RESEARCH ARTICLE

An eye-to-hand magnet effect reveals distinct spatial interference in motor planning and execution

Brian A. Richardson · Tyler Cluff · James Lyons · Ramesh Balasubramaniam

Abstract An important question in oculomanual control is whether motor planning and execution modulate interference between motion of the eyes and hands. Here we investigated oculomanual interference using a novel paradigm that required saccadic eye movements and unimanual finger tapping. We examined finger trajectories for spatial interference caused by concurrent saccades. The first experiment used synchronous cues so that saccades and taps shared a common timekeeping goal. We found that finger trajectories showed bilateral interference where either finger was attracted in the direction of the accompanying saccade. The second experiment avoided interference due to shared planning resources by examining interference caused by reactive saccades. Here, we observed a lesser degree of execution-dependent coupling where the finger trajectory deviated only when reactive saccades were directed toward the hemifield of the responding hand. Our results show that distinct forms of eye-to-hand coupling emerge according to the demands of the task.

B. A. Richardson (✉) · T. Cluff · R. Balasubramaniam
Sensorimotor Neuroscience Laboratory, McMaster University,
1280 Main Street West, Hamilton, ON L8S 4K1, Canada
e-mail: richab2@mcmaster.ca
URL: http://sensorimotor.mcmaster.ca

J. Lyons · R. Balasubramaniam
Department of Kinesiology, McMaster University,
Hamilton, ON, Canada

B. A. Richardson · T. Cluff
McMaster Integrative Neuroscience Discovery and Study
(MiNDS), McMaster University, Hamilton, ON, Canada

Present Address:
T. Cluff
Laboratory of Integrative Motor Behaviour (LIMB),
Centre for Neuroscience Studies, Queen's University,
Kingston, ON, Canada

Introduction

In daily activities, our brains direct our eyes to relevant targets in the environment. This is often done in parallel with a manual task that may or may not share a cooperative goal. To organize coupling suitable for a given task, the ocular and manual motor systems must share sensorimotor resources. An important challenge for researchers has been to model the encoding of motor planning and execution in multi-effector actions (e.g., Carson 2005; Carson and Kelso 2004; Grefkes et al. 2008; Swinnen and Wenderoth 2004). The topic of inter-effector coupling, for which the involuntary case is termed interference, is perhaps best introduced in the context of inter-limb coupling. An exemplary demonstration is the spatial magnet effect evoked by simultaneous action of the two upper limbs: when a circle is drawn with one hand and a line with the other, each movement is distorted in the direction of the other limb's trajectory (Franz et al. 1991).

Bimanual limb movements are susceptible to interference for a few reasons. During planning, the anticipatory encoding of one limb's action can influence the action of the other limb (Franz and Ramachandran 1998; Diedrichsen et al. 2006). Other coupling effects emerge during execution and are blanketed under the term *motor overflow*. Overflow describes effector crosstalk processes where motor commands interfere online during the execution of simultaneous movements. Two subclasses of overflow that have separate physiological correlates and are termed *associated* movements of non-homologous (dissimilar) limbs, or *irradiation*

of motor commands to contralateral homologous (similar) muscle groups. It is important to distinguish these hierarchically organized mechanisms. Associated movements arise from intrahemispheric and transcallosal projections between cortical regions specialized for non-homologous effectors (Hoy et al. 2004). In contrast, incomplete decussation of the pyramidal corticospinal tract is the source of irradiation to contralateral homologous effectors (Carson 2005). In sum, interference between simultaneous limb movements is a combined function of crosstalk in action planning and two distinct types of interference that arise during the execution of motor tasks.

Defining a similar organizational model for oculomanual coupling is somewhat confounded by the different timescales of saccades and hand movements. Saccades are extremely fast and are completed in a fraction of the time required for upper limb motion. This minimizes their temporal overlap in coordinated tasks and limits the time available to integrate potential interference. Describing eye–hand interactions in a purely motoric framework is also difficult because the hand's actions often rely on visual perception and visuomotor transformations. Despite these paradigmatic caveats, it is apparent that oculomanual interactions emerge predictively due to overlapping motor planning resources (Kattoulas et al. 2008; Lünenburger et al. 2000; Snyder et al. 2002; van Donkelaar 1997, 2004). To our knowledge, oculomanual interference arising from motor overflow has not been clearly demonstrated. Although *irradiation* between eye and hand movements is not possible because the eyes and hands lack homologous muscle groups, an important question is whether the eyes and hands are susceptible to *associated* interference from the recruitment of common neural structures (i.e., motor overflow).

The brain structures responsible for ocular and manual motor control are predominantly specialized and separate (Graziano et al. 2002; Kalaska et al. 1997; Sparks 2002). While this regional motor specialization is evident in the activation of the frontal eye field and the primary motor cortex (Ferraina et al. 2002; Mushiake et al. 1996), it is incomplete at higher levels of the control hierarchy. Examples of brain regions that respond to multiple effectors are the premotor cortices, supplementary motor areas, supplementary eye fields, and posterior parietal cortices (Mushiake et al. 1996; Pesaran et al. 2010; Snyder et al. 2000; Levy et al. 2007). Compared to the primary motor areas, these secondary networks are associated with complex movement parameters like motor sequencing, learning patterns, and general functions of planning in both limb- and vision-centered reference systems (van Donkelaar et al. 2002).

The selective recruitment of these networks for reactive or predictive visual tracking is an exemplary case of how saccades are encoded differently depending on the behavioral context (Mort et al. 2003; Müri and Nyffeler 2008;

Shelhamer and Joiner 2003). Predictive saccades require sensorimotor planning to model and implement a series of timed movement goals. Advanced temporal planning is not required for reactive saccades because they lack a predictable timing structure. This is a key factor in our study because reactive and predictive saccades recruit separate brain regions, and these regions might encode actions with varying levels of effector specificity and in different effector-centric coordinate systems. For this reason, we hypothesized that eye–hand interactions might also be different when reactive and predictive saccades are combined with a manual task.

