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Target selection in eye–hand coordination: Do we reach to where we look or do we look to where we reach?

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Abstract During a goal-directed movement of the hand to a visual target the controlling nervous system depends on information provided by the visual system. This suggests that a coupling between these two systems is crucial. In a choice condition with two or more equivalent objects present at the same time the question arises whether we (a) reach for the object we have selected to look at or (b) look to the object we have selected to grasp. Therefore, we examined the preference of human subjects selecting the left or the right target and its correlation to the action to be performed (eye-, arm- or coordinated eye–arm movement) as well as the horizontal position of the target. Two targets were presented at the same distance to the left and right of a fixation point and the stimulus onset asynchrony (SOA) was adjusted until both targets were selected equally often. This balanced SOA was then taken as a quantitative measure of selection preference. We compared these preferences at three horizontal positions for the different movement types (eye, arm, both). The preferences of the ‘arm’ and ‘coordinated eye–arm’ movement types were correlated more strongly than the preferences of the other movement types. Thus, we look to where we have already selected to grasp. These findings provide evidence that in a coordinated movement of eyes and arm the control of gaze is a means to an end, namely a tool to conduct the arm movement properly.

Keywords Psychophysics · Eye movements · Hand movements · Reference frames · Eye–hand coordination

Introduction

Eye–hand coordination is of great importance in everyday life. We spend much of our time reaching for and manipulating objects under visual guidance. Whether we grasp a pen or catch a ball, very sophisticated calculations have to be carried out by the nervous system. In the case of eye–hand coordination, the nervous system depends on information provided by the visual system. Therefore a close coupling of these systems during coordinated movements can be expected.

Among others (for instance Fisk and Goodale 1985; Soechting et al. 2001) Neggers and Bekkering (2000) provided supporting evidence from psychophysical studies for a ‘yoking’ of the two systems. During a goal-directed movement of the hand they presented a new saccade target and instructed the subject to look at it as soon as possible. Subjects made the second saccade not until offset of the hand movement. Thus, foveal information about the position of the first target is required until the end of the arm movement. However, when the subjects had been instructed to perform a coordinated movement of both eyes and arm to the new target, eye movements could be elicited during the ongoing arm movement (Goodale et al. 1986; Prablanc and Martin 1992; Lünenburger et al. 2000; Neggers and Bekkering 2002). Saccades accompanied by coordinated arm movements are faster (Snyder et al. 2002); ‘faster’ meaning that the main sequence (Bahill et al. 1975) of saccade dynamics is altered during coordinated eye–arm movement tasks. Interestingly, if the arm movement occurs simultaneously but in the opposite direction, no change in the timing of the saccade is observable. Thus, a common task for both systems is necessary for establishing a close coupling.

A site capable of mediating this sort of coupling may be the midbrain superior colliculus (SC): it contains an oculomotor map, and modulations of neurons related to arm movements have been observed (Werner 1993). For half of those ‘reach-neurons’, lying in the intermediate

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layers of the SC, discharge is coded in an oculocentric frame of reference. The other half, lying in the deeper visuomotor layers of the SC, discharge in relation to arm movements is irrespective of ocular gaze (Stuphorn et al. 2000). Activation of these 'reach-neurons' is probably mediated by motor-related cortical areas via projections from the premotor cortex (Fries 1984, 1985; Werner et al. 1997) and parietal cortex (Asanuma et al. 1985).

