Inter-individual differences in preferred directions of perceptual and motor decisions

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Abstract

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 inter-individual differences and 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 observed in tasks that involved motion, like the smooth pursuit eye movement, apparent motion and structure-from-motion tasks. The weakest effects were observed 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 are 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 was not correlated between any of the six tasks 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 2D stimuli, which allow different 3D interpretations, such as the Necker cube (Necker, 1832; Long & Toppino, 2004) or structure-from-motion (Wallach & O'Connell, 1953; Andersen & Bradley, 1998).

A lot of these motor and perceptual decisions are decisions about different directions and it could be useful to have preferences for certain directions. Such preferences could save time and cognitive effort when the alternatives are otherwise indistinguishable. 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 an example for perceptual biases. 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).

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. 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 areas 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. 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, in which we measured directional preferences for four motor tasks (saccadic and smooth pursuit eye movements, movements of the left and right thumb) and two perceptual tasks (structure-from-motion and apparent motion). 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 1A**). Each axis was presented ten times, except in the thumb movement experiments, where each axis was only presented five times. In the eye movement and thumb movement tasks we interspersed single-target trials 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 one hour, in a random order. To estimate the stability of directional preferences, some of the observers repeated the experiments after about one, four and twelve weeks.

In a separate saccade-latency experiment, we interleaved double-target trials and pro- and anti-saccade single-target trials, to distinguish between visual and motor effects. In the anti-saccade task, observers are required to execute a saccade in the opposite direction of a flashed stimulus (Hallett, 1978). This is a usefull paradigm to distinguish between visual and motor effects, because visual target direction and eye movement direction are disentangled. In this experiment, directional preferences were measured along 6 axes with a separation of 30°. Pro- and anti-saccade targets could appear at one of 12 possible directions, which were presented each 25 times, to achieve a better resolution of latencies for the different directions.

Subjects. 30 naïve 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). 28, 21 and 18 observers repeated the experiment one, two, or three times, respectively, about one, four and twelve weeks after the first measurement. 22 additional observers participated in the saccade-latency experiment. We had to exclude one observer because she/he did not show any directional preferences.

Equipment. Observers were seated in a dark room facing a 21-inch SONY GDM-F520 CRT monitor driven by an Nvidia Quadro NVS 290 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 x 1024 pixels this results in 28 pixels/dva. The luminance of white, gray, and black pixels was 87, 14.6, and 0.04 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) 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 x 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. In the smooth pursuit task, two random-dot kinematograms (RDK), each consisting of 157 dots, were shown

in a circular aperture of 10 dva radius. 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 quadratic area of 10 x 10 dva. Dot velocity was following a sinusoidal function to generate the orthographic projection of a rotating cylinder. Dot size and speed were identical to the smooth pursuit task. 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. 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 half-way to the next dot by 0.4 dva. This is consistent with a motion of 4 dva/s in two possible directions. In the saccade-latency experiment, the fixation target was red if an anti-saccade was required, green if a pro-saccade was required and grey if one of two targets had to be selected.

Experimental procedure. Observers had to fixate a red combination of bulls eye and cross hair (Thaler, Schütz, Goodale, & Gegenfurtner, 2013) and press an assigned button on the game pad to the 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 two dva radius. In the eye movement tasks, the fixation target disappeared after a random interval of 750 to 1,500 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 one second. 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 of four dva. A trial in the thumb movement tasks ended when the game pad stick exceeded an eccentricity of 7.5 dva.

> Insert **Figure 1** *about here.*

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. Saccades were removed from the velocity traces by linear interpolation. 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. We excluded single trials 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 less than 50% of the trials in the session were valid. This happened for one session in the saccade task, for ten sessions in the smooth pursuit task and three sessions in the thumb movement tasks. In the saccade-latency experiment, trials were excluded if the saccade direction deviated more than 90° from the required direction. There were not enough valid anti-saccade trials for two observers and not enough valid pro-saccades for one observer.

Modeling and statistical analysis. We calculated the preference for each of the tested axes as the proportion of choices in the respective directions (**Figure 1B**). We used a cosine model with two free parameters to extract the overall preferred direction (θ_m) and the magnitude of preferences (b):

$$y = 10^b \cos(\theta - \theta_m) \tag{1}$$

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 cannot not be distinguished with the directional 15° resolution of the data. The model responses were transformed into proportion of choices using a logit model:

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

With this model we could explain 93.9% (median) of the variability in directional choices (**Figure 1C**). The model produced a reliable estimate of the preferences since the Spearman-brown corrected split-half reliabilities amounted to 0.77 for magnitude and 0.93 for direction (**Figure 1D**).

To model saccade latency distributions in the saccade-latency experiment, we used modified version of the LATER model (Carpenter, 2012), in which evidence is accumulated at a normally distributed rate until a decision threshold is reached. The start and threshold values and the minimum response latency were fixed at 0, 1000 and 35 ms, respectively. We fitted the mean (μ_p, μ_n) and the standard deviation (σ_p, σ_n) of the accumulation rate, separately for preferred and non-preferred directions. The cumulative latency distributions for preferred (F_p) and non-preferred (F_n) directions can be calculated by cumulative normal distributions:

$$F_p\left(l, \mu_p, \sigma_p\right) = 1 - \frac{1}{\sigma_p\sqrt{2\pi}} \int_{-\infty}^{\frac{1000}{l-35}} e^{\frac{-(t-\mu_p)^2}{2\sigma_p^2}} \, dt \tag{3}$$

$$F_n(l, \mu_n, \sigma_n) = 1 - \frac{1}{\sigma_n\sqrt{2\pi}} \int_{-\infty}^{\frac{1000}{l-35}} e^{\frac{-(t-\mu_n)^2}{2\sigma_n^2}} \, dt \tag{4}$$

We assumed that the latency distribution in double-target trials results from a competition between the preferred and non-preferred direction. The LATER unit with higher accumulation in one trial determines the response latency and the choice of direction. The combined latency distribution (F_d) is the probability that one of the two later units reaches a certain latency and can be calculated as the multiplication of the individual distributions (F_{pd} & F_{nd}):

$$F_d = 1 - F_{pd}\left(l, \mu_{pd}, \sigma_{pd}\right) F_{nd}(l, \mu_{nd}, \sigma_{nd}) \tag{5}$$

