Chapter 4

Unraveling the informational basis of anchoring in rhythmic visuomotor tracking

Manuscript submitted as:
Roerdink, M., Bank, P. J. M., Peper, C. E., & Beek, P. J. (submitted). Unraveling the informational basis of anchoring in rhythmic visuomotor tracking
Abstract

Rhythmic movements are often anchored on particular points in the movement cycle as evidenced by regions of reduced trajectory variability. In rhythmic unimanual visuomotor tracking such anchor points are known to depend on gaze direction. In the present experiment, we examined the informational basis of this form of visuomotor anchoring by dissociating information regarding the timing and required spatial location of movement reversals, respectively. To this end, participants tracked an oscillating target signal in an in-phase and antiphase mode with and without concurrent visual feedback, while fixating their gaze at either the left or right target turning point. In line with the notion of gaze anchoring (which predicts that gaze and hand movements co-align), hand movements were always anchored on the foveated endpoint, particularly in the presence of visual feedback. For in-phase tracking only a single anchor point was discernible in the movement cycle, putatively because spatial and temporal information coincided at the point of gaze. For antiphase tracking, in contrast, anchoring was evident at both the foveated and non-foveated endpoint, particularly in the absence of visual feedback. Presumably, in this condition, anchoring at the foveated endpoint was related to spatial information (i.e., gaze anchoring) while anchoring at the non-foveated endpoint was based on target-related timing information. Anchor points were accompanied by increased temporal endpoint variability, presumably reflecting error correction associated with anchoring. Collectively, the results underscored that anchoring is a generic aspect of rhythmic coordination, and that the number of anchor points and their location depends on the prevailing task constraints.
Introduction

In rhythmic limb movements, regions of reduced trajectory variability are often observed as evidenced by a local thinning of the phase portraits at one or both movement reversal points (Chapters 2-3; Byblow & Chua, 1998; Byblow et al., 1994, 1995; Carson et al., 1994; Fink et al., 2000). Such local compressions of variability have been interpreted as reflections of informational, mechanical, or intentional constraints acting upon the ensuing rhythmic control. According to Beek (1989) they reflect points or regions in the perceptual-motor workspace where useful task-specific information is available, for instance for proper movement timing. It has also been suggested that such points possess functional task-specific mechanical properties that may be utilized in performing a rhythmic task (Chapter 3), for instance to store and release energy. In both accounts, the points and regions in question have been called "anchor points" to indicate that they serve as "intentional attractors" or "organizing centers" within and for the complete movement cycle (Beek, 1989).

Previous studies on visuomotor tracking manipulated both mechanical and informational constraints by instructing participants to manually track a rhythmically oscillating visual target signal in different wrist postures and under different visual configurations (Chapters 2-3; Byblow et al., 1995; Carson et al., 1994). In those studies, support was found for systematic relations between local compressions of endpoint variability (indicating anchor points) and either type of constraint. For example, for tracking with the wrist in a flexed posture—which alters the relative length of wrist flexor and extensor muscles and hence mechanical neuromuscular properties—flexion endpoint variability was reduced, suggesting that movements were oriented consistently at peak flexion, supposedly to fuel counteracting passive moments of elongated extensor muscles (Chapter 3). In an extended posture the converse was true, whereas in a neutral posture these differential effects were absent (Chapter 3). Regarding the informational constraints, gaze fixation at one of both target turning points was found to reduce the excursion variability around the associated movement endpoint (Chapters 2-3), whereas such a differential effect across endpoints was absent when gaze was fixated in between the turning points or when participants visually pursued the target signal (Chapter 2). These effects of mechanical and informational constraints on anchoring proved to be independent of each other (Chapter 3).