The sensorimotor transformation required for target selection and development of movement plans for both effectors (looking and reaching) occurs most probably in the posterior parietal cortex (PPC) which is located anatomically as well as functionally between visual and motor cortical areas. Supporting evidence is provided by the observation that patients with bilateral parietal lobe damage have difficulties in pointing to positions they are not allowed to look at (Carey et al. 1997). Instead, they point to the position they are already looking to. In human as well as in monkey PPC distinct regions were identified in which activity correlated with the planning of certain movement types, e.g. saccades, reach or grasp (Seal and Commenges 1985; Murata et al. 1996; Snyder et al. 1997). The response fields of neurons in parietal areas LIP (lateral intraparietal) and PRR (parietal reach region) are coded in eye-centred coordinates, independently from sensory input modality (vision, audition) and subsequent motor action, e.g. reach or saccade (Grunewald et al. 1999; Linden et al. 1999; Mazzoni et al. 1996; Stricanne et al. 1996; Batista et al. 1999; Cohen and Andersen 2000). The signal is gain-modulated by the position of eye, head or limb. Gain mechanisms play an important role for multisensory space representation as well as for decision making and attention and emanate from the properties of the coordinate transforming network. The above mentioned leads to the assumption that space is most likely represented differently in several (cortical) areas which build this network in the PPC and can be read corresponding to the movement plan and the actual requirements of the task (Pouget et al. 2002). A tight coupling of the visual and (manual) motor system is probably established at the SC, where the alteration of the main sequence is thought to occur after the plan to perform a coordinated movement has been developed and implemented in the PPC (Snyder et al. 2002).

Although the strong influence of an arm movement on saccades has been demonstrated, the influence of combined movements on target selection remains to be investigated. Gielen et al. (1984) showed that subjects always move eyes and arm in the same direction when confronted with two simultaneously appearing targets. We asked whether the eye movement in such a condition plays a leading or an assisting role, as posed earlier by Carey (2000). In other terms: Do we reach to where we look or do we look to where we reach? Are these two partners with equal priority acting together or is one system serving the other? If two equivalent stimuli are presented simultaneously, subjects have a spontaneous preference (bias) for one particular stimulus. This bias

depends on several parameters, e.g. the size of the stimuli, their eccentricity (Lévy-Schoen 1969, 1974; Findlay 1980) or the position in peripersonal space. The effector used for choosing one of the targets also influences the preference (Scherberger et al. 2003). This can be adapted to compare the preferences when making eye, arm or coordinated eye–arm movements, assuming that a certain preference is generated by a certain activated network: if preferences were alike for a couple of the movement types under study, predictions regarding relationships could be made. In case the preferences for combined movements resembled those for solitary arm movements, we would look to where we are about to reach. If it was the other way around, the saccadic system is likely to govern the manual system. If no relationship were to be observed, the systems would be independent. Thus, the comparison should reveal information about the fine adjustment of action planning in a coordinated goal-directed movement of eyes and arm. To provide a quantitative measure for preferences we employed the following psychophysical procedure: Two targets were presented at the same distance to the left and right of a fixation point and the stimulus onset asynchrony (SOA) was adjusted using the adaptive procedure PEST (parameter estimation using sequential testing, Taylor and Creelman 1967) until both targets were selected equally often. This balanced SOA is then taken as a quantitative measure of selection preference. We compared these preferences at three horizontal positions for the different movement types (eye, arm, both).

Materials and methods

Subjects

Twelve right-handed subjects, seven women and five men (ages 23–60 years), participated in this study. The data of one subject (female) had to be excluded due to unstable performance (<75% correct). Lateralization was assessed with a questionnaire according to Ehrenstein and Arnold-Schulz-Gahmen (1997). All participants had normal or corrected-to-normal vision and gave their informed consent prior to their inclusion in the study. Experiments have been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

The task was introduced to the subjects with the help of a written instruction in order to provide equal information for each participant.

Setup

Subjects were seated at a table in a dimly lit room resting their head on a chin-rest. A cylindrical board was positioned in front of the subject (distance = 42 cm) such that the axis of the hypothetical cylinder coincided

with the rotation axis of the head (Fig. 1a). Fourteen light-emitting diodes (LEDs, diameter 5 mm) and seven push-buttons [diameter 3 cm, i.e. 4° visual angle (va)] were mounted on the board (Fig. 1b). The push-buttons were horizontally aligned with an equal spacing of 10° va. Two LEDs (red and green) were countersunk above each button which were only visible when switched on.