Since the latencies in double-target trials were larger than in single-target trials (**Figure 4**), we needed to add an inhibition. In our model the two target locations inhibit each other by a certain percentage (K_i) of their own accumulation rate. Hence the mean and standard deviation of the individual LATER units have to be adjusted by the weighted value of the competing unit:

$$\mu_{pd} = \mu_p - K_i\mu_n \tag{6}$$

$$\mu_{nd} = \mu_n - K_i\mu_p \tag{7}$$

$$\sigma_{pd} = \sqrt{\sigma_p^2 + (K_i\sigma_n)^2} \tag{8}$$

$$\sigma_{nd} = \sqrt{\sigma_n^2 + \left(K_i\sigma_p\right)^2} \tag{9}$$

Finally we have to calculate the proportion of choices for the preferred direction in double-target trials. This can be expressed as the cumulative probability that the difference between the cumulative distributions for non-preferred and preferred directions is smaller than zero:

$$F_c = \frac{1}{\sigma_d\sqrt{2\pi}} \int_{-\infty}^{0} e^{\frac{-(t-\mu_c)^2}{2\sigma_c^2}} dt \tag{10}$$

$$\mu_c = \left(\mu_n - K_i\mu_p\right) - \left(\mu_p - K_i\mu_n\right) \tag{11}$$

$$\sigma_c = \sqrt{\sigma_n^2 + \left(K_i\sigma_p\right)^2 + \sigma_p^2 + (K_i\sigma_n)^2} \tag{12}$$

The circular statistics toolbox (Berens, 2009) was used for circular measurements. To test whether preferred directions were distributed uniformly we used a Hodges-Ajne test for circular data (Hodges, 1955; Ajne, 1968). To test correlations between the magnitude of preferences we used a Pearson correlation. To test correlations between preferred directions we used a circular correlation coefficient analogous to a Pearson correlation coefficient (Jammalamadaka & Sengupta, 2001). 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 and tasks. Based on the proportion of choices for the different directions, we estimated the preferred direction and the magnitude of preferences (**Figure 1**, **Equations 1 & 2**). The strongest directional preferences were estimated in the structure-from-motion task with an

average magnitude of 1.01 ± 0.57 (**Figure 2**, **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 of 20°. The weakest directional preferences were estimated for choices made by the left thumb (0.47 ± 0.67) and saccadic eye movements (0.15 ± 0.39). 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 (0.86 ± 0.69), apparent motion (0.83 ± 0.47) and right thumb preferences (0.74 ± 0.61). In all tasks, the majority of observers showed a magnitude of larger than zero[1], which means that most of the observers had pronounced preferences for a certain direction.

*Insert **Figure 2** about here.*

Although most of the observers showed directional preferences, it is possible that each of them had a different preferred direction (**Figure 2**, **Table 1**). Thus we analyzed the distribution of preferred directions across observers and compared them to a uniform distribution. Across observers, saccadic eye movements showed significant upward preferences (111° ± 60°, $P = 0.002$). 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 = 0.591). 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° ± 41°, $P = 0.001$). 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 tended to be preferred in the apparent motion task (-71° ± 63°), but the distribution was not significantly different from a uniform distribution ($P = 0.061$). While rightward decisions were preferred with right thumb movements (17° ± 58°, $P = 0.005$), leftward decisions were

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[1] Since we used a logarithmic parameter to quantify the magnitude of preferences, a value of zero does not represent a complete absence of preferences.

preferred with left thumb movements ($153° \pm 68°$, $P = 0.030$). These results show that all tasks led to directional preferences.

Correlations between tasks

In the next step we analyzed whether the directional preferences for the different task were related amongst each other for individual observers. If the directional preferences in the different tasks are caused by a central decision mechanisms, the preferred directions could be related.

First we analyzed whether the magnitude of preferences were correlated for different tasks (**Table 2**). There were trends for positive correlations between the saccade task and the apparent motion task ($r(28) = 0.317$, $P = 0.094$), between the saccade task and the right thumb ($r(25) = 0.296$, $P = 0.142$), between the saccade task and the left thumb ($r(27) = 0.319$, $P = 0.098$) and between the right and the left thumb ($r(26) = 0.366$, $P = 0.060$). All other correlations were very low, even compared to the median reliability of 0.77 (**Figure 1D**), and not significantly different from zero. 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.

We also analyzed whether preferred directions in different tasks were related (**Table 3**). Negative correlations were present for smooth pursuit and structure-from-motion task ($r_c(19) = -0.692$, $P = 0.006$) (**Figure 3A**) and the right and left thumb ($r_c(26) = -0.590$, $P = 0.004$) (**Figure 3B**). 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 (right: $r_c(25) = 0.240$, $P = 0.179$; left: $r_c(27) = 0.224$, $P = 0.230$), although the visual stimuli were

identical in these tasks. There was also no correlation between the two perceptual tasks ($r_c(29)$ = -0.021, $P = 0.905$) and the two eye movement tasks ($r_c(18) = 0.338$, $P = 0.166$). Since the preferred directions were not related between most of the tasks, it is unlikely that they have a common origin.

> Insert **Figure 3** about here.

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. Thus we analyzed response latencies for reactions to single targets and for decisions between two targets in the eye and thumb movement tasks (**Figure 4A**).

> Insert **Figure 4** about here.

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 parameters, 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 decision 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 random-dot kinematograms (Heinen & Watamaniuk, 1998; 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; $t(28) = 1.19$, $P = 0.246$). These results indicate that 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. Consistently with this hypothesis, there was a negative correlation between magnitude of preferences and the decision costs for saccadic eye movements ($r(28) = -0.55$, $P = 0.002$) and for smooth pursuit eye movements ($r(19) = -0.47$, $P = 0.035$) (**Figure 4B&C**). These results show that directional preferences facilitated the decisions in double-target trials at least for eye movements.

Stability over time

Some of the observers repeated the experiment after one, four and twelve weeks so that we were able to measure the stability of directional preferences over time. These three intervals allowed us to measure the stability on different time scales from a couple of days to several weeks. Since the intervals between measurements increased, we can also distinguish between possible effects of repetition and passed time.

First we calculated the differences in magnitude between successive measurements to test whether the directional preferences increased or decreased with time or repetition (**Figure 5A**). The results showed a trend for an interaction between measurement interval and task ($F(10, 68.06) = 1.15$, $P = 0.079$). There was a significant increase in the magnitude of directional preferences between the first and the second measurement for the saccade task (0.28 ± 0.40, $t(23) = 3.40$, $P = 0.002$), the smooth pursuit task (0.37 ± 0.71, $t(19) = 2.37$, $P = 0.028$) and the structure-from-motion task (0.34 ± 0.61, $t(27) = 2.99$, $P = 0.006$). All other changes were not significantly different from zero. Hence the magnitude of directional preferences increased quickly for the eye movement and the structure-from-motion task only. This increase between the first and the second measurement could mean that observers were developing the preferences during the first and second measurement. However for the other

tasks, the preferences either developed very rapidly during the first measurement or they were already present before the first measurement.

In the next step, we calculated correlations between successive measurements to assess the inter-individual stability of the magnitude of preferences. All of the correlations were below 0.71 (**Figure 5B**), and nine of eighteen were not significantly different from zero. Compared to the median reliability of 0.77, some of the correlations were quite high. 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 case but also fluctuated over time in other cases.

