and 0.97 for magnitude and direction, respectively.

Gegenfurtner, 2013) and press an assigned button on the game pad to start the trial. In the perceptual and the thumb tasks, the fixation target remained visible throughout the trial and observers had to maintain fixation within a circle of a 2 dva radius. In the eye movement tasks, the fixation target disappeared after a random interval of 750 to 1500 ms and the eye movement targets appeared at the same time. In the smooth pursuit and the perceptual tasks, the visual motion was presented for 1 s. In the perceptual tasks, the observers had to select the perceived motion direction afterwards. A trial in the saccade task ended

when the eye position exceeded an eccentricity relative to the screen center of 4 dva. A trial in the thumb movement tasks ended when the game pad stick exceeded an eccentricity of 7.5 dva.

Data analysis

Eye velocity signals were obtained by digital differentiation of eye position signals over time. The eye position and velocity signals were filtered by a Butterworth filter with cutoff frequencies of 30 and 20

Hz, respectively. Saccade onset and offsets were determined with the EyeLink saccade algorithm. To avoid a contamination of pursuit velocity and pursuit direction by saccades, they were removed from the velocity traces. Eye velocity during a saccade was replaced by a linear interpolation between eye velocity 50 ms before saccade onset and 50 ms after saccade offset. This procedure was applied before the velocity signal was filtered. Pursuit onset was determined as the intercept of the best-fitting regression on the velocity trace (Schütz, Braun, & Gegenfurtner, 2007; Braun et al., 2008). Smooth pursuit decision was evaluated as the average eye movement direction in a 50-ms interval, 450 ms after target motion onset. Pursuit gain was calculated as the average ratio of eye and target speed between 400 and 700 ms after target motion onset.

Exclusion criteria

Single trials were excluded in the smooth pursuit task if the pursuit gain was lower than 0.5 or larger than 1.3 or if the pursuit latency was lower than 50 or larger than 400 ms. Trials in the perceptual and the thumb movement tasks were excluded if central fixation was not maintained. A whole session was excluded if fewer than 50% of the trials in the session were valid. This happened for 4% of the sessions in the each of the saccade and thumb movement tasks and for 22% of the sessions in the smooth pursuit task.

Modeling and statistical analysis

The preference for each of the tested axes was calculated as the proportion of choices in the respective directions (Figure 2B). We used a cosine model (Mamassian & Wallace, 2010) with two free parameters to extract the overall preferred direction (θ_m) and the magnitude of preferences (b):

$$y = 10^b \cos(\theta - \theta_m) \quad (1)$$

We used an exponential scaling parameter (b), because the distribution of parameter values was closer to a normal distribution on an exponential scale. The magnitude of preferences was constrained within -1 to 2 , because stronger preferences could not be distinguished with the 15° directional resolution of the data. The model responses were transformed into proportion of choices using a logit model:

$$p = \frac{e^y}{(1 + e^y)} \quad (2)$$

This model could explain 95% (median) of the variability in directional choices (Figure 2C), and it

produced a reliable estimate of the preferences since the Spearman-Brown (Brown, 1910; Spearman, 1910) corrected split-half reliabilities amounted to 0.81 for magnitude and 0.97 for direction (Figure 2D). To calculate split-half reliabilities, the model was fitted separately to odd and even trials and the resulting fits were correlated with each other. These reliabilities are an estimate of how well our methods measure the observer's preferences and represent an upper boundary to any intertask or temporal correlations.

The circular statistics toolbox (Berens, 2009) was used for circular measurements. Hodges-Ajne tests for circular data were used (Hodges, 1955; Ajne, 1968) to test whether preferred directions were distributed uniformly. Spearman correlations were used to test correlations between the magnitude of preferences. To test correlations between preferred directions, a circular correlation coefficient was used, analogous to a Pearson correlation coefficient (Jammalamadaka & Sengupta, 2001), with α and β as the two samples and μ_α and μ_β as their corresponding means.

$$p_c(\alpha, \beta) = \frac{\sum \sin(\alpha - \mu_\alpha) \sin(\beta - \mu_\beta)}{\sqrt{\sum (\sin^2(\alpha - \mu_\alpha)) \sum (\sin^2(\beta - \mu_\beta))}} \quad (3)$$

All correlation coefficients are reported twice, with and without correction for attenuation. To correct for attenuation, a correlation coefficient is divided by the geometric mean of the reliability of the correlated measurements (Spearman, 1904). Changes in the magnitude or direction of preferences between successive measurements were analyzed with linear mixed-effects models.