Gaze position was sampled with an EyeLink-System (SMI, Sensomotoric Instruments, Teltow/Berlin, D) at 250 Hz for each eye. Signals were calibrated by having the subjects fixate targets at known eccentricities.

Control of the LEDs and monitoring of the push-buttons (temporal resolution = 1 ms) were accomplished through a custom-made device which was connected to a PC's parallel port. For the experimental protocol CORTEX (Cortex: A Program for Computerized Real Time Experiments, Laboratory of Neurophysiology, NIMH, Version 5) was used.

Experimental protocol

The task was colour coded: If a red LED was illuminated an eye-movement was required; the correct response to the illumination of a green LED was an arm-movement.

All trials began with the illumination of a fixation item (referred to as FP, fixation point). After a variable delay of 100–350 ms either one or two choice targets were illuminated. Between two consecutive trials there was a variable pause of 100–1,500 ms.

When an eye- or coordinated-movement was required, the FP disappeared with target onset, during isolated arm movements it remained illuminated for the purpose of fixation-maintenance.

In the eye-movement-only condition, both the FP and choice targets were red LEDs. The subject was required first to look at the FP and then to look at a choice target. Gaze position recording was used only to control fixation and determine which target was chosen.

For the solitary arm-movement condition the FP consisted of a red and a green LED while the choice targets for the arm were green LEDs. The task of the participant was first to look at the red LED and touch the push-button indicated by the green LED at the FP. Subjects were then required to choose a target with the arm. Fixation was held stable at the FP throughout the trial.

If coordinated eye- and arm-movements were required, both the FP and the choice targets consisted of a red and green LED. The subject made combined eye and arm movements to first the FP and then to a choice target.

Every block (eye-, arm-, coordinated-movement) was composed equally of single and double-target trials. The position of the fixation item varied between -20°, 0° and +20° va. In single stimulation trials (when only one choice target was visible) the FP and

the target could be spaced from 10° to 50° va. In the double-stimulation trials a second target was presented in the opposite direction of the first target at a distance of 10° from the FP.

The second choice target could be either switched on simultaneously with the first one or with a variable time delay with respect to the first. The time delay is called SOA and was altered with every decision of the participant using the adaptive staircase procedure 'parameter estimation using sequential testing' (PEST). The participant was instructed to choose the target that appeared first. Subsequently, the less preferred target was switched on earlier. The time delay between the onset of the two targets was then adjusted separately for each FP until the subject chose both targets equally often (Taylor and Creelman 1967, for a review see Gescheider 1997). This time delay was then called the balanced time delay (BTD). Initial time delay was 0 ms, the initial step size was 100 ms, thereafter the step size was adjusted according to the rules of the PEST procedure. Each block consisted of 192 trials: 32 double stimulation trials at three different FPs and 96 single stimulation trials. The measurements were repeated three times for each participant at similar times of the day.

Data analysis

The SOA was plotted against the trial number to get an impression of the performance of the subject (Fig. 1c).

The sought-after measure was the SOA for which the probabilities of left or right target choices are 0.5 (i.e. the BTD). The BTD was determined off-line by modelling the relationship between the preference of the observer and the stimulus intensity (i.e. SOA) (Fig. 1d). The psychometric function fit using the logistic distribution

$$P(\text{SOA}, \alpha, \beta) = \frac{1}{1 + \exp\left(\frac{z - \text{SOA}}{\beta}\right)}$$

where P is the probability of a rightward choice at a given SOA and assuming a binomial distribution (that is, the probability for a leftward choice is $1 - P$), provided the parameters α and β , where BTD is defined as α (Scherberger et al. 2003) and β is the slope of the function at $P(\text{SOA}) = 0.5$.

The BTD was determined for three FPs in each of the three conditions.

For the evaluation, raw data were used as well as normalized data to compare the data of different subjects among each other.