In conjunction with these two types of saccades, our study assessed finger kinematics while participants executed periodic tabletop tapping. Saccading was performed in the horizontal axis while the tapping motion was vertical, and we hypothesized that the finger trajectory would deviate laterally in the direction of a concomitant saccade. Another noteworthy property of oculomanual control is that saccades are predominantly encoded in the hemisphere contraversive to their horizontal direction, whereas motor neurons projecting to the limbs arise primarily from the hemisphere contralateral to the associated limb. It is therefore reasonable to hypothesize that saccades in either direction might interact differently with the movements of either hand. For this reason, and for controlling potential handedness effects, our experiments included unimanual responses with both hands.

A prevailing model of discrete short-interval sensorimotor timekeeping posits that one timing network is entrained to externally specified intervals while timing output generalizes to motor and perceptual networks from a single reference signal (*c.f.* Hazeltine et al. 1997). Motor planning is necessary for timing responses with external pacing cues and we hypothesized that synchronous saccades and finger movements would share these planning resources and increase the likelihood of eye–hand crosstalk in motor planning (Experiment 1). Finger tapping was repeated in Experiment 2, but we used aperiodic visual stimuli to cue reactive saccades. In contrast to the first experiment, Experiment 2 was based on a dual-task design with independent goals for eye and hand movements. Research has shown that each goal in a dual task can be encoded separately in the brain (Charron and Koechlin 2010), that minimal temporal interference is observed when saccades and tapping are cued by different events (Sharikadze et al. 2009), and that predictive but not reactive saccades engage internal timing networks (Shelhamer and Joiner 2003). We reasoned that making reactive saccades in combination with periodic tapping would minimize common planning resources shared by both actions, thus enabling a dissociation of oculomanual interference that arises during motor planning and execution.

Our results demonstrated an eye-to-hand magnet effect wherein saccades attracted the finger trajectory in the direction of the eyes' motion. Interestingly, spatial interference

affected both the left and right fingers when eye–hand responses were performed synchronously in Experiment 1, but we observed only weak oculomanual interference when saccades were directed to the hemifield of the tapping hand in Experiment 2.

Materials and methods

Participants and experimental apparatus

Nineteen healthy individuals were recruited from the local student body, consented to participate in the study, were naïve to the goals of the experiment, and received monetary compensation for their time. The following procedure was approved by the McMaster University Research Ethics Board. Participants sat comfortably at a table, kept the palms of their hands flat on the table with their index fingers pointing forward, and faced a computer display 60 cm away. Visual stimuli were presented on a 17-inch cathode ray tube monitor (640 × 480 @ 125 Hz) connected to a Windows XP PC workstation, and auditory stimuli were played through desktop speakers. The protocol was programmed and presented using the Experiment Builder software bundled with the Eye-Link II head-mounted eye tracker (SR Research Ltd., Osgoode, Ontario). The eye tracking system sampled gaze position at 250 Hz. Three-dimensional finger trajectories were recorded at 250 Hz using 14 mm reflective markers attached to the fingertip, and a ten-camera (MX-T040) motion capture system (Vicon Motion Systems, Lake Forest, CA). Computer-generated TTL pulses and a recording of the auditory pacing tones synchronized the two data streams via analog inputs to the Vicon system.

In both experiments, we presented trials in a pseudorandomized order, repeating each condition once per block, and repeating blocks to derive within-subject performance measures. The two experimental protocols are summarized in Fig. 1 by an illustration of the time series of stimulus and response events.

Behavioral task—Experiment 1

Participants ($N = 10$) performed unimanual finger tapping in synchrony with horizontal saccades. In separate trials, unimanual finger tapping was executed with the left or right index finger in time with auditory metronomic pacing tones (50 ms duration, 1 kHz pitch sinus wave, 5 ms volume envelope at onset). Participants also made alternating leftward and rightward saccades to track periodic visual stimuli on the display screen, in time with every tap. This saccade target (5 mm diameter, red in color) jumped between two locations separated by 20° of visual angle (±10° with respect to subject's centered gaze). The timing of visual pacing was
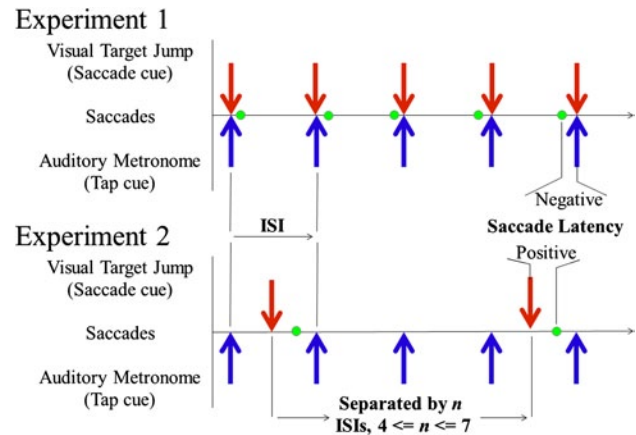