Results

Directional preferences

In this study we compared directional preferences for different perceptual and motor tasks. Based on the proportion of choices for the different directions, we estimated the preferred direction and the magnitude of preferences (Figure 2; Equations 1 and 2). The strongest directional preferences (b) were present in the structure-from-motion task with an average magnitude of 1.02 ± 0.56 (SD ; Figure 3; Table 1). This is a very strong effect, because it means that the preferred direction was chosen over the opposite direction in 100% of the trials. Furthermore the directional tuning of preferences was very precise, because the transition between 15% to 85% choices occurred within an angle

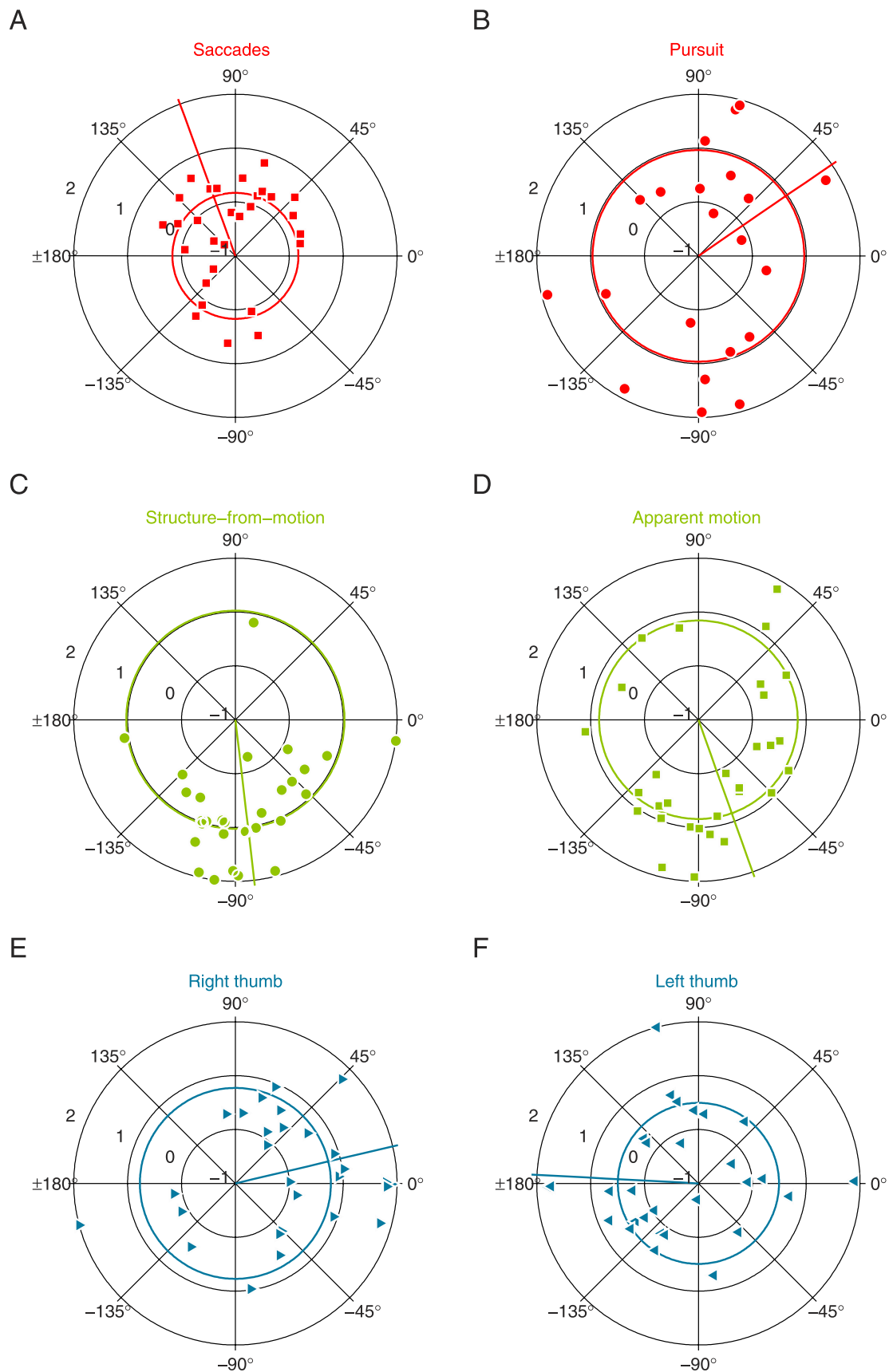


Figure 3. Individual directional preferences. Magnitude of preferences and preferred directions are shown in polar coordinates. Symbols represent data of individual observers. The colored circle represents the average magnitude across observers. The colored line represents the average preferred direction across observers.

Task	Magnitude	Direction
Saccade	0.17 ± 0.37	$110^\circ \pm 64^\circ$ (0.087)
Smooth pursuit	0.96 ± 0.73	$34^\circ \pm 76^\circ$ (0.466)
Structure-from-motion	1.02 ± 0.56	$-83^\circ \pm 39^\circ$ (0.001)
Apparent motion	0.84 ± 0.46	$-70^\circ \pm 62^\circ$ (0.020)
Right thumb	0.77 ± 0.65	$13^\circ \pm 59^\circ$ (0.003)
Left thumb	0.50 ± 0.64	$177^\circ \pm 71^\circ$ (0.208)

Table 1. Average magnitude and direction of preferences. *Note:* p -values for a Hodges-Ajne test against a uniform distribution are given in parentheses for the direction of preferences.

of 20° . The weakest directional preferences were estimated for choices made by the left thumb (0.50 ± 0.64) and saccadic eye movements (0.17 ± 0.37). Even this constitutes a considerable bias, because the preferred direction was still chosen in 80% of the trials. Intermediate magnitudes were found for smooth pursuit (0.96 ± 0.73), apparent motion (0.84 ± 0.46), and right thumb preferences (0.77 ± 0.65). Hence, there were substantial preferences in all measured tasks.