To compare the data of the three different conditions, the area lying between the six data points of each pair of conditions (arm-eye, arm-coordinated, eye-coordinated) was calculated separately (Fig. 2). This area should be small if the difference between the preferences of two conditions is small. Great differences in preferences should result in a larger area. The Wilcoxon

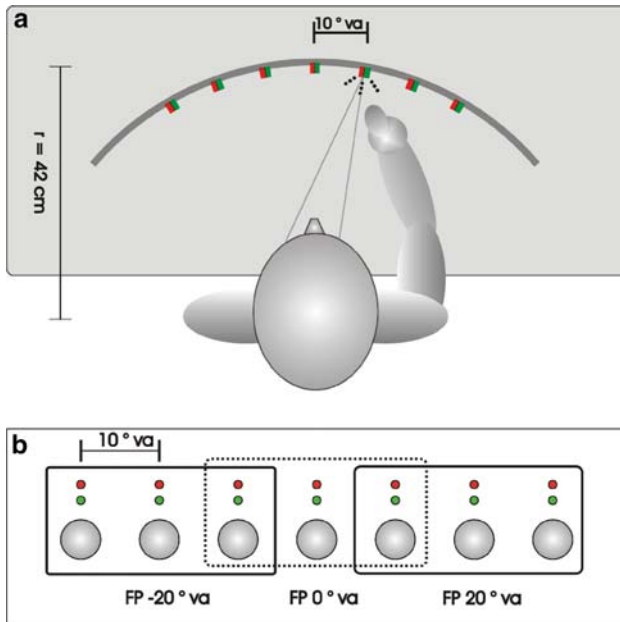


Fig. 1 Experimental setup and data analysis. **a** The subject is seated at a table in front of a cylindrical board, containing red/green LEDs and touchbars. The distance to the board was 42 cm and the space between the neighbouring LEDs/touchbars was 10° va. Gaze position on the board was measured by an infrared camera system (250 Hz). **b** Frontal view of the board. Two LEDs (red and green) were countersunk above each touchbar. The three fixation positions with the adjacent choice targets are indicated by the rectangles. *FP* fixation position, *va* visual angle. **c** Target selection with SOA: Algorithm, left (red dots) and right target selections (green dots) in a block of 32 trials. SOA (left target onset-right target onset, positive values indicate that the left target appeared first) is adapted using the adaptive procedure PEST and converges toward the BTD, for which left and right targets are selected equally often. **d** Logistic function fit. Circles probability of a leftward choice at a given SOA. Sigmoid curve maximum-likelihood estimate of the logistic distribution. Vertical line BTD, defined as the SOA for which the logistic distribution reaches half-maximum (50% rightward choices, horizontal line). BTD balanced time delay, SOA stimulus onset asynchrony (see Materials and methods)

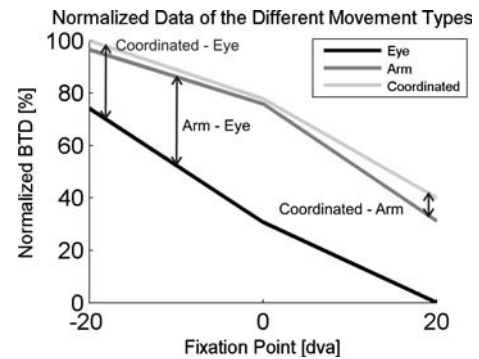
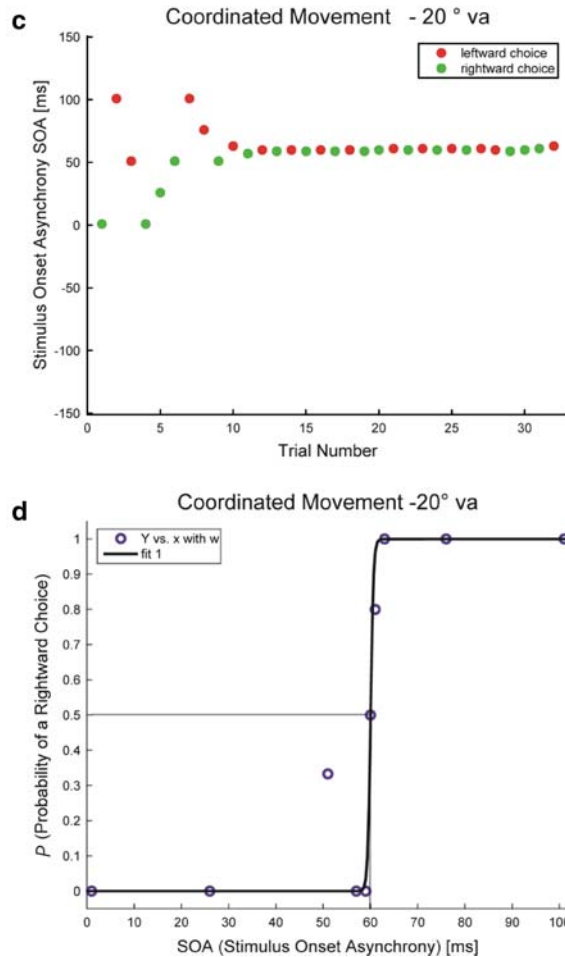