Fig. 1 Experimental protocol: typical series of stimulus and response events for Experiments 1 and 2. *Blue arrows* indicate the onset of auditory metronome cues. The separation between arrows represents the inter-stimulus interval (ISI), which was varied between 500, 750, and 1,000 ms. As shown in the figure, the tapping portion of Experiments 1 and 2 tasks was identical. The timing of visual target jumps is represented by the red arrows, each of which cues a saccade that is represented as a *green dot*. Although it is not discernible from the figure, successive saccades in both experiments are made in alternating directions between the two target locations. In Experiment 1, each visual target jump is synchronized with a metronome beep and tap. Over the first few intervals, participants synchronize their saccades to the metronome stimulus, resulting in reactive saccades that quickly transition to predictive saccades characterized by negative response latencies. In Experiment 2, the visual target jumps are at irregular times, and without a periodic timekeeping goal, the saccades are reactive. These reactive saccades are characterized by positive response latencies. Since the timing of visual target jumps in Experiment 2 was adjusted for the expected reaction time (~200 ms), saccades in both experiments occurred at approximately the same relative time in the tap-to-tap cycle

synchronized with auditory tones, and in separate trials, we varied the pacing rate between fast (500 ms), medium (750 ms), and slow (1,000 ms) inter-stimulus intervals (ISI). Each trial consisted of a series of 26 intervals. We also included a control condition wherein finger tapping was repeated with the auditory metronome while participants fixated gaze on a stationary target centered on the display screen. Tapping in this control condition was included to establish the lateral deviation of finger trajectories without accompanying saccades. In total, twelve trial conditions (3 × ISI, 2 × HAND, 2 × EYE-TASK) were presented twice over two blocks of trials. Since timed saccades are generally predictive of their temporal goal, we anticipated that most saccades would occur while the finger was off the table immediately prior to each tap.

Behavioral task—Experiment 2

Finger tapping and saccading were cued separately so their execution occurred at the same instant, but in response to

different events. In replication of the manual component of Experiment 1, we instructed participants ($N = 9$) to synchronize only finger tapping with the auditory pacing metronome. Unimanual finger tapping was again executed using either the left or right index finger, at 500, 750, and 1,000 ms ISIs. While the tapping task was repeated, the saccading cues were modified to produce reactive—not predictive, nor rhythmic—visual tracking. In Experiment 2, we cued reactive saccades with alternating visual targets that jumped at unpredictable and pseudorandomized times, once every 4th–7th tapping interval. The precise timing of these target jumps relative to the auditory tapping cues was structured so that saccades would likely occur between taps. In contrast to the negative latency of predictive saccades in Experiment 1, here we expected that saccade latency would be positive due to normal reaction time. The illustration in Fig. 1 contrasts the timing structure of auditory and visual stimuli, saccades, and taps between experiments.

Because of the unpredictable timing of these visual stimuli, reactive saccades do not require a discrete and predictable temporal goal specified in advance by motor planning networks. Unlike Experiment 1, in Experiment 2, there is no aspect of the task that encourages an overlapping representation of saccades and tapping movements by planning-related control networks.

Each trial was terminated when 10 saccades had been executed in each direction, which was a variable duration since saccades were spaced at pseudorandom intervals (i.e., coinciding with every 4th–7th tapping movement). This totaled in six task conditions ($3 \times$ ISI, $2 \times$ HAND) that were all repeated over six blocks of trials.

Data analysis

The gaze and finger trajectory data were imported into MATLAB® (Mathworks Inc., Natick, MA), temporally aligned, and analyzed using scripts developed in our laboratory. We smoothed the finger trajectory data with a 5-sample equally weighted moving average filter (bidirectional), with successive windows advanced by one sample. The coordinate system defined positive displacement in the rightward direction of the horizontal axis and upward on the vertical axis. Each tapping event was detected by examining the vertical component of the finger trajectory to determine the moment at which the fingertip speed fell below 15 mm/s after its peak downward acceleration. The times when the finger was in mid-flight were determined by finding peak upward acceleration, then looking recursively for the first preceding sample where the speed was below 15 mm/s.

We used a single measure to quantify spatial interference in the finger trajectory, which was the series of values describing the horizontal fingertip translation between successive taps. To compute this measure, we recorded the Euclidean coordinates where each tap contacted the table and took the difference between the landing positions of successive taps to determine the tap-to-tap fingertip translation. Examining motion in the horizontal axis was our variable of interest because it is parallel to the primary axis of the saccades. Consequently, we expected that any aspect of saccadic planning or execution that was encoded with directional specificity would cause the finger trajectory to deviate in the horizontal axis.

In Experiment 1, we analyzed the series of horizontal finger displacements using the unbiased estimate of lag-1 autocovariance between successive finger taps. Since alternating left–right saccades were executed in-phase with successive taps, this first analysis examined whether a similar left–right trend was expressed in the landing position of successive finger taps. Significantly, negative autocovariance values would indicate that the translation vector between two taps was generally directed opposite to the preceding tap. The magnitude of the autocovariance function is then proportional to the size of alternating back and forth displacements. As illustrated in Fig. 1, the saccading in Experiment 2 was not executed synchronously with each tap. For this reason, the lag-1 autocovariance measure would not objectively characterize tapping behavior in Experiment 2. While it would be possible to assemble a series of tap-to-tap displacement values extracted from the responses that did have an accompanying saccade, the following analyses better characterize the statistics of individual responses.

The autocovariance measure in Experiment 1 is our first analysis, and thus helps to determine the proper conditioning of the data for the subsequent steps of analyses for both experiments. To explain this logic, consider that our hypotheses predicted that the horizontal component of the finger trajectory would be biased in the direction of the accompanying saccade. It is later discussed in the results section of our manuscript that we confirmed lag-1 autocovariance returned a significantly negative value. This implies that when making saccades—but not when maintaining fixation—the finger is indeed entrained to a left–right alternating pattern that can be observed in the landing positions of successive taps. However, an implicit caveat is that the autocovariance function is unable to determine whether the back and forth trend in fingertip positions is positively correlated with the direction of the accompanying saccade. The autocovariance analysis lends support for a tap-to-tap alternating trend in the series of fingertip displacements between taps. In other words, determining whether this displacement is directionally congruent with saccades requires analyses of our data at the level of individual taps. The next analyses discussed below must account for the direction of finger displacement as it relates to the direction of the accompanying saccade.