> Insert **Figure 5** about here.

In the following we analyzed whether the preferred directions changed over time. We calculated the average absolute change in preferred direction between successive measurements (**Figure 5C**). There was a significant effect of measurement repetition ($F(2, 167.83) = 4.28$, $P = 0.015$), where the changes were larger for the first repetition ($29° ± 39°$) than for the second ($22° ± 27°$) and third ($18° ± 25°$). This suggests that the individual preferences stabilized with more experience with the tasks. There was also a significant difference between different tasks ($F(5, 89.14) = 7.54$, $P < 0.001$), with the smallest changes in the smooth pursuit ($15° ± 27°$) and the structure-from-motion task ($12° ± 22°$). These values show that the observers very precisely preferred the same directions in these tasks over several weeks. To assess the inter-individual stability of the preferred directions, we calculated circular correlation coefficients between successive measurements. Here all correlations reached high values of more than 0.63 (**Figure 5D**), expect the correlation between the first and the second measurement in the saccade task ($r_c(24) = 0.25$, $P = 0.263$).

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.

Effect of saccade latencies on saccade preferences

Upward choices were preferred in the saccadic eye movement task. Theoretically, this choice preference for upward saccades could be caused by anisotropies of saccade latencies, which have been shown to be shorter for upward than for downward targets in several studies (Heywood & Churcher, 1980; Honda & Findlay, 1992; Schlykowa, Koffmann, Bremmer, Thiele, & Ehrenstein, 1996). Previous studies also compared latencies of pro- and anti-saccades for different directions (Goldring & Fischer, 1997; Bell, Everling, & Munoz, 2000; Dafoe, Armstrong, & Munoz, 2007). Since latency anisotropies in anti-saccades were much weaker than for pro-saccades, these studies remain inconclusive about the origin of the effect.

Insert **Figure 6** about here.

Here we repeated the saccade experiment with more single-target trials, to achieve a better resolution of saccade latencies and with additional anti-saccades trials, to disentangle visual from motor effects. Directional preferences were estimated with the same model as before. For double-target trials and single-target trials with pro-saccades, there was again a trend for a negative relationship between the magnitude of preferences and the decision costs (r(19) = -0.39, *P* = 0.088). There was no such relationship for anti-saccades (r(18) = 0.26, *P* = 0.282).

To analyze the latencies for the different directions more closely, we first converted the proportion of choices to a scale from minus one to one (**Figure 6A**). These converted preferences were multiplied by the latencies for pro- and anti-saccades (**Figure 6B**), separately for each axis. As a result, latencies for non-preferred directions are counted negative, latencies for preferred directions are counted positive and latencies for non-biased directions are not counted at all (**Figure 6C**). The sum of this function across directions yields an estimate of the latency differences between preferred and non-preferred directions (**Figure 6D**). The average latency difference for pro-saccades was -2.13 ± 2.21 ms and significantly smaller than zero (t(19) = 4.31, *P* < 0.001). This means that pro-saccade latencies were indeed slightly longer in the non-preferred directions. For the anti-saccades the latency difference

was -0.58 ± 4.35 ms and not significantly different from zero (t(19) = 0.59, *P* = 0.565). The results of this analysis indicate that pro-saccade latencies were slightly smaller for preferred than for non-preferred directions. For anti-saccades, the results were mixed, so that it is not possible to distinguish between visual and motor preferences.

*Insert **Figure** 7 about here.*

The measured latency differences between pro-saccades in preferred and non-preferred directions were quite small. In order to test whether these small latency differences actually could cause the directional preferences, a more elaborate analysis of latency distributions is necessary. To this end we fitted a LATER model (Carpenter, 2012) to the latency distributions. First we dichotomized all single-target directions into preferred or non-preferred directions according to the double-target preferences, which resulted in two latency distributions for preferred and non-preferred directions. Two separate LATER units were fitted to these latency distributions in single-target trials (**Figure 7**). For these LATER units the mean and standard deviation of the accumulation rate were determined independently. To predict directional preferences and the latency distribution for the double-target trials, we combined these two LATER units by mutual inhibition. In each trial, the faster one of the two LATER units determined the chosen direction and also the latency of the response.

Consistently with the average latency differences, the accumulation rate was faster for preferred (8.93 ± 1.41) than for the non-preferred directions (8.43 ± 1.36, t(20) = 3.12, *P* = 0.005). There was no difference in the standard deviation of the accumulation rate (preferred: 2.13 ± 0.50, non-preferred: 2.13 ± 0.56, t(20) = 0.01, *P* = 0.990). For the single-target trials we were able to explain 97 ± 4 % of the variability in the cumulative latency distribution for the non-preferred directions and 97 ± 3 % for the preferred directions (**Figure 8B**). The mutual inhibition in the combined LATER model for double-target trials was 0.33 ± 0.09. With that model we could accurately predict the latency distribution (**Figure 8C**). The model could explain 95 ± 4 % of the variability in the cumulative latency distribution. Although the predicted latency (185 ± 22 ms) was significantly shorter (t(20) = 6.53, *P* < 0.001) than the measured latency (195 ± 27 ms), they were highly correlated (r(20) = 0.98, *P* < 0.001).

Contrary to the latency, the model could not accurately predict the choice preferences. The predicted preference was 0.59 ± 0.11 and significantly smaller ($t(20) = 5.28$, $P < 0.001$) than the measured preference of 0.73 ± 0.09 ms. There was no correlation between measured and predicted preferences ($r(20) = 0.29$, $P = 0.202$).

> *Insert **Figure 8** about here.*

The simple race between two LATER units, connected by mutual inhibition could account for the observed latency distribution but not for the choice preferences in the double-target trials. Hence, the directional preferences could not be explained by latency anisotropies alone and an additional factor favoring one direction over the other is necessary.

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 2**), with the strongest preferences in the structure-from-motion task. The distribution of preferred directions showed that there were consistent preferences across observers in some tasks (structure-from-motion and thumb movements) and idiosyncratic preferences in other tasks (smooth pursuit eye movements and apparent motion) (**Figure 2**). Even in tasks with consistent biases across observers, there were strong inter-individual 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). 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 4**). This means that the directional preferences were clearly beneficial to quickly initiate saccades or smooth pursuit in the case of target conflict. This is in contrast the thumb movement tasks and to perceptual ambiguity, where reaction times to ambiguous stimuli are not delayed compared to unambiguous stimuli (Takei & Nishida, 2010). A detailed analysis of latency distributions in the saccade task showed that the

directional preferences were not a direct consequence of latency anisotropies (**Figure 7** & **Figure 8**).