Fig. 2 Illustration of the enclosed area. **a** Normalized BTDs at the three fixation points for each task. Data of one session are given as an example. Thick dark line 'eye', gray line 'arm', light gray line 'coordinated'. The enclosed area between the respective normalized BTDs at the three fixation positions of the tasks 'eye', 'arm' and 'coordinated' is indicated by the arrows. Units of area are arbitrary due to normalization. BTD balanced time delay (see Materials and methods)

Results

The experiments had the aim to study the relationship between both subsets of a coordinated movement of eye and arm: control of gaze and control of the arm. Therefore the preference for one of two appearing targets was measured in terms of BTD, i.e. the time needed to compensate for a selection bias. Preferences were collected for movements of eyes, arm and both eye and arm. The horizontal fixation position was varied between -20° and 20° va with respect to the head.

Influence of fixation position

The determined preferences for the left or right target of all subjects under the three conditions (eye-, arm-, coordinated-movement) are presented in Fig. 3. A

matched-pairs signed-ranks test was used to test for significant influences of different parameters, level of significance was $\alpha = 0.05$.

positive value for BTD corresponds to preference of the right target when targets are presented simultaneously. The three columns show the data for the three different fixation positions (-20° , 0° , 20° va).

A main effect was found for fixation position as displayed in Fig. 4. Fixation on the left side primary led to selection of the target to the right of the fixation point (median BTD: 67.33 ms), fixation on the right to selection of the left target (median BTD: -2 ms). Fixation straight ahead led to a slightly higher preference for the right target (median BTD: 25.13 ms, see also table 1. This effect was found regardless of the movement type and was highly significant ($P < 7.4 \times 10^{-14}$, Wilcoxon matched-pairs signed-ranks).

Movement type

Table 1 contains the median values for each condition. The data of the three fixation points are pooled. The median BTD for target selection by means of eye movements was lowest with 13.72 ms (-0.93 ms, 43.40 ms), for arm movements 28.43 ms (-7.70 ms, 61.40 ms) and for the coordinated movement 28.90 ms (-3.31 ms, 60.85 ms), respectively. The slope of the logistic function used to determine the BTD did not vary systematically with the various conditions. Statistically, subjects did not have different ($P = 0.69$) preferences when selecting a target with the arm alone or with a coordinated movement of arm and eye. The preferences for target selection with an eye movement differed statistically from those for an arm movement ($P = 0.044$). The comparison of the preferences for ‘eye’ and

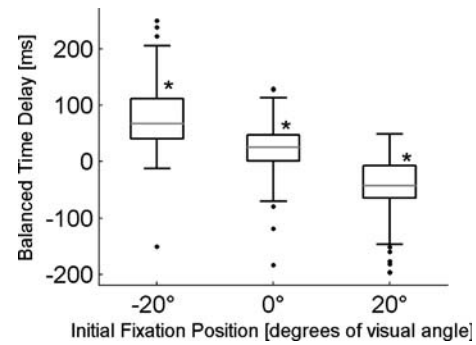


Fig. 4 Influence of fixation position on target selection. *Boxes* show data pooled for all three tasks according to fixation position. Median values with the respective lower and upper quartile are given. Whiskers extend to $\pm 1.5 \cdot IQR$ at most. *IQR* inter quartile range. The *asterisk* indicates a statistically significant difference to the other two data sets. A positive value for BTD indicates preference for the right target if targets were presented simultaneously