Although most of the observers showed directional preferences, it is possible that each of them had a different preferred direction (Figure 3; Table 1). To test this hypothesis, the distributions of preferred directions were compared to uniform distributions. Across observers, saccadic eye movements showed a trend for upward preferences ($110^\circ \pm 64^\circ$, $p = 0.087$). The distribution of preferred directions for smooth pursuit eye movements showed two modes, one at upward and one at downward motion. However the distribution was not significantly different from a uniform distribution ($p = 0.466$). This means that there was no consistent preference for a specific smooth pursuit direction across observers. A clear preference for downward rotation was present in the structure-from-motion task ($-83^\circ \pm 39^\circ$, $p < 0.001$). Such an overall preference for downward rotation is consistent with the previously reported bias to perceive downward motion in front in a transparent motion display (Mamassian & Wallace, 2010). Similarly, downward motion was preferred in the apparent motion task ($-70^\circ \pm 62^\circ$, $p = 0.020$). While rightward decisions were preferred with right thumb movements ($13^\circ \pm 59^\circ$, $p = 0.003$), leftward decisions tended to be preferred with left thumb movements ($177^\circ \pm 71^\circ$, $p = 0.208$). These results show that all tasks led to directional preferences.

Correlations between tasks

If these directional preferences in the different tasks are caused by a central decision mechanism, the preferred directions and the magnitude of preferences could be related between tasks. Hence we asked

whether the directional preferences for the different tasks were correlated amongst each other for individual observers.

In the following, correlations between the magnitude of preferences for different tasks are reported (Figure 4; Table 2). There were significant correlations between the saccade task and the right thumb task and between the two thumb tasks. Besides there were trends for positive correlations between the saccade task and the apparent motion task and between the saccade task and the left thumb. All other correlations were very low, even compared to the median reliability of 0.81 (Figure 2D), and not significantly different from zero. This was not due to insufficient reliability of the measurements because even the disattenuated correlation coefficients were clearly below 0.5 in these cases. Hence the magnitude of directional preferences was quite different for different tasks. This rules out the possibility that the magnitude of preferences is a global trait of the observer.

In the following, circular correlations between preferred directions in different tasks are reported (Figure 4; Table 2). Negative correlations were present for smooth pursuit and structure-from-motion tasks and the right and left thumb. Negative circular correlations indicate an axis-symmetric relationship between these tasks. Preferred directions for smooth pursuit and structure-from-motion were axis-symmetric to the horizontal axis, and thumb movements were axis-symmetric to the vertical axis. Interestingly there was no correlation between saccades and thumb movements, although the visual stimuli were identical in these tasks. There was also no correlation between the two perceptual tasks and the two eye movement tasks. This was not caused by insufficient reliabilities because even the disattenuated correlation coefficients were clearly below 0.5. Since the preferred directions were not related between most of the tasks, it is unlikely that they have a common origin.

Effect of preferences on latencies

Response latencies are typically longer for choice reactions than for simple responses to one stimulus (Donders, 1969; Lévy-Schoen, 1969; Sternberg, 1969; Ratcliff & Rouder, 1998). If strong directional preferences facilitate decisions amongst equivalent choices, response latencies should increase less compared to simple responses. To test this hypothesis, we analyzed response latencies for reactions to single targets and for decisions between two targets in the eye and thumb movement tasks (Figure 5A).

As expected, the latencies for saccades were shorter in single-target trials (168 ± 32 ms) than in double-target trials (188 ± 37 ms; $t[28] = 7.79$, $p < 0.001$). Of course, saccade latencies depend on different stimulus param-