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In rhythmic visuomotor tracking the hand must be at a particular location at a particular time, which requires task-specific spatiotemporal information. The observed gaze-related anchoring may be attributed to two distinct sources of information available at the point of gaze. First, target-related timing information is available at the foveated target turning point. This spatiotemporal information specifies the required timing of the associated movement reversal which may evoke anchoring in the originally proposed sense (Beek, 1989), implying that hand movements are consistently oriented to a particular point in the movement cycle based on target-related timing information picked up at the point of gaze. Second, the spatial location where hand movements must be steered to is specified or coded by the point of gaze. From discrete visuomotor tasks we know that movements are not only more accurate in the direction of foveation (e.g., Prablanc et al., 1979) but also that foveal fixation remains locked to the target until it is reached (Neggers & Bekkering, 2000). This forced co-alignment of eye and hand, called gaze anchoring (Neggers & Bekkering, 2000), testifies to a strong bidirectional visuomotor coupling (Neggers & Bekkering, 2001) that is independent of visual information of the moving limb (Neggers & Bekkering, 2001; see also Prablanc et al., 1986). Also in rhythmic visuomotor tracking tasks eye and hand movements appear to be intimately coupled and to assist task performance (Chapters 2-3; Koken & Erkelens, 1992; Leist et al., 1987), thereby utilizing spatial location information specified or coded by the point of gaze.

The present study aimed at dissociating between these two sources of information (i.e., information about the precise timing of a movement reversal point and information about the spatial location of a particular movement reversal point, both available at the foveal fixation point) to uncover the informational basis of anchor points in visuomotor tracking while controlling for possible interfering mechanical effects. The dissociation between spatial and temporal endpoint variability may be instrumental in this regard, because the latter is expected to be associated with target-related timing information, whereas the former is expected to be associated with both sources of information. By comparing spatial and temporal variability associated with the foveated and non-foveated target turning points, we determined the contributions of the two sources of information to anchoring. For in-phase tracking (i.e., target and hand move along), we expected a reduction of spatial and temporal endpoint variability at the foveated endpoint, because in this mode...
Both sources of information are available at the point of gaze. For antiphase tracking (i.e., target and hand move in opposite directions), we not only expected reduced spatial variability at the foveated endpoint (due to gaze anchoring) but also reduced spatial and temporal endpoint variability at the non-foveated reversal point, because in this mode target-related timing information available at the point of gaze may be used to control movement reversals at the non-foveated endpoint. Because a spatial co-alignment of eye and hand is the defining characteristic of gaze anchoring (Neggers & Bekkering, 2000, 2001), we expected a further reduction of spatial endpoint variability at the point of gaze for tracking with concurrent movement-related visual feedback, allowing for a direct spatial co-alignment of gaze and the visual feedback representing the hand movement. This facilitating effect of feedback on gaze anchoring was expected to be independent of tracking mode (in-phase or antiphase).

Methods

Twelve healthy adults participated (three male, nine female, mean age 24 years, age range: 20-48) after giving informed consent. All were right-handed (Oldfield, 1971) and had normal or corrected to normal vision. The study was approved by the local ethics committee.

The participant’s right forearm rested on a tabletop with adjustable supports to prevent forearm movement. The right hand was strapped against a flat vertically-oriented manipulandum (fingers extended) mounted on a potentiometer aligned with the wrist joint, allowing wrist flexion and extension movements in the horizontal plane only. A horizontal cover prevented vision of the moving hand. The range of motion of the wrist was determined (i.e., the maximal flexion and extension positions were held for about five seconds) and the individual midpoint (4.5° ±0.8° flexion relative to the hand being aligned with the forearm) was used for neutral offset correction (see below).

A harmonically oscillating target signal was presented on a horizontal semicircular projection bow, consisting of a continuous array of 448 light-emitting diodes (LEDs), positioned 1.5 meter in front of the participant. Concurrent visual feedback of the wrist angle could be provided by using a laser pointer attached to the manipulandum, pointing just below the target trace (for a schematic representation of the experimental setup see Figure 3.2 in Chapter 3). To avoid systematic influences on endpoint variability due to variations in the contents under embargo.
The relative contribution of flexor and extensor muscles (Chapters 2-3), the frontoparallel position of the LED bow was adjusted for each individual to ensure that the laser pointed at the center of the LED bow when the wrist was in its individually determined neutral position. LED coordinates were calibrated to potentiometer data for offline comparison of target and tracking signals (both in °, sampling rate: 1000 Hz).