To determine whether mean displacement was significant in the direction of the accompanying saccade, we derived the SACCADE DIRECTION factor by grouping the lateral fingertip deviation from taps associated only with saccades in one direction or the other. In both experiments, displacement values associated with each tap were pooled together for calculating the mean with respect to the factors of HAND (2 levels: left and right), PACING RATE (3 levels: 500, 750, and 1,000 ms), and SACCADE DIRECTION (2 levels: leftward and rightward). For comparisons of data acquired within each experiment, we used repeated measures analysis of variance (ANOVA) to identify significant main effects and interactions involving the relevant factors.

We must also consider that the autocovariance analysis in Experiment 1 indicated the fingertip moved in opposite directions between successive taps. To test the hypothesis that fingertip displacement depends on the direction of the accompanying saccade, we must invert the sign of the displacement values for only the taps corresponding to saccades in one direction. Since our motion capture system defined positive horizontal motion toward the participants' right, we inverted the sign of the displacement data collected when accompanying saccades were directed toward the left. Consequently, when positive displacement values are observed with either the *left* or *right* level of the SACCADE DIRECTION factor, the interpretation is that positive values represent fingertip displacement in the same horizontal direction as the accompanying saccade, and negative values suggest the finger moved opposite to the saccade's direction. ANOVA significance was set to a threshold of $p < 0.05$, and significant main effects were corrected for multiple comparisons using Bonferroni's criterion. We also performed additional post hoc one-sample t tests on the null hypothesis that any of the observed motion in the fingertip was significant in magnitude whatsoever. Here, one-sample t tests against a test value of 0 mm determined whether fingertip translation was different from the null hypothesis that no horizontal fingertip displacement occurred.

To analyze data related to our hypotheses, we must constrain our analysis to taps that are associated with specific instances of saccading behavior. While these constraints were applied identically to the repeated measures analysis of data from both experiments, the following criteria were irrelevant for the autocovariance analysis as it required an uncut series of finger tap responses. Firstly, the most important factor to control for is that overflow-related effects from saccades occurred within the time window when they could theoretically interfere with finger-related motor commands. For this reason, we only analyzed tapping movements where the accompanying saccade was initiated and terminated while the finger was in motion, that is, at no point was the finger in contact with the table during the saccade. These inclusion criteria were important because any oculomanual interference that might occur due to overflow naturally requires that there are in fact motor commands descending to the finger that may be affected by the saccadic command. To implement these criteria, we used gaze data to determine when a saccade occurred: onset threshold $>30°/s$ and $5,000°/s^2$, offset $<30°/s$.

It was also important that our analyses avoided oculomanual interference from eye movements unrelated to the primary saccading task. When saccades considerably overshoot a visual target, the oculomotor system performs *secondary corrective saccades* immediately following and in the direction opposite to the primary saccade. Naturally, as our methods intend only to model the interference effects related to the execution of reactive saccades, and planning and execution of voluntary timed saccades, any interference from secondary movements must be avoided. Accordingly, we included the fingertip displacement associated with a given tap when no secondary saccades occurred before the finger landed on the table. Lastly, displacement data were not included from taps when the accompanying saccade amplitude was more than $\pm 5°$ in error from the target. This last exclusionary criterion was instated because typical saccading behavior falls within this range, and larger errors may indicate the saccade was initiated toward some distracting stimuli.

We also analyzed our data for statistics that were descriptive of general ocular and manual behavior. Our analyses are all contingent on the accurate classification of saccades in Experiment 1 as predictive and timed, which is different than the expected reactive behavior in Experiment 2. Every saccade was analyzed for its temporal asynchrony with respect to the timing of the associated visual target jump. Asynchrony was measured in milliseconds and was negative when a saccade's onset preceded the target jump and positive when saccade onset followed the target jump. Moreover, we quantified subjects' general proficiency for tapping in all conditions and in both experiments by measuring the mean and variance of inter-response intervals (IRI).

Averaged trajectories of the fingertip paths plotted in Fig. 2 were computed by extracting fingertip position time series when the fingertip was not in contact with the table. Each in-flight trajectory was computed from each tap made by each subject, time-normalized by upsampling the number of points in each tap's trajectory to the length of the tap with the most data points. From these data, we computed a grand average 2D trajectory as well as the confidence interval by deriving the standard error of the mean—the sample standard deviation divided by the root of the number of samples. Since the mean and confidence were computed from the pooled data from within and between subjects, the error range is representative of cumulative variability in the expression of the interference effect at both levels.
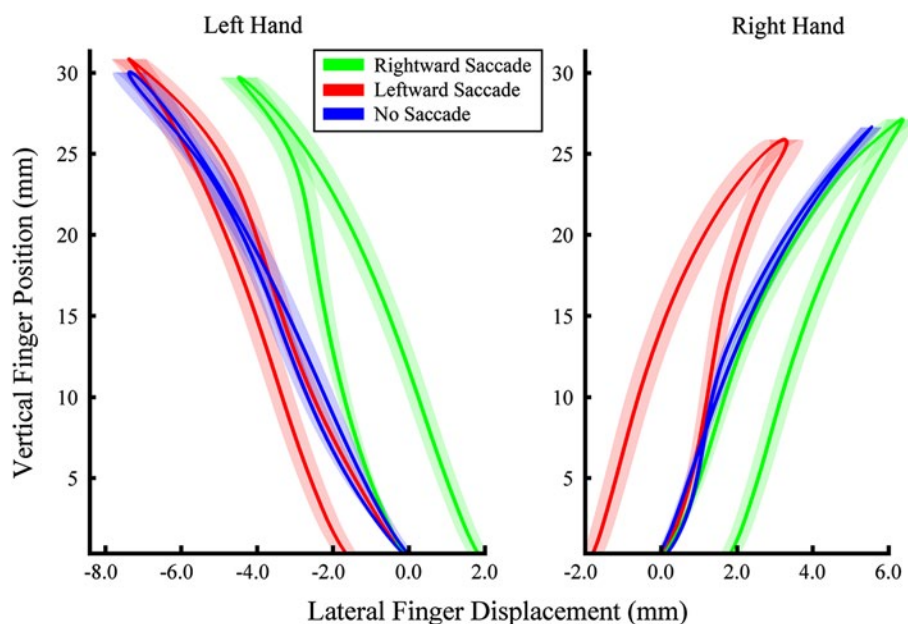
Fig. 2 Finger trajectories from Experiment 1: averaged finger trajectories from 500 ms ISI trials in Experiment 1 when subjects saccaded rightward (*green*), leftward (*red*), or maintained fixation (*blue*). *Left hand* responses are plotted in the *left panel*, and *right hand* responses in the *right panel*. The fingertip paths were derived from the time-normalized trajectory of all taps grouped over all participants (see "Materials and methods"). Importantly, the shaded area represents the standard error in the horizontal dimension computed across individual taps for all subjects. The start positions were normalized to lift from the origin (0 mm) on the *horizontal axis* to enable comparison across subjects. Negative values correspond to leftward fingertip displacement. From this illustration, it is evident that in control tapping (*blue*) when no saccade is made, the finger returns to the *horizontal axis* (lands on the table) in nearly the same place from where it was lifted. Saccading while tapping (*red* and *green*) caused the finger to land at some horizontal distance away from where it began the upward phase, in the direction of the concomitant saccade