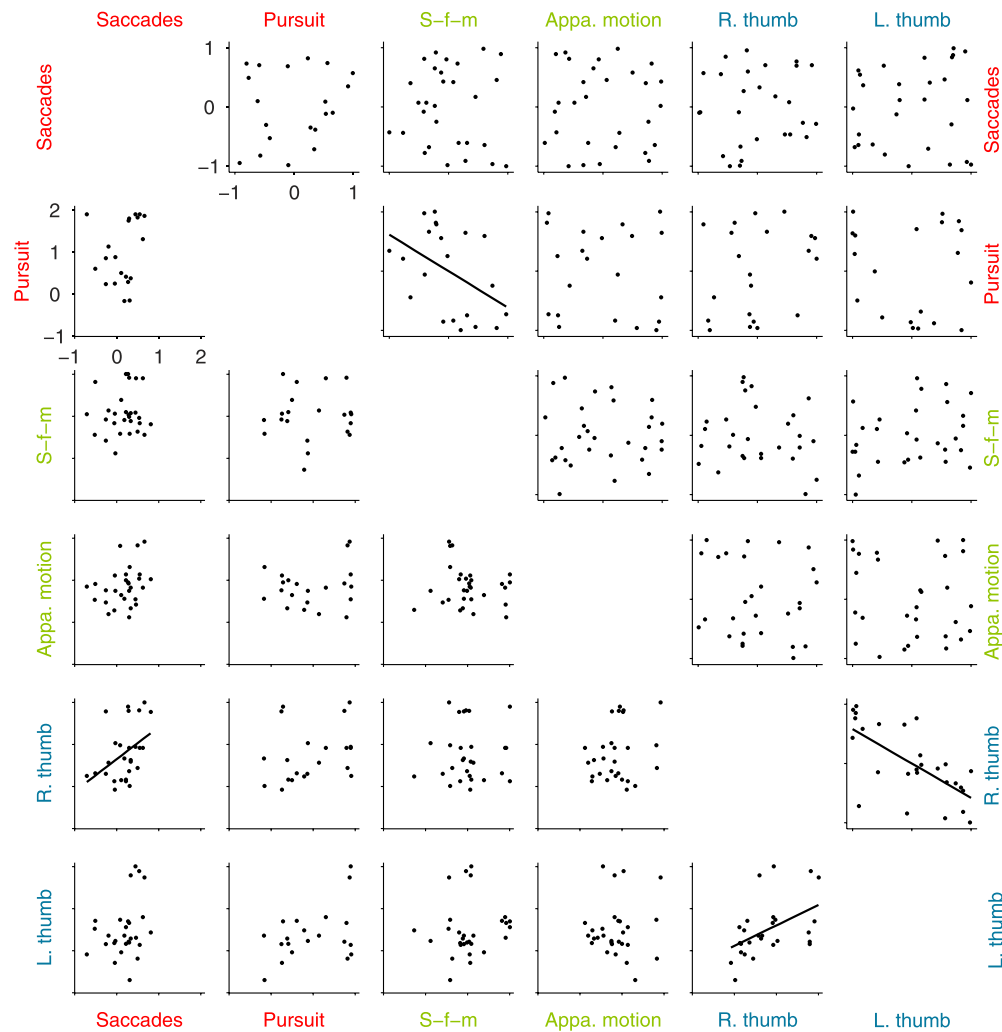


Figure 4. Correlations between preferences for different tasks. Regression lines are displayed for significant correlations. Correlations for preferred directions are located above the identity diagonal; correlations for magnitude of preferences are located below the identity diagonal. For preferred directions, x- and y-values represent the sine of the difference between the preferred directions in the respective task and their mean (Equation 3).

ters, such as spatial frequency and contrast (Ludwig, Gilchrist, & McSorley, 2004), but in general the observed latencies were at the lower end of the typical range of about 120 to 350 ms for saccades (Carpenter, 1988). This indicates that observers were executing reactive saccades and that the directional preferences were not caused by a cognitive strategy to prefer certain directions. Also smooth pursuit latencies were shorter in single-target trials (132 ± 23 ms) than in double-target trials (174 ± 33 ms; $t[19] = 7.27$, $p < 0.001$). These latencies are in the typical range of smooth pursuit latencies with RDKs (Heinen & Watamaniuk, 1998; Krauzlis & Adler, 2001; Schütz, Braun, Movshon, & Gegenfurtner, 2010). Right thumb latencies tended to be shorter in single-target (472 ± 106 ms) than in double-target trials (490 ± 118 ms; $t[26] = 1.89$, $p = 0.071$). Left thumb latencies were not significantly different for single

(497 ± 126 ms) and double-target trials (505 ± 120 ms; $t[28] = 1.17$, $p = 0.251$). Hence the decision costs in double-target trials were mainly present in the eye movement tasks. The longer latencies of thumb movements might provide enough time such that the target selection can be accomplished without adding any further delay to the movement.

Since eye movement latencies were significantly longer in double-target than in single-target trials, directional preferences could actually facilitate the eye movements in double-target trials and reduce the decision costs. Consistent with this hypothesis, there was a negative correlation between the magnitude of preferences and the decision costs for saccadic eye movements, $r(28) = -0.58$, $p = 0.001$, and for smooth pursuit eye movements, $r(19) = -0.45$, $p = 0.047$ (Figure 5B, C), but not for thumb movements (all $ps > 0.340$).

	Saccades	Pursuit	Structure-from-motion	Apparent motion	Right thumb	Left thumb
Saccade		0.17 [0.23] (0.439)	−0.04 [−0.05] (0.828)	−0.04 [−0.04] (0.808)	0.07 [0.08] (0.667)	0.11 [0.12] (0.588)
Pursuit	0.31 [0.35] (0.188)		− 0.45 [− 0.57] (0.019)	−0.09 [−0.11] (0.715)	0.26 [0.34] (0.190)	−0.07 [−0.09] (0.727)
Structure-from-motion	0.04 [0.05] (0.835)	−0.03 [−0.04] (0.886)		−0.01 [−0.01] (0.966)	−0.13 [−0.14] (0.468)	0.27 [0.28] (0.147)
Apparent motion	0.34 [0.41] (0.069)	0.05 [0.05] (0.837)	−0.08 [−0.10] (0.658)		−0.11 [−0.12] (0.559)	−0.13 [−0.14] (0.489)
Right thumb	0.42 [0.59] (0.028)	0.30 [0.39] (0.192)	−0.08 [−0.10] (0.702)	0.13 [0.18] (0.507)		− 0.67 [− 0.71] (0.002)
Left thumb	0.29 [0.35] (0.136)	0.22 [0.26] (0.341)	0.19 [0.23] (0.310)	−0.08 [−0.10] (0.661)	0.53 [0.75] (0.005)	

Table 2. Correlation of the preferences for different tasks. *Note:* Correlations for preferred directions are located above the identity diagonal; correlations for magnitude of preferences are located below the identity diagonal. Values are given in the following format: uncorrected correlation coefficient [Correlation coefficient corrected for attenuation] (uncorrected p -values). Significant correlations are printed in bold.