Participants were instructed to foveate at either the left (L) or right (R) target turning point and to track the target signal (30 cycles, oscillation frequency: 1 Hz, amplitude: 15°, i.e., movement range: 30°) either in phase (IP: hand moving along with the target signal) or in antiphase (AP: hand moving opposite to the target signal), and either with (FB) or without (NF) concurrent visual feedback of the wrist angle. The eight experimental conditions were performed five times each. Trials were presented in blocks with feedback (FB, NF) providing the first level of blocking (2 × 20 trials; order counterbalanced over participants). For each feedback block the four combinations of gaze direction (L, R) and tracking mode (IP, AP) were presented in blocks, also in counterbalanced order.

Before commencing a trial, participants moved their hand to the starting position, which was indicated by two LEDs (1 cm apart), under visual guidance of laser feedback. The laser was subsequently switched off (NF trials) or remained on (FB trials). The target signal always started at the fixation position, which was indicated by a single LED. Participants were instructed to foveate at this position throughout the trial. Gaze was monitored using a webcam.

Wrist angle data were low-pass filtered (cut-off 12.5 Hz) and the first three seconds were excluded from analysis to eliminate possible transient effects. From the following 25 complete movement cycles dependent variables were calculated. Tracking performance was quantified by the oscillation center (to control for potentially confounding shifts in wrist posture between NF and FB conditions (Chapter 2)), tracking amplitude, and tracking accuracy (i.e., square root of the mean continuous squared error between target and tracking signals [RMSE]; for AP trials the target signal was first inverted, see Chapter 2). In addition, the relative phase between target and hand movement was determined by subtracting the continuous phase of the wrist oscillations from that of target oscillations (for AP trials the target signal was inverted). Mean relative phase (negative values indicating that the hand was leading the target signal in time) and its transformed circular variance (TCV; reflecting the
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as evidenced by smaller differences between movement and target amplitudes (target: 15°, FB: 13.5°, NF: 17.6°; $F(1,8) = 7.77, p < 0.05, \eta^2 = 0.49$), smaller RMSE between target and tracking movements (FB: 4.6°, NF: 9.0°; $F(1,8) = 89.93, p < 0.001, \eta^2 = 0.92$), and smaller phase advance of the tracking hand relative to the required phase relation (FB: -14.6°, NF: -18.8°; $F(1,8) = 7.60, p < 0.05, \eta^2 = 0.49$). TCV was not affected by feedback, but the effect of tracking mode indicated that IP tracking was more stable than AP tracking (IP: 14.1°, AP: 16.3°; $F(1,8) = 14.81, p < 0.005, \eta^2 = 0.65$). Tracking performance was not affected by gaze direction nor were there any significant interactions.

The effects of the eight conditions on spatial endpoint variability are shown in the phase portraits in Figure 4.1. The 2 (Feedback) × 2 (Tracking Mode) × 2 (Gaze Direction) × 2 (Endpoint: flexion, extension) repeated measures ANOVA revealed significant effects of feedback ($F(1,8) = 41.77, p < 0.001, \eta^2 = 0.84$) and tracking mode ($F(1,8) = 16.28, p < 0.005, \eta^2 = 0.67$), demonstrating lower overall spatial endpoint variability for tracking with feedback (FB: 1.53°, NF: 2.56°) and AP tracking (IP: 2.16°, AP: 1.93°). The Feedback × Tracking Mode interaction tended towards significance ($F(1,8) = 5.10, p = 0.054, \eta^2 = 0.39$), suggesting that the difference in overall spatial endpoint variability between IP and AP tracking was more pronounced without (IP: 2.77°, AP: 2.35°) than with feedback (IP: 1.56°, AP: 1.51°). In addition, the Gaze Direction × Endpoint interaction was significant ($F(1,8) = 32.51, p < 0.001, \eta^2 = 0.80$). Post hoc paired-samples t-tests indicated lower left (1.80°) than right (2.20°) spatial endpoint variability when gaze was foveated on the left side, and lower right (1.94°) than left (2.25°) spatial endpoint variability when gaze was foveated on the right side, consistent with the notion of gaze anchoring. The Gaze Direction × Tracking Mode × Endpoint interaction ($F(1,8) = 50.81, p < 0.001, \eta^2 = 0.86$) indicated that the Gaze Direction × Endpoint interaction was less pronounced for AP than IP tracking. Moreover, the Gaze Direction × Feedback × Tracking Mode × Endpoint interaction ($F(1,8) = 6.74, p < 0.05, \eta^2 = 0.46$) revealed that the Gaze Direction × Endpoint interaction was completely absent for AP tracking without feedback (Figure 4.2a).