Results

Saccading—temporal analysis

Our two experiments differed in the type of saccading behavior associated with each tracking paradigm, and so we must first examine whether subjects performed saccades as we anticipated. In Experiment 1, visual stimuli alternated periodically requiring that short-interval timekeeping was engaged to reproduce predictive saccades at accurate times. We computed the mean latency of saccades relative to the synchronized audiovisual stimuli in Experiment 1 ($M = -80.87$ ms, SD $= 74.23$). From this negative latency, or any latency values <80 ms—,that is, the shortest time required to evoke a saccade in response to an external visual cue (Wenban-Smith and Findlay 1991)—one can infer that the saccades must have been encoded by predictive motor plans.

In Experiment 2, saccade timing was unpredictable and each saccade temporally followed the presentation of the visual cues. We expected that saccading behavior would be reactive and initiated after the visual target jumped. The saccade latency data ($M = 211.02$ ms, SD $= 39.82$) confirmed that saccades were reactive in Experiment 2.

Finger tapping—temporal analysis

Our protocol was constructed so that the only change between Experiment 1 and 2 was the method we used to cue saccades. To confirm that only the saccading task changed, we must demonstrate that subjects performed the tapping component of the tasks similarly in both experiments. To quantify tapping accuracy, we measured the mean inter-response interval (IRI) and mean within-trial IRI variance (varIRI). From these data, we performed repeated measures ANOVA with factors HAND × PACING RATE. Only the main effect of PACING RATE reached significance for Experiment 1 ($F(2,18) = 16,154.99$, $p < 0.001$) and Experiment 2 ($F(2,16) = 196,704.12$, $p < 0.001$). We also found a significant main effect for PACING RATE in varIRI for Experiment 1 ($F(2,18) = 14.08$, $p < 0.001$) and Experiment 2 ($F(2,16) = 13.31$, $p < 0.001$).

We then used independent samples t tests to determine whether the tapping behavior was similar between experiments, at each level of the PACING RATE factor. At 500 ms pacing, IRI ($M_{Exp1} = 500.67$ ms, SD $= 8.22$; $M_{Exp2} = 504.72$ ms, SD $= 1.41$) was not significantly different between experiments. We did observe a significant between-experiment difference in IRI at 750 ms pacing

$(t(17) = -6.11, p < 0.001; M_{Exp1} = 746.65$ ms, SD = 3.75; $M_{Exp2} = 755.31$ ms, SD = 2.09), and also at 1,000 ms pacing $(t(17) = -2.69, p = 0.016; M_{Exp1} = 998.10$ ms, SD = 9.18; $M_{Exp2} = 1,006.53$ ms, SD = 2.08). There were no significant differences in varIRI between experiments. While these statistics show that subjects produced tapping intervals with a slightly longer duration in Experiment 2, the difference is very small (~8 ms or 1 % of the interval duration) and unlikely to indicate that any pertinent differences in the tapping strategy between experiments to confound our primary investigation of spatial interference.

Inclusion/exclusion of individual finger taps

We recorded the number of finger taps from each trial used in deriving the mean displacement values for each subject and in each condition. In Experiment 1, on average, 27.98 taps (SD = 9.00) were used to compute within-condition mean displacement of the fingertip position from multiple trials. Based on the total number of cues presented (26 per trial multiplied by two trial blocks, 52 total), this means that approximately 53.8 % of taps were paired with saccades that were acceptable for inclusion in our analyses. In Experiment 2, on average, 46.11 taps (SD = 11.13) were used to calculate the mean displacement values in Experiment 2 analyses, which is approximately equivalent to 88.7 % of recorded taps.

The difference in these numbers between experiments can be explained by the methods of cueing saccades. The high percentage of taps included for Experiment 2 analysis is likely because we optimized the presentation schedule of the visual stimuli. Reactive saccade cues were structured so that saccades would likely occur when the finger was in mid-flight, and we accounted for typical reaction time in our calculations. In Experiment 1, we cannot explicitly optimize the timing of saccades, as they are instead initiated as a function of each participant's ability to make accurately timed eye movements. Moreover, there is cycle-to-cycle variability in any motor timekeeping task. Because we cannot otherwise control the task to account for this normal range of responses, it is a natural consequence that fewer responses occur in the specific time window that is pertinent in which to examine spatial interference according to our current protocol.