These results suggest that directional preferences might facilitate the decisions in double-target trials at least for eye movements.

Stability over time

Some of the observers repeated the experiment after 1, 4, and 12 weeks so that the stability of directional preferences over time could be assessed. These three intervals allowed measurement of the stability on different time scales from a couple of days to several weeks. The intervals between successive measurements were increased, such that possible effects of passed time and number of repetition could be distinguished. If preferences build up with repetitions, one would expect larger correlations in the last intervals than in the first intervals. However, if preferences decay over time, one would expect smaller correlations in the last than in the first intervals, because the last intervals were larger than the first intervals.

Differences in magnitude between successive measurements were calculated to test whether the directional preferences increased or decreased with time or repetition (Figure 6A). There were no effects of measurement interval, $F(2, 181.67) = 1.96$, $p = 0.144$, or task, $F(5, 91.91) = 1.04$, $p = 0.399$, suggesting that there were no systematic differences in the magnitude of direction preferences between measurements or tasks. Correlations between successive measurements were

calculated to assess the interindividual stability of the magnitude of preferences. All of the uncorrected correlation coefficients were below 0.77 (Figure 6B), and 7 of 18 were not significantly different from zero. Compared to the median split-half reliability of 0.81, some of the correlations were quite high, and several disattenuated correlation coefficients reached values above 0.9 (Figure 6C). There was no trend over the different measurement intervals, and there were also no consistent differences between the different tasks, except that the correlations were large and significant for the saccade task. Hence the magnitude of directional preferences was stable in some cases but also fluctuated over time in other cases.

To analyze whether the preferred directions changed over time, the average absolute change in preferred direction between successive measurements was calculated (Figure 6D). There was a significant effect of measurement repetition, $F(2, 157.88) = 3.69$, $p = 0.027$, where the changes were larger for the first repetition ($29^\circ \pm 37^\circ$) than for the second ($22^\circ \pm 26^\circ$) and third ($20^\circ \pm 25^\circ$). This suggests that the individual preferences stabilized with more experience with the tasks. There was also a significant difference between different tasks, $F(5, 88.49) = 7.92$, $p < 0.001$, with the smallest changes in the smooth pursuit ($16^\circ \pm 27^\circ$) and the structure-from-motion task ($13^\circ \pm 22^\circ$). These values show that the observers very precisely preferred the same directions in these tasks over several weeks. To assess the interindividual

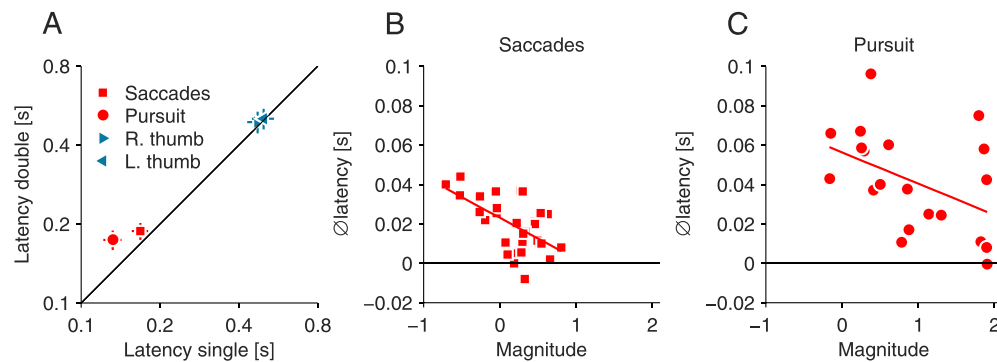


Figure 5. Effect of preferences on latencies. (A) Latencies in double-target trials over latencies in single-target trials. Average data across observers is shown. Error bars represent 95% confidence intervals. (B) Latency costs of double-target trials over magnitude of preferences for saccadic eye movements. (C) Latency costs of double-target trials over magnitude of preferences for smooth pursuit eye movements. Symbols represent data of individual observers. (B and C) The colored line represents a linear regression.

stability of the preferred directions, circular correlation coefficients between successive measurements were calculated. Here all uncorrected correlation coefficients reached values of more than 0.48 (Figure 6E), except the correlation between the first and the second measurement in the saccade task, $r_c(24) = 0.21$, $p = 0.336$. Relative to the median reliability of 0.97,

most of the disattenuated correlation coefficients exceeded 0.9 (Figure 6F).

The repeated measurements showed that the preferred directions were remarkably stable over more than two months. However the magnitude of these preferences was less stable and could fluctuate on a short time scale.