Figure 4.2. Effects of gaze direction (L, R) and tracking mode (IP, AP), performed with (FB) and without feedback (NF) on spatial endpoint variability (a) and oscillation center (b). Asterisks indicate significant differences between flexion and extension endpoint variability within a condition, as determined by paired-samples t-tests.
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For the oscillation center, asterisks indicate a significant shift away from 0°, as determined by a one-sample t-test ($p < 0.05$).

Motivated by this four-way interaction, the relative contribution of both sources of information on spatial endpoint variability was further examined by a number of strategic comparisons across conditions (Table 4.1; see also Figures 4.1, 4.2a). First, the impact of target-related timing information available at the fixation point was isolated by comparing spatial variability of the non-foveated endpoint between IP and AP tracking. Endpoint variability was significantly lower in the non-foveated direction for AP than for IP tracking, especially for NF tracking. Second, the impact of information about the spatial location of a movement reversal at the fixation point was isolated by comparing spatial variability of the foveated endpoint between IP and AP tracking. No differences were observed between the tracking modes.

For temporal endpoint variability the main effect of tracking mode ($F(1,8) = 40.41, p < 0.001, \eta^2 = 0.83$) indicated that the timing of movement reversals was overall more variable in AP (45.9 ms) than in IP (37.5 ms) tracking. The effect of feedback tended towards significance ($F(1,8) = 3.75, p = 0.089, \eta^2 = 0.32$) suggesting that overall temporal endpoint variability was larger for tracking with (43.3 ms) than without feedback (40.2 ms). The Gaze Direction × Endpoint interaction ($F(1,8) = 6.34, p < 0.05, \eta^2 = 0.44$) indicated larger temporal endpoint variability at the foveated endpoint (42.8 vs. 40.6 ms). The Gaze Direction × Feedback × Endpoint interaction tended towards significance ($F(1,8) = 4.77, p = 0.060, \eta^2 = 0.37$) suggesting that this difference was more pronounced for tracking with feedback (45.3 vs. 41.3 ms) than for tracking without feedback (40.4 vs. 40.0 ms).

Table 4.1. Strategic comparisons between IP and AP non-foveated endpoint variability (isolating target-related timing information) or foveated endpoint variability (isolating spatial location information) using paired-samples t-tests.

<table>
<thead>
<tr>
<th>Target-related timing information</th>
<th>endpoint conditions</th>
<th>difference</th>
<th>$t$</th>
<th>$d.f.$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SDext FB-IP-L - FB-AP-L</td>
<td>0.25°</td>
<td>2.86</td>
<td>8</td>
<td>0.021</td>
<td></td>
</tr>
<tr>
<td>SDflex FB-IP-R - FB-AP-R</td>
<td>-0.07°</td>
<td>0.58</td>
<td>8</td>
<td>0.581</td>
<td></td>
</tr>
<tr>
<td>SDext NF-IP-L - NF-AP-L</td>
<td>0.74°</td>
<td>3.36</td>
<td>8</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td>SDflex NF-IP-R - NF-AP-R</td>
<td>0.57°</td>
<td>3.71</td>
<td>8</td>
<td>0.006</td>
<td></td>
</tr>
</tbody>
</table>

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SDflex FB-IP-L - FB-AP-L 0.04° 0.66 0.526
SDext FB-IP-R - FB-AP-R -0.04° 1.07 0.314
SDflex NF-IP-L - NF-AP-L 0.08° 0.35 0.734
SDext NF-IP-R - NF-AP-R 0.27° 1.91 0.092

SDflex: flexion endpoint variability; SD ext: extension endpoint variability; FB: feedback; NF: no feedback; IP: in-phase; AP: antiphase; L: left gaze; R: right gaze