Repetitions of the experiment after 7, 21 and 56 days showed that the magnitude of preferences could fluctuate over time, but that the directions of preferences were remarkably stable over time (**Figure 5**). Hence the inter-individual differences in the preferred directions were not just accidental variations between observers, but stable behavioral and perceptual differences. Having a flexible magnitude of preferences however might be important for adaptive behavior in different contexts. 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. 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).

Although there were pronounced directional preferences for the individual observers in all tasks, there were very few correlations between preferences in different tasks. 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. Either way, directional preferences seem to be present in most tasks and are possibly a general principle of response selection.

Several explanations for anisotropies in perceptual and motor tasks can be found in the literature. They cover a wide range of topics from physiological properties such as the strength of inter-hemispheric connections (Genc, Bergmann, Singer, & Kohler, 2011), asymmetries of D2 receptors (Tomer et al., 2013) and differences between the upper and lower visual field (Previc, 1990, 1996) to cultural influences, such as reading direction (Morikawa & Mcbeath, 1992). While some of these hypotheses allow idiosyncratic preferences, others predict consistent preferences across a population. However all of them

predict stable preferences, that do not change substantially over time, because differences in brain structure 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 brain structure or cultural differences, 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.

Thumb movements

There was a negative correlation of preferred directions for choices with the left or the right thumb (**Figure 3B**). Across observers, rightward choices were preferred with the right thumb and leftward choices were preferred with the left thumb (**Figure 2E & F**). 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 (right thumb towards the right) than for abducting (right thumb towards the left) thumb movements (Bourbonnais, Forget, Carrier, & Lepage, 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). In this sense, the results could be interpreted as evidence that an adducted end state is more comfortable than an adducted end state.

We did not find a latency advantage for observers with strong directional preferences in thumb movement tasks, contrary to the results for saccadic and smooth pursuit eye movements. The absence of a latency advantage suggests that the directional preferences in thumb movements tasks were not caused by a directional prior that facilitates conflict resolution. Instead they might result from a post-stimulus prediction of the mechanical costs of the movements and their end-state comfort.

Saccadic eye movements

Upward and leftward choices were preferred in the saccadic eye movement task (**Figure 2A**). 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 than for downward targets/ saccades (Heywood & Churcher, 1980; Honda & Findlay, 1992; Schlykowa, et al., 1996). This leads to the hypothesis that the directional preferences in double-target trials are caused by latency anisotropies. Our analysis of saccade latency distributions however showed that the directional preferences were not caused entirely by latency differences between

preferred and non-preferred directions (**Figure 7** & **Figure 8**). The simple race model with two LATER units, connected by mutual inhibition was able to accurately predict latencies but underestimated preferences in double-target trials.

Smooth pursuit eye movements

Although the individual preferences were quite pronounced for smooth pursuit eye movements, no direction was consistently preferred across observers (**Figure 2B**). 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 more prevalent and pronounced than horizontal asymmetries for pursuit target preferences.

Structure-from-motion

In the structure-from-motion task, observers preferentially viewed downward motion in the front and upward motion in the back (**Figure 2C**), which is consistent with the 3D 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 a 3D percept (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 3D shape is resolved.

The perceived rotation direction of structure-from-motion stimuli can be decoded from activity in the middle temporal 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 task, 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 a previous study 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). 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

There was a trend for downward preferences in the apparent motion task (**Figure 2D**), but the distribution of preferred directions was not significantly different from a uniform distribution. 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 preference showed inter-individual differences that were stable over several weeks. Eye movement choices were facilitated by strong directional preferences. This indicates that directional preferences are a widely used mechanism to deal with ambiguous choices, facilitating decisions for some tasks.