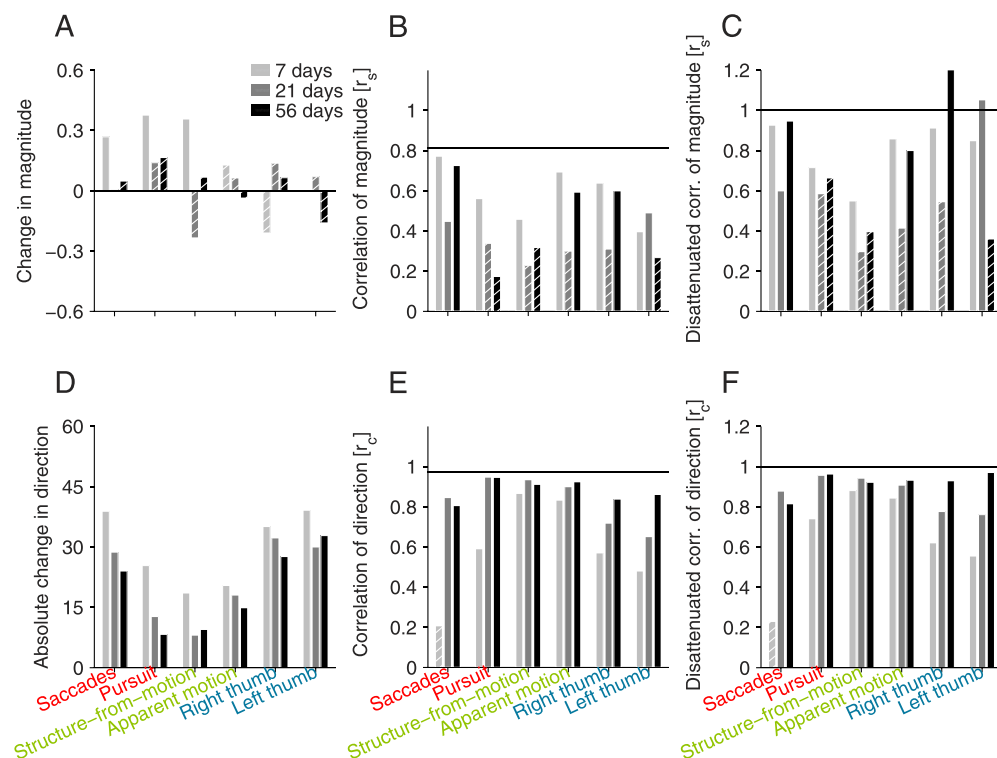


Figure 6. Stability over time for successive measurements separated by 7, 21, and 56 days. (A) Mean difference between magnitude in successive measurements. Positive values indicate an increase in magnitude with time. (B) Correlation of magnitudes. (C) Disattenuated correlation of magnitudes. (D) Mean absolute differences in preferred directions in successive measurements. (E) Correlation of directions. (F) Disattenuated correlation of directions. (A–F) Hatched bars represent values that were not significantly different from zero. (B and E) The horizontal line represents the median split-half reliability from Figure 2D.

Discussion

General findings

In this study we measured directional preferences for motor decisions between equivalent alternatives and for ambiguous, bistable perceptual tasks. We found pronounced preferences in all six tasks (Figure 3), with the strongest preferences in the structure-from-motion task. These results indicate that directional preferences might be a general principle of response selection. The distribution of preferred directions showed that there were consistent preferences across observers in some tasks (structure-from-motion, apparent motion, and right thumb movements) and idiosyncratic preferences in other tasks (saccadic eye movements, smooth pursuit eye movements, and left thumb movements; Figure 3). Even in tasks with consistent biases across observers, there were strong interindividual differences. Hence it is important to consider data of single observers and not just averages across observers, even in such seemingly simple tasks (Wilmer, 2008).

Although there were pronounced directional preferences for individual observers in all tasks, there were very few correlations between preferences in different tasks (Figure 4). Preferred directions were only related between the smooth pursuit and structure-from-motion task as well as the two thumb movement tasks. This means that there are either separate decision mechanisms for different perceptual and motor tasks or that a shared decision mechanism receives stimulus-, task-, or effector-specific input (Gottlieb et al., 2009; Cisek, 2012).

The analysis of latencies in trials with one or two potential targets showed that observers with a strong directional preference needed less time to solve the target conflict in the two eye movement tasks (Figure 5). This means that the directional preferences might be beneficial to quickly initiate saccades or smooth pursuit in the case of target conflict. This is in contrast to the thumb movement tasks and to perceptual ambiguity, where reaction times to ambiguous stimuli are not delayed compared to unambiguous stimuli (Takei & Nishida, 2010).

Repetitions of the experiment after 1, 4, and 12 weeks showed that the magnitude of preferences could fluctuate over time, but that the direction of preferences was remarkably stable over time (Figure 6). Hence the interindividual differences in the preferred directions were not just accidental variations between observers, but stable behavioral and perceptual differences. The pronounced fluctuations in preference magnitude can be interpreted in two ways: Obviously they could just represent noise in the sense that the magnitude of preferences is not under precise control and randomly

varies from time to time. Alternatively, this flexibility might represent active control to adapt behavior to the specific context and affordances. While directional preferences can be very helpful to facilitate decisions in ambiguous settings, they would definitely harm performance in settings that require a fine discrimination between small stimulus differences (Mamassian & Wallace, 2010). It would be interesting to test whether the magnitude of preferences can be experimentally manipulated by changing the discriminability of stimuli in a task. A previous study showed that directional biases in the depth ordering of transparent motion can be moderately shifted by manipulating the usefulness of directional biases for a visual search task (Chopin & Mamassian, 2011). However, since the context remained identical in our experiments, one would not expect any adaptive changes. Hence it is most likely that the changes in the magnitude of preferences represent rather random fluctuations than adaptive processes.