The oscillation center was analyzed to verify that our neutral wrist position offset correction procedure was successful. The absence of a main effect of feedback (FB: 0.27°, NF: -0.49°; $F(1,8) = 1.01, p > 0.05, \eta^2 = 0.12$) revealed that this was the case. (Note that 0° indicated the neutral position.) Unexpectedly, however, significant Tracking Mode × Gaze Direction and Feedback × Tracking Mode × Gaze Direction interactions ($F(1,8) = 11.26, p < 0.01, \eta^2 = 0.58$ and $F(1,8) = 14.51, p < 0.005, \eta^2 = 0.64$, respectively) were found. Post hoc analyses indicated unexpected systematic shifts in oscillation center (dashed lines in Figure 4.1), which differed significantly from 0° in most conditions (Figure 4.2b). For FB tracking, oscillation center was always shifted in the gaze direction, whereas in NF conditions shifts were generally larger and depended on tracking mode as well (see Figures 4.1, 4.2b): for IP tracking left gaze resulted in a shift to the left and right gaze in a shift to the right whereas the converse was observed for AP tracking.

Discussion

In the present study, we sought to uncover the informational basis of anchoring in rhythmic visuomotor tracking by teasing apart spatial and temporal sources of information available at the point of gaze. Tracking mode was manipulated and spatial and temporal endpoint variability was assessed to dissociate between these sources of information.

The results underscored the notion that, in general, rhythmic movements are not controlled continuously but contain clearly discernible control or anchor points at task- and constraint-dependent locations (Chapters 2-3; Beek, 1989; Byblow & Chua, 1998; Byblow et al., 1994, 1995; Carson et al., 1994; Fink et al., 2000). As expected, anchor points were strongly gaze-dependent, with lower spatial variability at the foveated endpoint. Furthermore, gaze-related anchoring proved to be independent of tracking mode, since spatial endpoint variability in the foveation direction did not differ between IP and AP tracking (Table 4.1).

Moreover, as anticipated, the reduction in spatial endpoint variability was more

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pronounced in the presence of concurrent movement-related visual feedback (again irrespective of tracking mode), providing further support for the notion that gaze-related spatial information was specified or coded by the point of gaze to co-align the associated movement reversal with the point of gaze fixation (i.e., gaze anchoring, Neggers & Bekkering, 2000, 2001).

Gaze anchoring furnishes non-temporal information regarding the spatial location of a movement reversal. However, also target-related timing information is required in rhythmic tracking, which is also available at the point of gaze. Therefore, also a reduction in temporal endpoint variability was expected for IP tracking at movement reversals in the direction of foveation. However, the opposite effect was observed. In AP tracking, reduced temporal variability was expected at the non-foveated endpoint, reflecting the utilization of target-related timing information available at the point of gaze. Also this prediction was not borne out. For this tracking mode we further anticipated reduced spatial variability at the non-foveated endpoint, which was indeed observed (Table 4.1), especially for tracking without feedback where differences in spatial variability across endpoints vanished completely (Figures 4.1, 4.2a).

Thus, although we expected reduced temporal variability at foveated endpoints for IP tracking and at non-foveated endpoints for AP tracking, we found the opposite. As wrist oscillations were performed at a much lower frequency than in Chapter 3, i.e., 1.0 vs. 1.8 Hz, the observed increase in temporal variability may have reflected error corrections aimed at getting the hand to the correct location, at the expense of its precise timing. This phenomenon was most prominent at the foveated movement reversal for tracking with visual feedback (i.e., reduced spatial variability at the expense of increased temporal variability), suggesting a dominant role of processes underlying gaze anchoring (Neggers & Bekkering, 2000, 2001). Moreover, error correction also appeared implicated in anchoring to target-related timing information as spatial variability at the non-foveated endpoint was significantly smaller for AP tracking than for IP tracking without feedback (Table 4.1, Figures 4.1, 4.2a) at the expense of overall increased temporal variability.