Acknowledgments

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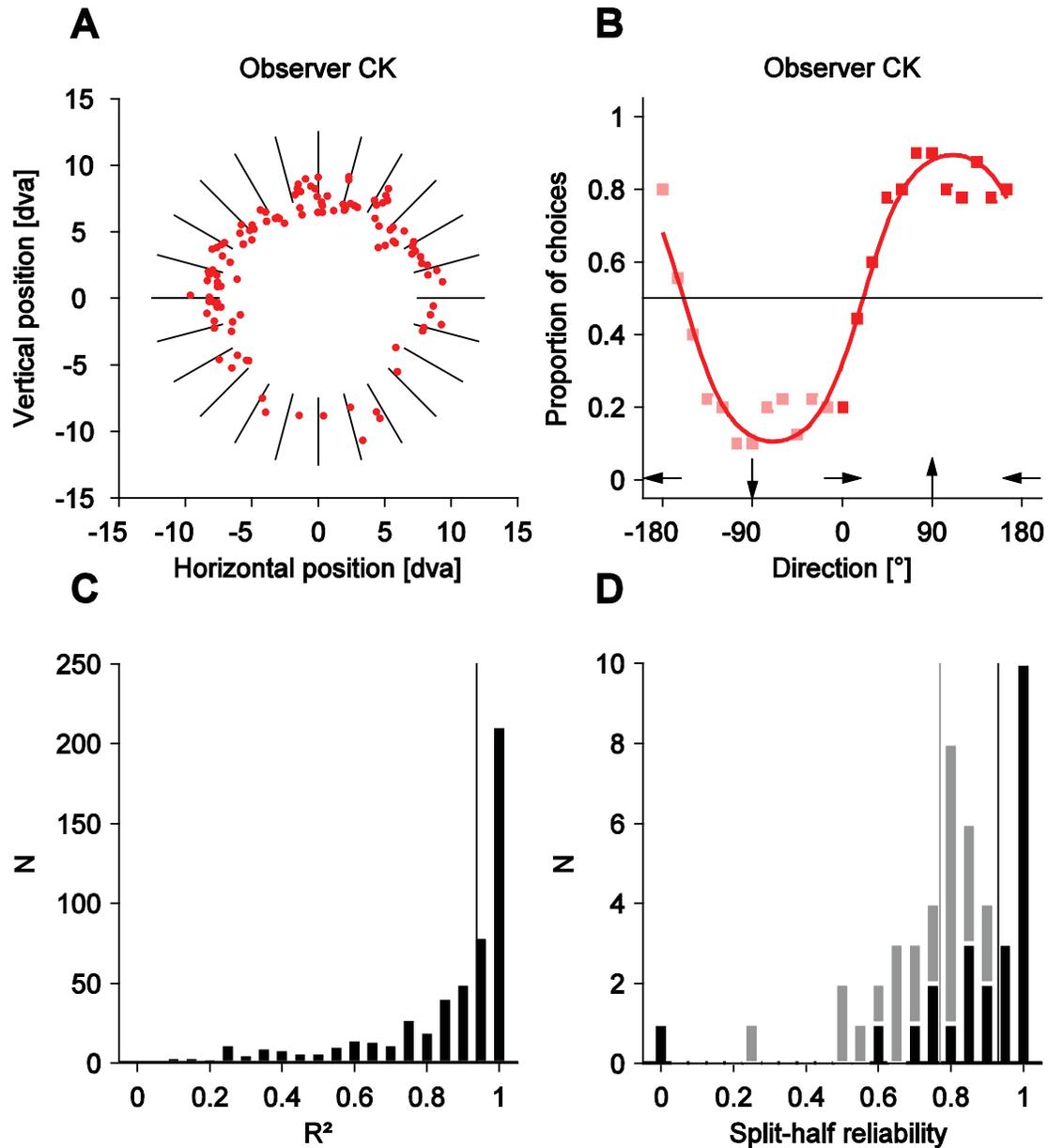
Figure 1: Analysis of directional preferences. (**A**) Saccade endpoints for observer CK. The black lines indicate the centers of the presented stimuli. In each trial two stimuli at opposite directions were shown. If there would be no directional preference, saccade endpoints should be distributed equally in all directions. (**B**) Proportion of saccade choices for observer CK based on the saccade endpoints from **Figure 1A**. The data points plotted in light color are calculated as the differences to unity of the proportions plotted in dark color. 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 0.93. (**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 0.77 and 0.93 for magnitude and direction, respectively.
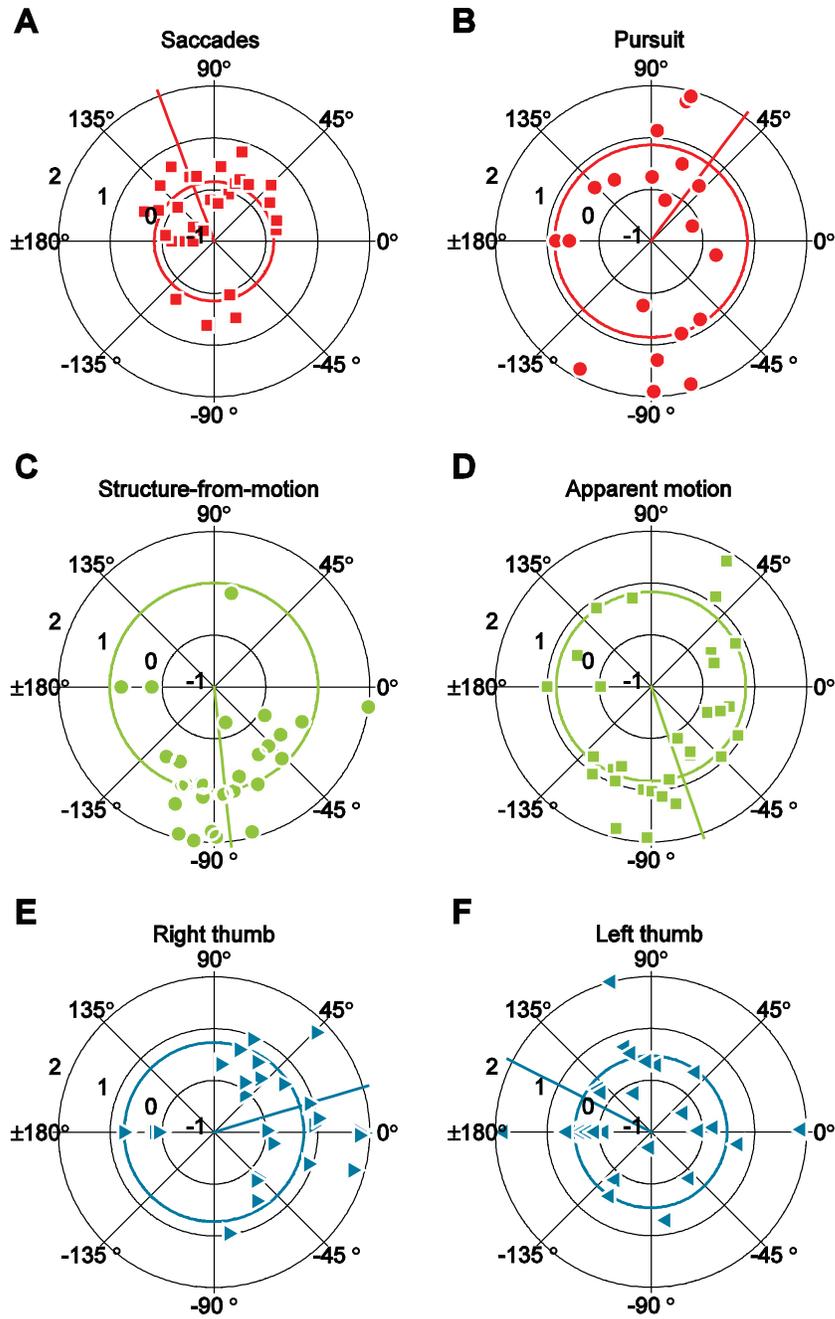
Figure 2: Individual directional preferences. Magnitude of preferences and preferred directions are shown in polar coordinates. Symbols represent data of individual observers. The colored circle represents the average magnitude across observers. The colored line represents the average preferred direction across observers.