Potential sources of directional preferences

Anisotropies in perceptual and motor tasks could result from different causes at different descriptive levels, ranging from physiological properties, such as the strength of interhemispheric connections (Genc, Bergmann, Singer, & Kohler, 2011), asymmetries of dopamine D2 receptors (Tomer et al., 2013), and sensory differences between the upper and lower visual field (Previc, 1990, 1996), to biomechanical costs, such as muscle strength (Bourbonnais, Forget, Carrier, & Lepage, 1993), to evolutionary factors, such as natural scene statistics (Simoncelli & Olshausen, 2001; Geisler, 2008), and to cultural influences, such as reading direction (Morikawa & Mcbeath, 1992).

While physiological properties allow in principle idiosyncratic preferences, evolutionary factors and cultural influences predict consistent preferences across a population. This is in sharp contrast to our finding that there are large interindividual differences of preferred directions in all of the tasks. All of the mentioned hypotheses predict stable preferences that do not change substantially over time, because physiological properties, evolutionary factors, or cultural influences should not change in the short term. This is consistent with our finding that the preferred directions were highly stable over time. However, it is not consistent with our finding that the magnitude of preferences was not particularly stable over time.

Alternatively to relatively stable causes like physiological properties, evolutionary factors, or cultural influences, perceptual dominance has also been associated with sensory memory. Previous studies showed

that intermittent presentation of ambiguous stimuli stabilizes the perceptual dominance (Leopold, Wilke, Maier, & Logothetis, 2002; for a review see Pearson & Brascamp, 2008). This can be interpreted as some form of sensory memory that stabilizes subsequent percepts and leads to directional preferences. Detailed analysis of preferences revealed that there are memory effects on different time scales (Brascamp et al., 2008; Pastukhov & Braun, 2008; de Jong, Knapen, & van Ee, 2012) from seconds to minutes. Here we show that the direction of individual preferences can be stable in the long term even over several weeks.

In the following we will discuss the different preferences observed in the different tasks separately.

Thumb movements

There was a negative correlation of preferred directions for choices with the left or the right thumb (Figure 4; Table 2). Across observers, rightward choices were preferred with the right thumb, and leftward choices tended to be preferred with the left thumb (Figure 3). Interestingly there was no correlation with saccadic choices, which were measured with identical stimuli. This indicates that the directional preferences of the thumb choices were not caused by visual anisotropies, which would apply to saccades and left and right thumb movements in the same way.

Instead, the preferences of thumb choices might have been caused by anatomical asymmetries. For instance, the maximal available force is higher for adducting (in our case right thumb towards the right) (Figure 1F) than for abducting (right thumb towards the left) thumb movements (Bourbonnais et al., 1993). In this sense, the observed directional preferences could be interpreted as an effect of the expected mechanical properties of the movements. The most famous example for an influence of mechanical properties on choices is the end-state comfort effect, where grasping locations and orientations are chosen such that the posture at the end of the movements is comfortable (Rosenbaum et al., 1990). Consistent with these findings, an adducted end state could be more comfortable than an abducted end state.

Thumb movement latencies were similar for double-target and for single-target trials. This means that thumb movement planing could incorporate an additional target selection process without adding further delay. Consistently, there was no latency advantage for observers with strong directional preferences in thumb movement tasks, contrary to the results for saccadic and smooth pursuit eye movements.

Saccadic eye movements

Upward and leftward choices tended to be preferred in the saccadic eye movement task (Figure 3A).

Upward (Chedru, Leblanc, & Lhermitte, 1973; Previc, 1996; Zelinsky, 1996) and leftward preferences (Chedru et al., 1973; Zelinsky, 1996; Dickinson & Intraub, 2009; Foulsham, Gray, Nasiopoulos, & Kingstone, 2013; Nuthmann & Matthias, 2014; Ossandon, Onat, & Konig, 2014) have also been found in visual search tasks and viewing of natural scene images. Upward biases have been related to differences between the upper and lower visual fields (Previc, 1996), which differ in functional specialization (Previc, 1990) and neural representation (van Essen, Newsome, & Maunsell, 1984). Leftward biases have been related to the phenomenon of pseudoneglect (Dickinson & Intraub, 2009), where a leftward bias can be observed in perceptual tasks (Jewell & McCourt, 2000).

Several studies also reported shorter saccade latencies for upward rather than for downward targets/saccades (Heywood & Churcher, 1980; Honda & Findlay, 1992; Schlykova, Koffmann, Bremmer, Thiele, & Ehrenstein, 1996; reviewed in Greene, Brown, & Dauphin, 2014). Further research is necessary to test if directional preferences in double-target trials are caused by these latency anisotropies.