Experiment 1: Periodic saccading and tapping

When saccades and taps were planned and executed together in the synchronous timing task, the finger's path was attracted in the direction of the accompanying saccade. To help visualize this interference effect, Fig. 2 illustrates the data for a HAND × SACCADE DIRECTION interaction using averaged finger trajectories from the 500 ms pacing

condition, wherein we observed the most robust interference. The following statistics demonstrate the strength of spatial interference was equivocal when saccading in either direction, when tapping with the left or right hand, and that interference was strongest for faster pacing intervals.

An ANOVA of lag-1 autocovariance in series of fingertip translations revealed the finger was entrained to an alternating tap-left then tap-right trend. This pattern was significantly stronger $(F(1,9) = 10.83, p = 0.009)$ when saccading $(M = -5.67$ mm^2, SD = 4.56) than in control tapping $(M = -1.07$ mm^2, SD = 0.69). This was our first line of evidence that periodic saccades interfered with finger trajectory formation.

Next, repeated measures ANOVA determined whether horizontal deviations between taps were affected by the HAND, SACCADE DIRECTION, and PACING RATE factors. In all conditions, the fingertip displacement is reported in the context that positive values signify displacement in the direction of the accompanying saccade. A significant main effect of PACING RATE $(F(2,18) = 6.63, p = 0.007)$ demonstrated that spatial interference scaled such that saccading caused the largest interference effects at faster pacing intervals. This effect is illustrated in Fig. 3 and presented with additional statistics in Table 1. The data showed no significant main effects or interactions involving the SACCADE DIRECTION or HAND, confirming the strength of spatial interference was similar when saccading in either direction and when tapping with either the left or right hand.
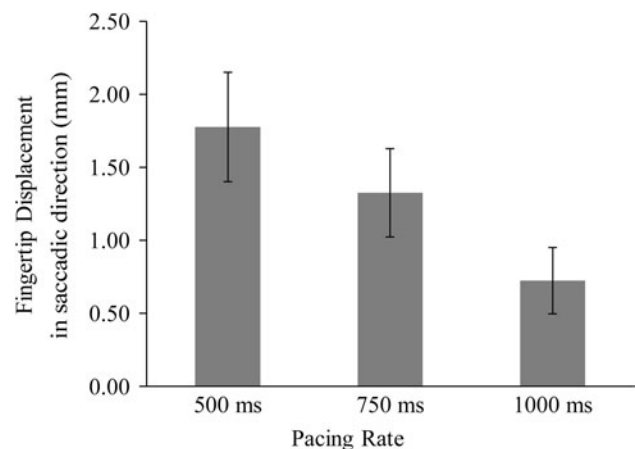
Fig. 3 Effect of pacing rate on horizontal fingertip displacements. The effect of PACING RATE is shown with error bars representing the standard error of the mean. At the faster 500 ms pacing rate (interstimulus intervals or ISI), the fingertip is more strongly attracted in the direction of the accompanying saccade, as compared with the slower 750 and 1,000 ms ISI. In addition to the data plotted in this figure, see Table 1 for the results of one-sample t tests showing that fingertip displacement in the direction of the concurrent saccade was significantly different from zero at all levels of the PACING RATE factor

Table 1 Descriptive statistics and t test scores from fingertip displacement

Experiment	Responding hand	Saccade direction	ISI	M	SD	p value	One-sample t score versus 0	d.o.f.
1	Both[a]	Both[a]	500	1.46	0.72	<0.001	6.440	9
			750	1.28	1.42	0.019	2.858	9
			1,000	1.09	1.13	0.014	3.037	9
2	Left	Left	All[a]	0.40	0.37	0.012	3.259	8
		Right		0.08	0.53	0.665	0.483	8
	Right	Left		0.08	0.25	0.337	1.022	8
		Right		0.50	0.25	<0.001	6.053	8

[a] Marginal means calculated after collapsing across the associated factor

While the interaction between the SACCADE DIRECTION × HAND factors did not reach significance, below we determine that the analogous interaction is of interest in characterizing behavior in Experiment 2. Consequently, Fig. 4a plots this interaction for Experiment 1, with which an intuitive visual contrast can be made to the analogous interaction in Experiment 2 results, Fig. 4b.

Our analyses have compared fingertip displacement between different experimental conditions, but we have not yet established whether we observed significant magnitude of displacement—indicative of *significant* spatial interference in the fingertip—in any direction. We must test the null hypothesis that no significant displacement occurred

Fig. 4 SACCADE DIRECTION × HAND interaction plot, Experiments 1 (**panel a**) & 2 (**panel b**). This interaction reached significance for Experiment 2 but not for Experiment 1. An illustration is useful to clarify the importance of the one-sample t tests (Table 1). As it is easy to see in this **panel b**, some instances of saccading in Experiment 2 failed to cause fingertip deviation that was significantly different from zero (Table 1, *bottom*). This an important contrast to make against Experiment 1, where the fingertip was always significantly attracted in the direction of the accompanying saccade (**panel a**, see also Fig. 3 and Table 1)

whatsoever, which is a separate task than using ANOVA to demonstrate how interference changed as a function comparing data within our nested model. As is standard practice with factors that do not meet statistical significance, we collapsed across the HAND and SACCADE DIRECTION factors and computed within-subject means. One-sample t tests against a test value of zero displacement indicated that at all remaining levels of PACING RATE, significant horizontal displacement of the finger did in fact occur, rejecting the null hypothesis that no significant displacement was observed (see Table 1). Familywise corrections for three comparisons maintain these results are significant at an experiment-wide error rate of $p < 0.0559$. In summary, we observed a significant spatial interference effect where the fingertip was attracted in the direction of accompanying horizontal saccades. Further, we determined that eye-to-hand spatial interference was significant at all pacing rates, and that the interference was significantly stronger at faster pacing intervals.