A

B
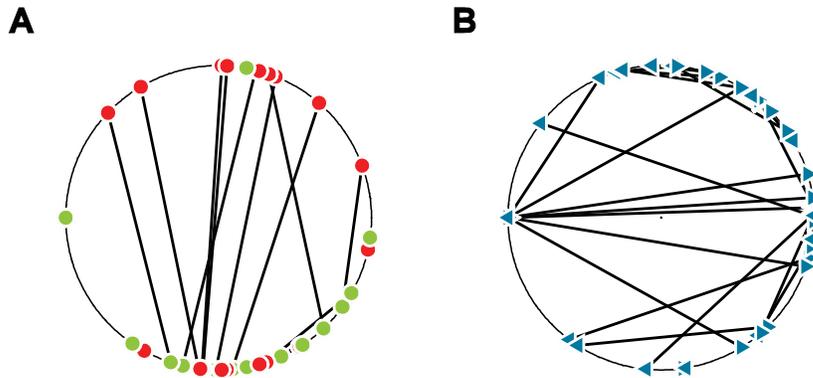
Figure 3: Correlation between preferred direction in different tasks. (**A**) Correlation between smooth pursuit (red) and structure-from-motion (green). (**B**) Correlation between right and left thumb movements. (**A & B**) Symbols represent data of individual observers. The black lines connect the preferred directions of one observer in the two tasks.
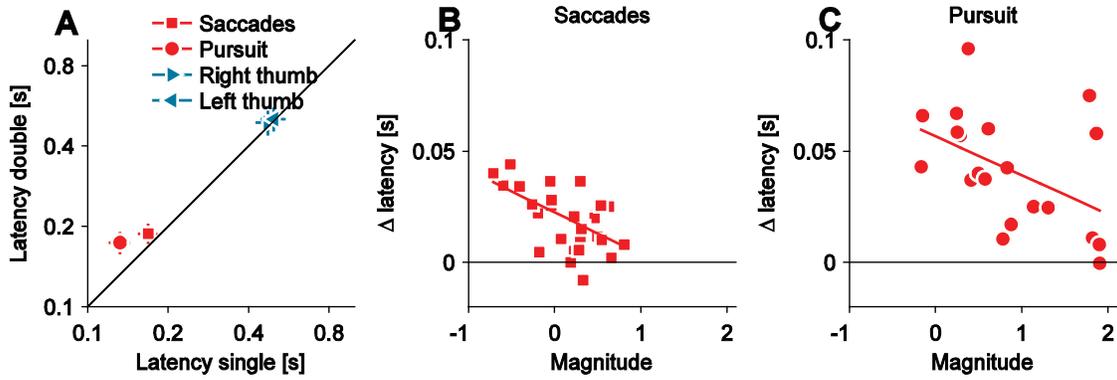
Figure 4: Effect of preferences on latencies. (**A**) Latencies in double target trials over latencies in single target trials. Average data across observers is shown. Error bars represent 95% confidence intervals. (**B**) Latency costs of double target trials over magnitude of preferences for saccadic eye movements. (**C**) Latency costs of double target trials over magnitude of preferences for smooth pursuit eye movements. (**B & C**) Symbols represent data of individual observers. The colored line represents a linear regression.
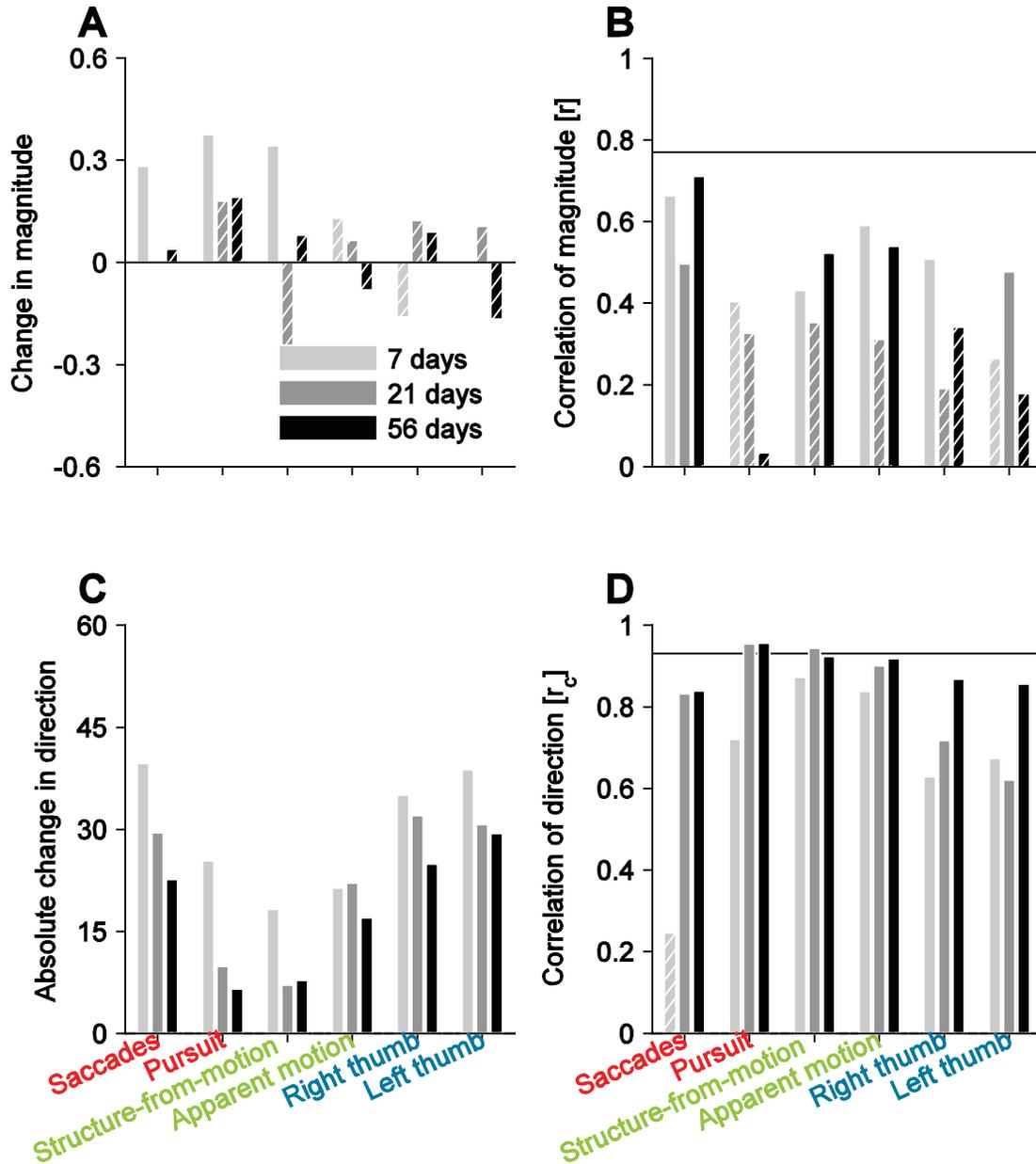
Figure 5: Stability over time for successive measurements separated by 7, 21 and 56 days.