Smooth pursuit eye movements

Although the individual preferences were quite pronounced for smooth pursuit eye movements, no direction was consistently preferred across observers (Figure 3B). However, most of the observers with strong preferences had a preference along the vertical axis, preferring either up- or downward movements. Vertical asymmetries have been reported for eye movement gain in smooth pursuit as well as in optokinetic nystagmus (OKN). Interestingly there are a lot of conflicting results in this field (reviewed in Ke, Lam, Pai, & Spering, 2013). Identical performance (Collewijn & Tamminga, 1984; Rottach et al., 1996; Takeichi et al., 2003) or advantages for upward (Baloh, Richman, Yee, & Honrubia, 1983) or downward motion (Ke et al., 2013) have been reported for smooth pursuit gain. Similarly, consistent advantages for upward (Takahashi, Sakurai, & Kanzaki, 1978; Lelievre & Correia, 1987; Van den Berg & Collewijn, 1988; Murasugi & Howard, 1989; Clement & Lathan, 1991; Ogino, Kato, Sakuma, Takahashi, & Takeyama, 1996; Garbutt et al., 2003) or downward motion (Baloh et al., 1983) or idiosyncratic asymmetries (Schor & Narayan, 1981; Calhoun, Lelievre, & Correia, 1983; Knapp, Gottlob, McLean, & Proudlock, 2008) have been reported for slow-phase eye velocity in OKN. Our

results emphasize that vertical asymmetries are also more prevalent and pronounced than horizontal asymmetries for pursuit target selection.

Structure-from-motion

In the structure-from-motion task, observers preferentially viewed downward motion in the front and upward motion in the back (Figure 3C), which is consistent with the 3-D interpretation of a cylinder rolling on the ground towards the observer. A previous study on transparent motion perception showed that downward motion is preferentially seen in the front, even when the display does not lead to the perception of a 3-D object (Mamassian & Wallace, 2010). Hence the preference in our study could be caused by a bias in the depth ordering of motion signals that happens even before the overall 3-D shape is resolved.

The perceived rotation direction of structure-from-motion stimuli can be decoded from activity in the middle temporal (MT) area (Andersen & Bradley, 1998; Bradley, Chang, & Andersen, 1998; Dodd, Krug, Cumming, & Parker, 2001) or its human homologue (Brouwer & van Ee, 2007). Intermittent presentation of structure-from-motion stimuli stabilizes perceptual dominance (Leopold et al., 2002), as well as neural activity in MT (Klink, Oleksiak, Lankheet, & van Wezel, 2012). Transcranial magnetic stimulation to area MT leads also to a stabilization of perceptual dominance, which has been interpreted as an interruption of the formation of new memory (Brascamp, Kanai, Walsh, & van Ee, 2010). Consistent with this view, the perceived rotation is also affected by working memory contents (Scocchia, Valsecchi, Gegenfurtner, & Triesch, 2013). Neurons in area MT are tuned for motion direction (Maunsell & Van Essen, 1983a) and binocular disparity (Maunsell & Van Essen, 1983b). A bias in the population, such that neurons that are selective for far depth and upward motion are more responsive or more numerous, could create the observed preferences in the structure-from-motion task. Interestingly there was a negative correlation between the directional preferences in the structure-from-motion and the smooth pursuit tasks, indicating axis-symmetric preferences for the two tasks. This suggests that there might be a common origin of the directional preferences in these tasks. In previous studies we found that a stronger motion signal, i.e., which is composed of more dots or directed opposite to an adapted direction, is preferred by smooth pursuit and also preferentially seen in the back (Schütz, 2011) and that the number of dots is overestimated for the surface in the back (Schütz, 2012). Hence the directional preferences in the smooth pursuit and the

structure-from-motion task could be generated by anisotropies in the representation of motion strength.

Apparent motion

Downward motion was also preferred in the apparent motion task (Figure 3D). For different apparent motion stimuli, different directional preferences with different origins have been reported previously. When vertical motion is tested against horizontal motion in the motion quartet (Neuhaus, 1930), the strength of callosal connections determines the preferred axes of motion (Genc et al., 2011). When testing left- against rightward motion, preferences are correlated with the reading direction (Morikawa & Mcbeath, 1992).

For a very similar stimulus as in this study, it has been shown that the perceived motion direction is primarily represented by neurons in the lateral intraparietal area (LIP) and less so by neurons in areas MST and MT (Williams et al., 2003). Interestingly, already neural activity before stimulus onset predicted the perceived motion direction. Subsequently it has been shown that microsaccade rate increases just before reversals in perceived motion direction and that the direction of microsaccades before stimulus onset is related to the subsequent perceived motion direction (Laubrock, Engbert, & Kliegl, 2008). In light of these studies, it is possible that the measured directional preferences in the apparent motion task are caused by an imbalance in neural activity in area LIP or by anisotropies in the direction of microsaccades, or by a third, common factor that affects both microsaccades and activity in area LIP. Since there was only a brief fixation period before stimulus onset in our experiment, it is unlikely that the directional preferences were entirely caused by microsaccades.

Summary

Directional preferences were observed in several perceptual and motor tasks. Most of these preferences showed interindividual differences that were stable over several weeks. Eye movement choices were facilitated by strong directional preferences. This indicates that directional preferences might be a widely used mechanism to deal with ambiguous choices, facilitating decisions for some tasks.

Keywords: saccadic eye movements, smooth pursuit eye movements, apparent motion, structure-from-motion, hand movements, decision making, directional preferences, individual differences

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