Experiment 2: Periodic tapping and reactive saccades

In contrast to the above results, eye–hand interactions in this experiment were different and the finger exhibited weaker attractions to reactive saccades. Similar to the analyses used in Experiment 1, we tested for effects or interactions involving HAND, PACING RATE, and SACCADING DIRECTION factors in the mean displacement of the fingertip in the direction of the accompanying saccade. Overall, no significant effects or interactions involving these factors were observed at $\alpha = 0.05$. In Experiment 2, the test for an effect of PACING RATE did not reach significance ($F(2,16) = 1.442$, $p = 0.266$). Consequently, in the case of Experiment 2, there is no significant scaling of the extent of interference at different inter-stimulus intervals of tapping.

It is also important to discuss the significant interaction between SACCADE DIRECTION and HAND in Experiment 2 ($F(1,8) = 5.820$, $p < 0.05$). In a visual inspection of the decomposed two-by-two interaction plot (Fig. 4b), we noted that the interference in Experiment 2 data
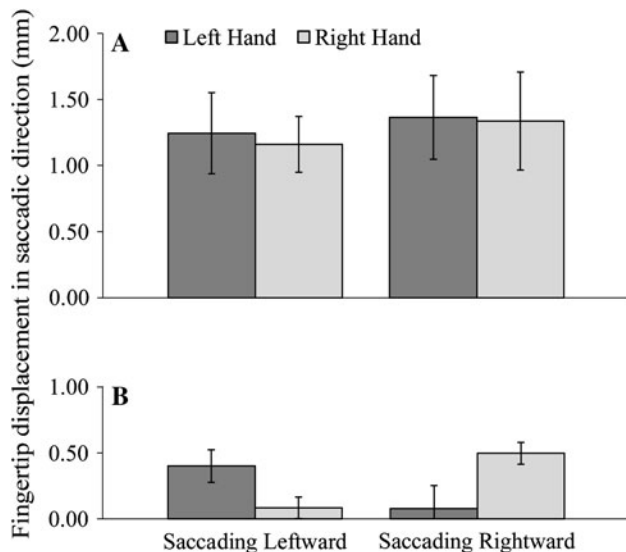
tended to be stronger when the responding hand was that in the hemispace in which the accompanying saccade was directed.

As discussed in the results section for Experiment 1, the ANOVA does not indicate whether the measured displacement was significantly different from zero, in any direction. Instead, one-sample t tests are used again in Experiment 2 to make this inference. Shown in Table 1, the only significant finger deviations observed in Experiment 2 occurred when saccading to the right caused the right finger to move rightward and saccading to the left caused the left finger to move leftward (see Table 1). These results remained significant after correcting for the familywise error rate across the four comparisons in Experiment 2 (i.e., corrected p's < 0.0125). The null hypothesis was not rejected and we cannot provide statistical support to significantly separate 0 mm of interference from the distribution of responses when saccading to the right and tapping with the left hand, or saccading to the left and tapping with the right hand.

Discussion

In the present study, we questioned whether a novel oculomanual paradigm could dissociate motor interference arising during motor planning and execution. The degree to which the brain recruited overlapping networks for controlling finger and eye movements was manipulated by the method of cueing saccades relative to a periodic finger tapping task. Our approach was motivated by evidence that timed, but not reactive saccades imposed demands on motor timekeeping networks (Joiner and Shelhamer 2006; Shelhamer and Joiner 2003). Moreover, timed saccades are voluntary and in comparison with reactive saccades involve different neural implementation (Mort et al. 2003; Müri and Nyffeler 2008).

Finger kinematics from both experiments demonstrated significant spatial interference. This was important for validating our task as a means to evoke unintentional eye-to-hand coupling. Since spatial interference in the finger trajectory was observed as lateral deviations toward the direction of a concurrent saccade, this coherence is perhaps best labeled as an eye-to-hand magnet effect due to its similarity to the interference observed in bimanual interactions (Franz et al. 1991; Franz and Ramachandran 1998). Another noteworthy characteristic of our timekeeping task is that visuomotor transformations were not required for tapping one's finger and thereby limited our focus to motoric interactions.

In order to attribute changes in eye–hand coupling dynamics to the modulation and effector-specific recruitment of motor planning, two points must be considered. First, varying the ISI of pacing cues in Experiment 1 led to a significant

effect in scaling the interference strength. By changing the time between successive responses, we are potentially manipulating the time available to plan each movement. If we may draw conservative parallels with the bimanual control literature, it is noteworthy that Heuer et al. (1998a, b), albeit in a discrete and goal-directed task, also demonstrated a period-dependent modulation of bimanual coupling. In both our experiment and those of Heuer et al., an increase in preparation time for simultaneous actions led to a reduction in interference. Determining whether the same neural mechanisms are responsible for these similar effects is beyond the scope of this study, but would be an interesting query for future investigations. Nonetheless, in our task, the temporal goal was the only variable constraining the coordination of eye and hand movements. Varying the timing of this temporal goal directly modulated the spatial interactions when joint motor planning was a possibility in Experiment 1. However, whether the modulation of interference manifests as a function of limiting the time to decouple two jointly planned actions is not certain. Determining this would require other experimental conditions to control for motor planning time with various types of voluntary saccades, perhaps using delayed movements in a memory-guided oculomotor task.