‘coordinated’ movements produced not quite a statistically significant difference ($P = 0.0737$), but this P -value is lower by a factor of ~ 10 compared to the P -value for preferences of arm and coordinated eye–arm movement ($P = 0.69$).

Interactions/relationships between movement types

The scatterplots in Fig. 5 compare the preferences for the three different movement types. Data from the different fixation positions are pooled again. The dotted line corresponds to $x = y$, the solid line marks the linear

Fig. 3 Determined BTDs of all subjects and sessions in the three tasks. Three successive data points are obtained in the three subsequent sessions with one subject. *Solid lines* mark the median values of each data set. *Upper row* BTD ‘eye’ movement task at -20° va, 0° va (straight ahead) and $+20^\circ$ va. *Middle row* BTD ‘arm’. *Lower row* BTD ‘coordinated’. *BTD* balanced time delay (see Materials and methods), *va* visual angle, *m* median value

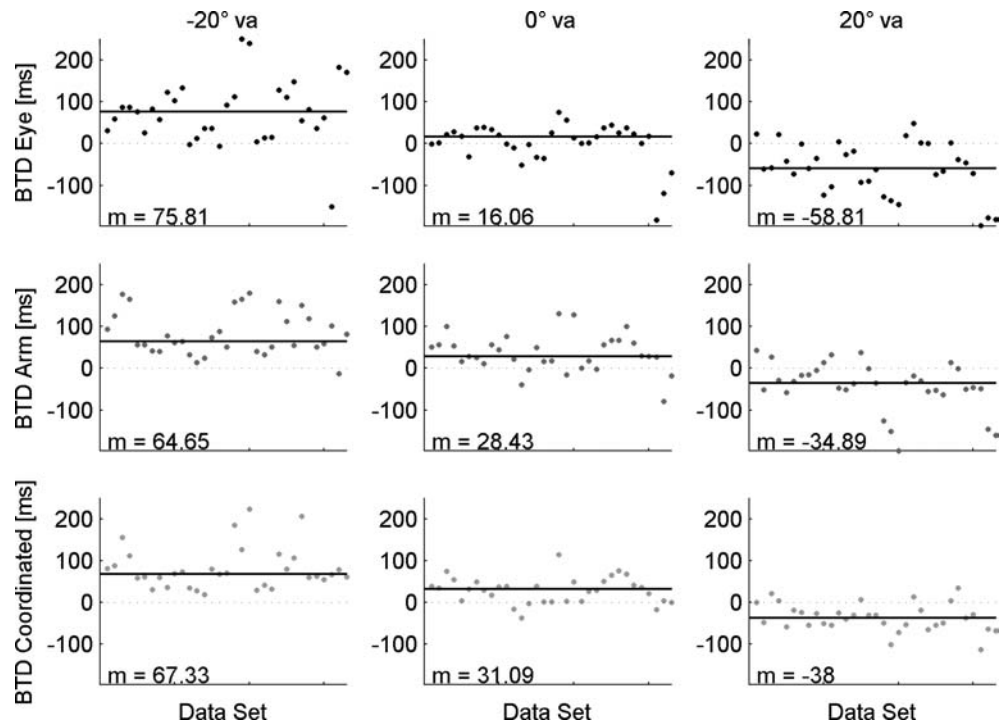
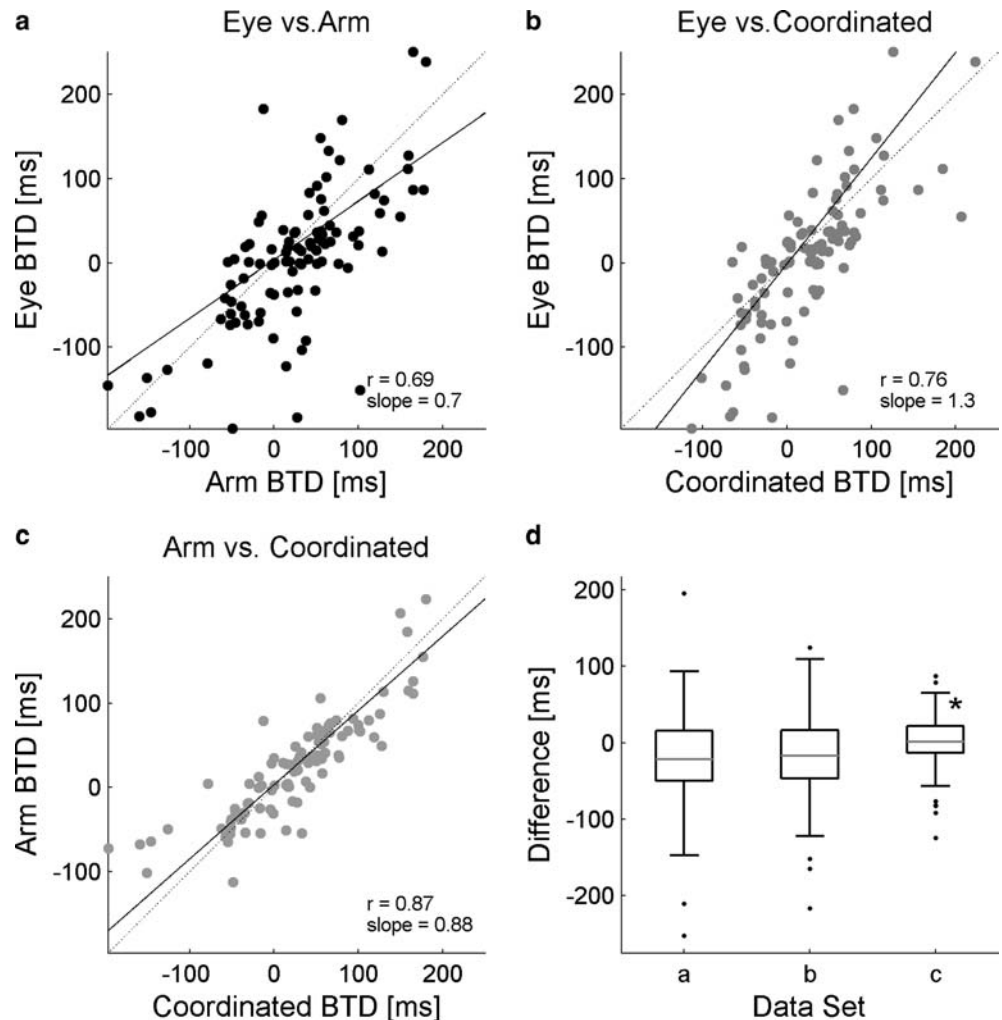


Table 1 Effect of fixation position and preference with respect to condition

	FP -20° va	FP 0° va	FP 20° va
BTD [ms]	67.33 (40.43, 111.63)	25.13 (0.73, 47.58)	-2 (-3.79, -.16)
BTD [ms]	13.72 (-0.93, 43.40)	28.43 (-7.70, 61.40)	28.90 (-3.31, 60.85)

Median BTD with respect to fixation position and movement condition; Values in parentheses are the upper and lower quartile; *BTD* balanced time delay (positive value corresponds to an overall preference for the right target); *va* visual angle