(**A**) Mean difference between magnitude in successive measurements. Positive values indicate an increase in magnitude with time. (**B**) Correlation of magnitudes. (**C**) Mean absolute differences in preferred directions in successive measurements. (**D**) Correlation of directions. (**A – D**) Hatched bars represent values which were not significantly different from zero. (**B & D**) The horizontal line represents the median split-half reliability from **Figure 1D**.
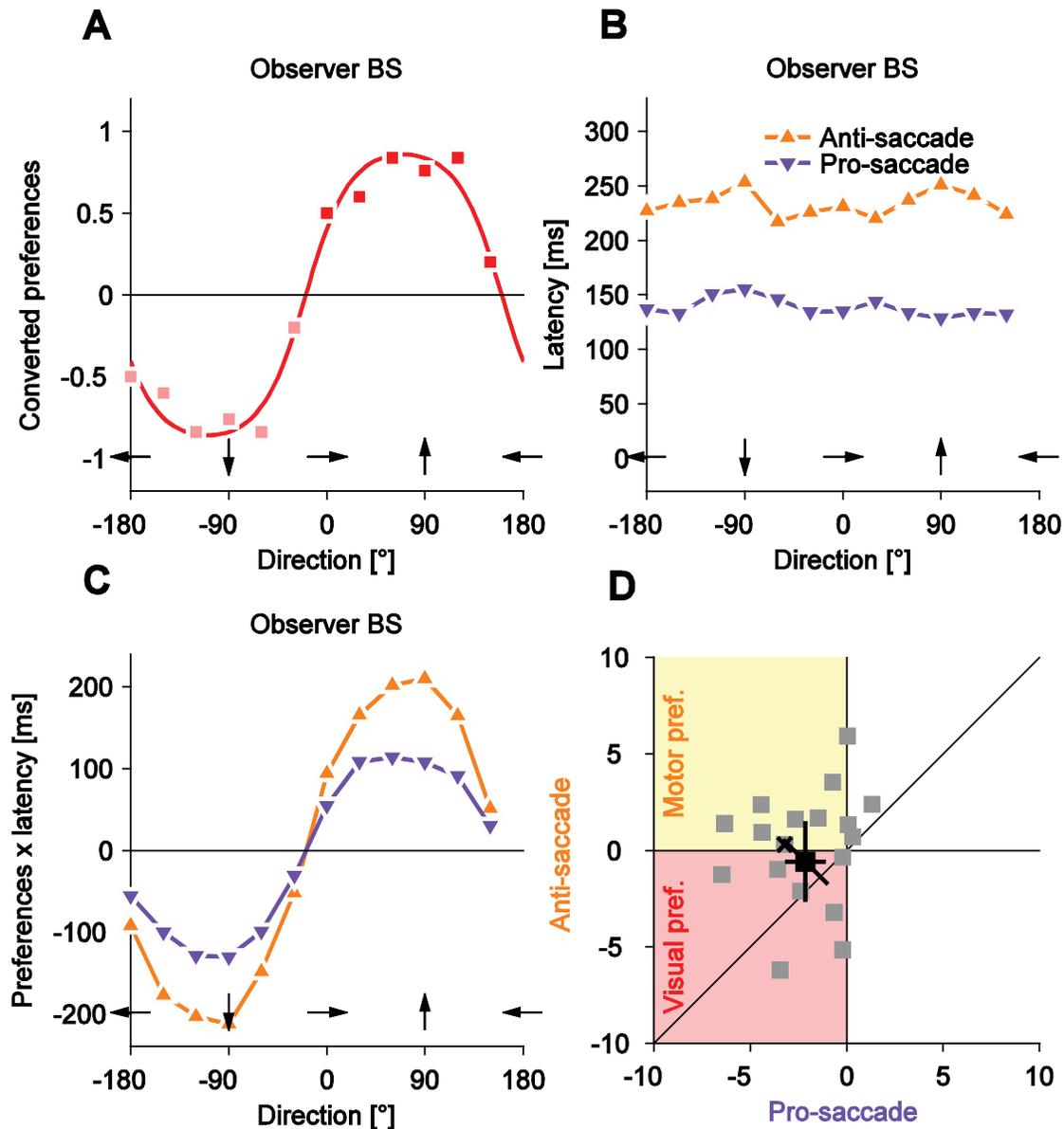
Figure 6: Correlation of latencies of pro- and anti-saccades and pro-saccade preferences. (**A**) Converted preferences of observer BS. Proportion of choices are multiplied by two and unity is subtracted to obtain a range from minus one to one. (**B**) Latencies of pro- and anti-saccades over visual target direction. (**C**) Multiplication of the converted preferences from **A** and saccade latencies from **B**. (**D**) Latency differences for pro-saccades and anti-saccades, generated by summing the functions in **C**. The gray squares represent data of individual observers. Observer BS is marked by a cross. The black square represents the average across observers. The error bars indicate 95% confidence intervals. Negative values indicate lower pro-saccade latencies in the preferred than in the non-preferred direction. The red-region