Whereas previous studies on anchoring were focused predominantly on the local thinning of phase portraits (Chapter 2; Beek, 1989; Byblow & Chua, 1998; Byblow et al., 1994, 1995; Carson et al., 1994), the present results suggest that temporal endpoint variability may be informative about the formative processes underlying anchoring.
underlying anchoring. We therefore submit that both aspects should be addressed in future studies of anchoring behavior (see also Chapter 3).

Overall, the timing of movement reversals was more variable in AP tracking than in IP tracking while overall spatial endpoint variability was smaller. This indicated that for AP tracking, particularly without feedback, two control or anchor points (with associated error correction) are implicated in the movement cycle: one at the foveated endpoint and one at the non-foveated endpoint. We interpret this finding to imply that the former anchor point is associated with gaze anchoring (Neggers & Bekkering, 2000, 2001), while the latter anchor point reflects anchoring in the sense proposed by Beek (1989), who suggested that movements are steered to particular points in the movement cycle where task-specific information is available. According to this interpretation, anchoring of foveated movement reversals is based on spatial information encoded in the direction of foveation, while anchoring of movement reversals in the non-foveated direction is based on target-related timing information available at the foveated target turning point. IP tracking, in contrast, is governed by only one anchor point since both sources of information coincide at the point of gaze.

In general, anchor points are mediated by mechanical, informational, and intentional constraints, and observable anchoring phenomena in any given situation may be considered as the (additive) anchoring effects of those constraints. In the present study the mechanical constraint was controlled by keeping wrist posture neutral, so that any mechanical anchoring effects at peak flexion and extension were in balance (Chapter 3). Informational constraints were manipulated by systematically varying tracking mode, gaze direction, and movement feedback, yielding markedly different anchoring effects across experimental conditions. In IP tracking target-related timing information and gaze-related spatial information coincided at the point of gaze, resulting in pronounced anchoring at this point. In AP tracking without feedback, in contrast, anchoring effects associated with the two sources of information were equally balanced over both movement reversals, resulting in two distinct anchor points rather than one. Finally, in AP tracking the facilitating influence of visual feedback outweighed the gaze anchoring effect relative to that based on target-related timing information, thereby introducing an imbalance in anchoring across movement reversals in favor of the foveated one.

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The obtained insights into the number of control points with inherent error correction and their location may have profound implications for the understanding of phase transitions as studied in coordination dynamics (Beek et al., 1995; Kelso, 1995). As has been demonstrated repeatedly, phase transitions in visuomotor tracking from the less stable AP to the more stable IP tracking mode can be induced by gradually increasing target frequency (Chapter 2; Byblow et al., 1994; Wimmers et al., 1992). It has been claimed that such phase transitions have an informational basis (Beek, 1989; Kugler, 1986; Wimmers et al., 1992) and that they are due to thresholds in the associated information processing demands (Rosenbaum, 1991). These claims can now be made more specific on empirical grounds. As explained, rhythmic AP tracking involves two anchor points and the associated error corrections presumably introduce considerable information processing demands. As tracking frequency increases, this processing load increases until it reaches a threshold value inducing a transition to IP tracking to relieve the computational burden: two anchor points coalesce to one at the foveated endpoint.

As we were interested in uncovering the informational basis of anchoring in visuomotor tracking we controlled for effects of wrist posture on endpoint variability (Chapters 2-3). Although this control was successful, some unexpected effects were observed (Figures 4.1, 4.2b). The oscillation center was shifted in the direction of gaze (by approximately 1-2°) for FB tracking, which may (in combination with the slightly smaller movement amplitude) be attributed to the identified error correction inherent to gaze anchoring, leading to a small error between prescribed and actual movement reversal positions. For NF tracking the oscillation center shifted in the direction of the non-foveated endpoint in the antiphase mode. These shifts were more pronounced and may have assisted participants to also utilize mechanical properties available at the anchored point (Chapter 3). Future EMG studies on rhythmic unimanual limb movements will help to identify the neurophysiological underpinnings of anchoring and the shifts in oscillation center that are often observed with increasing movement frequencies (e.g., Figure 2.8 in Chapter 2). The number and precise location of observable anchor points may be (co)determined by prevailing cost functions related to task performance (more anchor points may be beneficial) and task economy or computational burden (less anchor points may be more economical).
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