We can, however, infer that the scaling of spatial interference with changing ISI in Experiment 1 is related to motor planning in some way. Potential confounds are perhaps that ISI causes interference scaling by passive effects, such as biomechanical constraints that change with the speed of finger movements, or by modulating the control networks in ways unrelated to motor planning. For example, one may argue that changing the ISI leads to changing the movement speed. By extension, faster movements are perhaps less controlled (*c.f.* Elliott et al. 2001) and could be influenced more strongly by a similar source of interference. However, should this have been the case, it would also be expected that finger trajectory interference should be modulated by pacing rate in both experiments, which it was not. Moreover, we provided data that tapping was otherwise performed identically in both experiments. The tapping task was purposefully kept identical between the two experiments and the inter-response interval (IRI) data reasonably equated the timing accuracy of finger tapping at all levels of ISI in both experiments. Trajectory formation of finger movements in both experiments should thus be comparable as the kinematic profile is known to emerge as a function of the accuracy of the response with respect to the timekeeping goal (Balasubramaniam et al. 2004; Torre and Balasubramaniam 2009). This provides reasonable support for inferring that the scaling of interference with changing pacing rate is an effect related to the interaction of the timekeeping goal with motor planning-dependent interference processes.

The next step is to characterize the interference that emerged as a function of online motor overflow. In the first

experiment, saccades in either direction caused significant deviations in the finger trajectory when tapping with either hand. This contrasted results from the second experiment where saccades only attracted the finger of the responding hand located in the hemifield toward which saccades were directed. These results demonstrated that associative motor overflow accounted for an interference pattern that was weaker and lateralized.

The difference in coupling patterns is particularly interesting when one considers the neurophysiology of the related motor areas. Each hand is controlled primarily by the contralateral motor cortex and saccades by the oculomotor networks in the hemisphere contraversive to their horizontal direction. The lateralized interference effects we observed in Experiment 2 suggested that reactive saccades influenced only the motor coding of finger movements controlled by the same hemisphere. Conversely, in Experiment 1, the bilateral spatial interference was characterized by a widespread divergence of saccadic coding to manual motor networks in both hemispheres. This is an intriguing result considering the temporal goal that synchronized the execution of saccades and taps in Experiment 1 did not impose any spatial constraints, yet we observed different spatial interference patterns between experiments.

One possible explanation for the generalized planning interference is the observation that bimanual goals encoded in motor planning can induce widespread modulation of cortical motor interconnectivity, often in a generalized manner, and with distributed effects (Bestmann et al. 2008; Grefkes et al. 2008; Tallet et al. 2010). Our results might suggest that oculomanual planning is accomplished through a more generalized set of brain networks that are together less specifically associated with the control of the eyes *or* the limbs. In addition to demonstrating the generalization of motor planning-related interference to the trajectory of either hand, our results also suggest a broad spatiotemporal representation at a higher level of goal specification. A noteworthy finding in our experiments is that we observed spatial interference when the common goal for eye and hand movements was specified in the temporal domain. In this case of generalized recruitment, the brain areas related to planning the temporal goal also related to the parameterization of spatial variables in the same task. It is also possible that the brain areas related to planning spatial and temporal parameters are separate, but instead that their recruitment occurs in a generalized fashion regardless whether the coordinated variable is specified in the temporal or spatial domain.

Future investigations may seek to explain how planning modulates the state of oculomanual networks. For example, we cannot infer whether the bilateral form of coupling was due to co-parameterization of both actions in a single motor planning stream that later diverges, or instead whether planning-related networks exerted top–down modulation on the functional state of interhemispheric cross-effector networks. These are two distinct cases of a theoretical model of planning-related crosstalk. The former would mean coupled parameters were programmed *then* propagated via diverging cortical pathways to effector-specific networks (e.g., Akam and Kullmann 2010), while the latter would indicate the functional state of hardwired brain networks was modulated by top–down control. The latter of these has already been described in bimanual coordination as the transcallosal facilitation and transfer of inhibition models (c.f. Hoy et al. 2004). Extending these models to oculomanual coordination would be an interesting avenue for future research.

It would also be prudent to consider the influence of attentional shifts. According to the premotor theory of attention, motor actions, and covert attentional shifts are closely related (Rizzolatti et al. 1987); however, we suggest an explanation based only on attentional shifts is unlikely. We make this claim because ocular tracking tasks similar to those used in our study have shown that attention seems to be simultaneously co-allocated to multiple target areas as opposed to periodically alternating (Baldauf and Deubel 2008). This could be construed as evidence that our study implicitly dissociated the influence of attentional shifts from the effects of executing saccades.

One could also raise the possibility of somatosensory feedback processes contributing to the eye–hand interference patterns, as in the case of a well-known model of bimanual coordination (Mechsner et al. 2001). However, the metrics of movements in both experiments were similar, and one could extend this to inferring the feedback is also similar, thus if feedback plays a role it would be in the way it is used. Further, a potential caveat in our design is that inadvertent head movements might have contributed to the interference effect. While we did not measure head movements, in primate research, it is only common for saccades *greater than* 20° in visual angle to have associated head movements (Tomlinson and Bahra 1986). Saccades in our experiments were cued to exactly 20° in visual angle, and we again draw attention to the fact that these metrics were consistent between experiments. Consequently, any factors that might validly explain the interference must also demonstrate a similar change in their presentation between experiments to explain the observed modulation in the strength and specificity of the spatial interference.

In sum, the hands and eyes have very different physical structure, musculature, inertial properties, and neural correlates of sensorimotor control. By designing this novel oculomanual control paradigm, we have demonstrated that planning and execution are separate levels in the sensorimotor control hierarchy from where the independent sources of eye–hand interference can emerge. Our study has provided well-formed evidence that oculomanual control is mediated by distributed brain networks, and that the cause

of interference between eye and hand movements depends on the overlap in networks recruited for the task at hand—and at eye. The susceptibility of oculomanual actions to spatial interference in planning was apparent only when we introduced a cooperative temporal goal and varied its pacing rate. Additionally, associated movements of the finger arising from saccade-related motor overflow also led to significant spatial interference and were dissociated from the crosstalk in motor planning. We speculate that further investigations of this eye-to-hand magnet effect with neuroimaging at macroscopic and microscopic scales, or that introduce other novel variations of our current task could provide unique insights into the neural mechanisms that mediate the task-dependent flow of oculomanual coding throughout the human brain.

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