marks values in which directional preferences are of visual origin. The yellow-region marks values in which directional preferences are of motor origin.
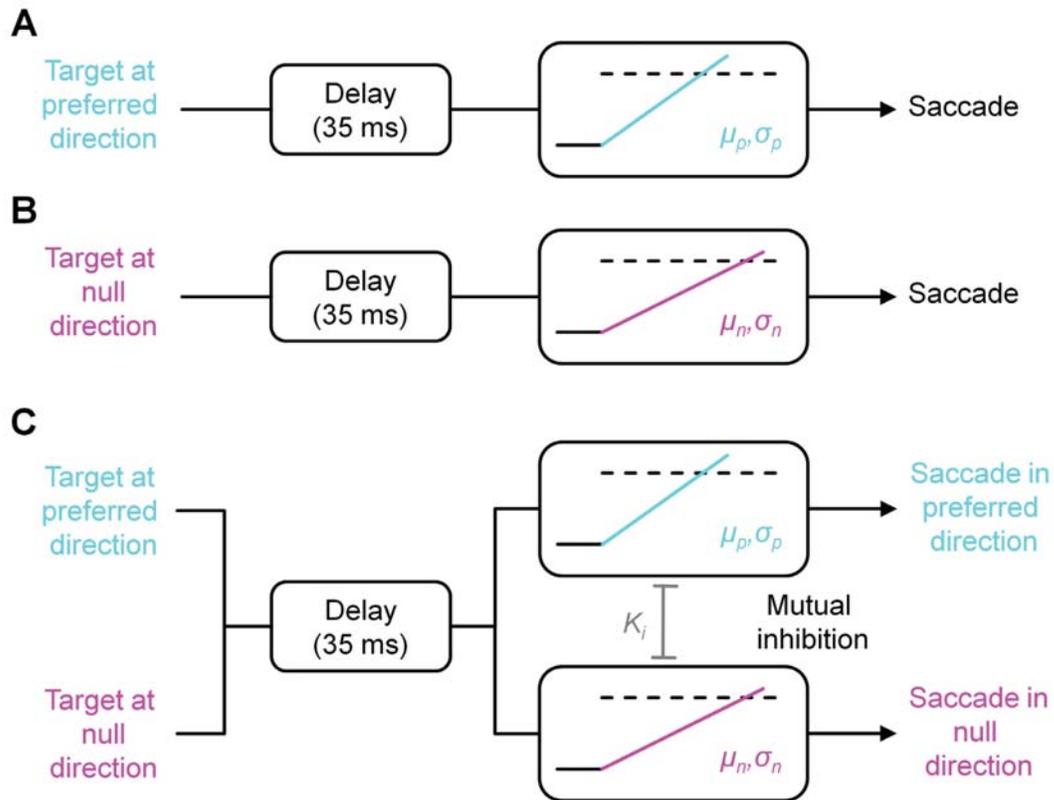
Figure 7: Illustration of LATER model of saccade latencies. (**A & B**) independent LATER units for preferred and non-preferred directions in single-target trials. The mean and standard deviation of the rate of accumulation are estimated. (**C**) Combination of the two LATER units by mutual inhibition to predict the latency distribution and choice preferences in double-target trials.
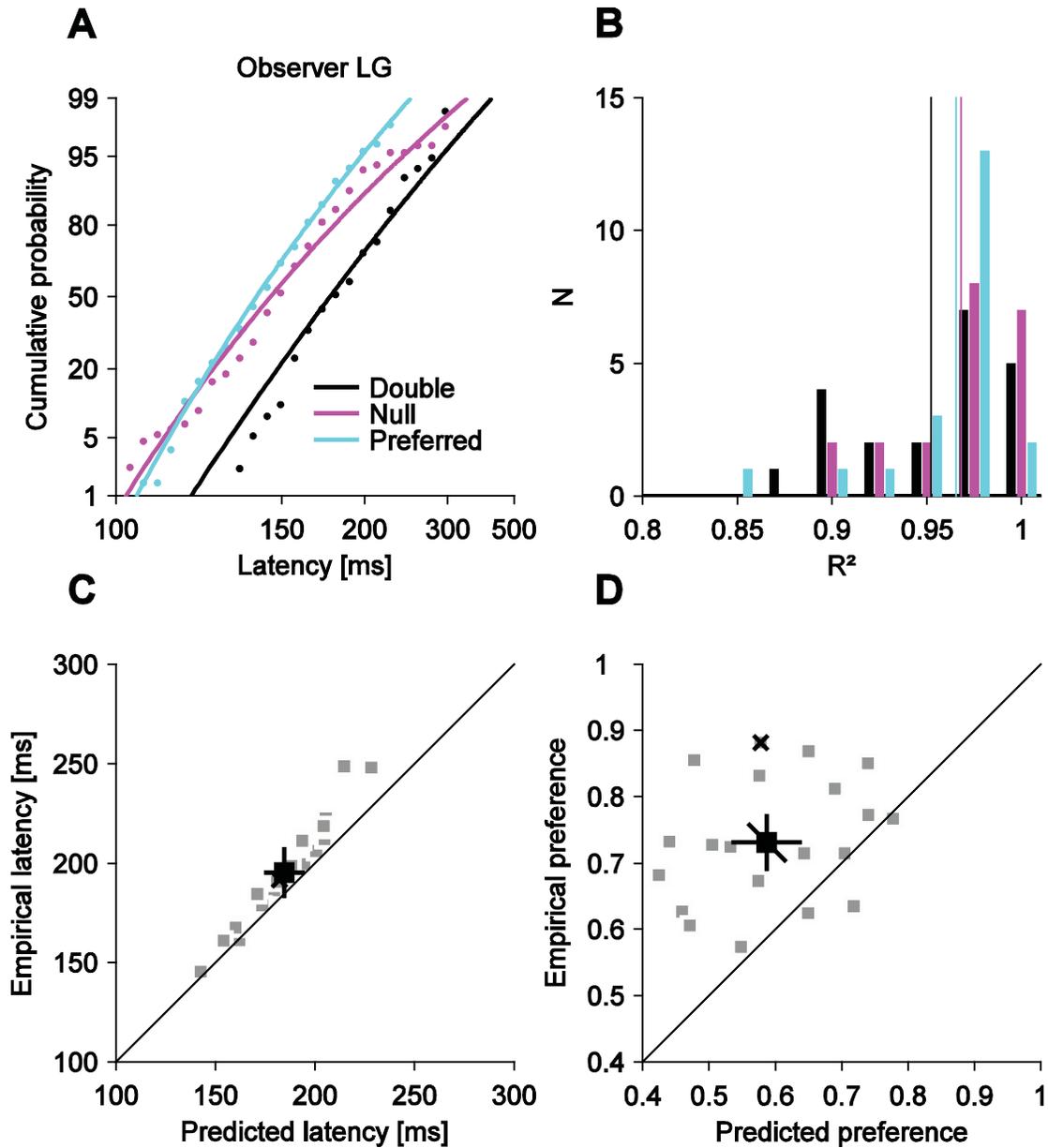
Figure 8: Results for the LATER model of saccade latencies. (**A**) Reciprobit-plot of saccade latencies for observer JK in single-target trials for preferred (cyan) and non-preferred (magenta) directions and in double-target trials (black). Dots represent empirical measurements, the lines represent model fits. (**B**) R² of the LATER model in single-target trials for preferred and non-preferred directions and in double-target trials. (**C**) Empirical latency in double-target trials over predicted latency from the model. (**D**) Empirical preference in double-target trials over predicted preference from the model. (**B-D**) Gray squares represent data of individual observers. Observer JK is marked by a cross. The black

square represents the average across observers. The error bars indicate 95% confidence

intervals.

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

Task	Magnitude	Direction [°]
Saccade	0.15 ± 0.39	111 ± 60 (0.002)
Smooth pursuit	0.86 ± 0.69	53 ± 77 (0.591)
Structure-from-motion	1.01 ± 0.57	-84 ± 41 (0.001)
Apparent motion	0.83 ± 0.47	-71 ± 63 (0.061)
Right thumb	0.73 ± 0.62	16 ± 58 (0.005)
Left thumb	0.47 ± 0.67	153 ± 68 (0.030)
Saccade (latency experiment)	0.20 ± 0.33	75 ± 56 (0.097)

Table 2: Correlation of the magnitude of preferences for different tasks. Uncorrected p-values are specified in parentheses.

	Smooth pursuit	Structure-from-motion	Apparent motion	Right thumb	Left thumb
Saccade	0.210 (0.388)	0.093 (0.632)	0.317 (0.094)	0.296 (0.141)	0.318 (0.099)
Smooth pursuit		0.040 (0.868)	0.249 (0.289)	0.006 (0.980)	0.214 (0.380)
Structure-from-motion			-0.094 (0.622)	0.082 (0.686)	0.044 (0.821)
Apparent motion				0.061 (0.762)	0.090 (0.642)
Right thumb					0.366 (0.060)

Table 3: Correlation of the preferred directions for different tasks. Uncorrected p-values are specified in parentheses. Significant correlations are printed in bold.

	Smooth pursuit	Structure-from-motion	Apparent motion	Right thumb	Left thumb
Saccade	0.338 (0.166)	-0.037 (0.851)	-0.065 (0.709)	0.240 (0.179)	0.224 (0.230)
Smooth pursuit		**-0.692 (0.006)**	-0.053 (0.824)	0.234 (0.295)	-0.157 (0.478)
Structure-from-motion			-0.021 (0.905)	-0.064 (0.704)	0.215 (0.226)
Apparent motion				-0.142 (0.475)	0.025 (0.896)
Right thumb					**-0.590 (0.005)**