Fig. 5 Comparison of preferences. **a–c** The determined BTDs for the different tasks are plotted against each other. Data from different fixation positions are pooled. *Dotted line* line of unity slope, *solid line* line of best fit (see Materials and methods), *r* correlation coefficient, *slope* slope of linear regression. **d** Median difference with lower and upper quartiles. The *asterisk* indicates a statistically significant difference to the other data sets. *a, b, c* Respective pair of datasets



regression with minimized x and y offsets (line of best fit). Correlation coefficient and slope of the regression for the respective data set are annotated. The data set which compares the movement types 'arm' to 'coordinated' bears the highest correlation coefficient as well as the slope that is nearest to 1. The data of the two other sets are somehow more scattered with greater distances to the line of unity slope. The boxplot shows the median difference between the data sets. It is smallest (1.37 ms (-3.19 ms, 21.45 ms)) between the preferences of the movement types 'arm' and 'coordinated'. The differences between the other combinations are -21.61 ms (-0.14 ms, 15.99 ms) for 'eye' minus 'arm' and

-17.34 ms (-7.07 ms, 16.44 ms) for 'eye' minus 'coordinated'. This demonstrates clearly that similar preferences exist for arm and coordinated movements. These results are summarized in Table 2.

Enclosed area

The enclosed area between each pair of datasets (see Fig. 2) was calculated. Figure 6 presents the results. The area between 'arm' and 'coordinated' is smallest. The other two areas are greater and statistically similar ($P = 0.4886$). Both differ significantly ($P < 0.0001$) from

Table 2 Relationships between movement types

	Eye–arm	Eye–coordinated	Arm–coordinated
Slope (line of best fit)	0.7	1.3	0.88
Correlation coefficient	0.69	0.76	0.87
Ratio	0.57 (0.04, 1.35)	0.71 (0.28, 1.80)	1.09 (0.69, 1.47)
Difference (ms)	−1.61 (−0.14, 15.99)	−7.34 (−7.07, 16.44)	1.37 (−3.19, 21.45)
Enclosed area	753 (457, 1246)	718 (507, 1039)	363 (284, 647)

Characteristics of different comparisons are given. Values in parentheses are the upper and lower quartile

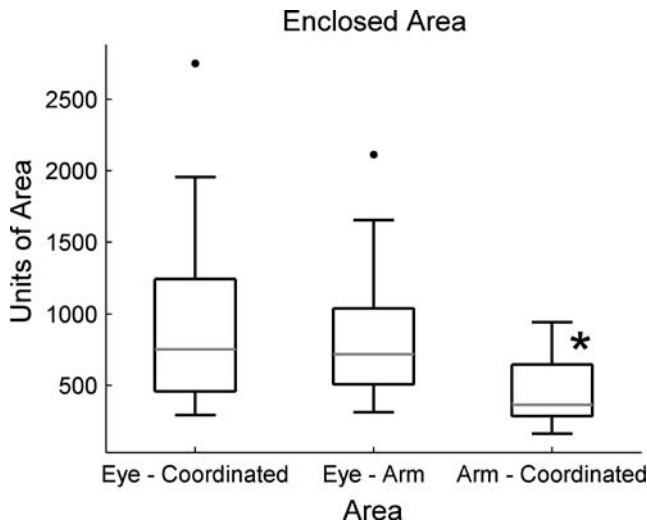


Fig. 6 Enclosed Area. Median dimensions of the area enclosed between the preferences of the different tasks (see Materials and methods). Median values with the respective lower and upper quartile are given. The *asterisk* indicates a statistically significant difference to the other data sets. Units of area are arbitrary

the former. This alternative view at the data confirms the similarity between left–right preferences in arm and combined eye–arm movements. The *P*-values of the parameters ‘difference’ and ‘area’ are given in Table 3.

Discussion

The presented experiments yielded two main results: preferences for one out of two possible targets were similar when subjects moved only the arm or made a coordinated movement of eyes and arm. This was true at

Table 3 Comparison of the difference of preferences and the enclosed area

	Eye–arm	Eye–coordinated	Arm–coordinated
Eye–arm		0.4886	0.00002
Eye–coordinated	0.8544		0.00007
Arm–coordinated	0.00086	0.00079	

For every pair of the data sets the difference between the raw data and the area enclosed between the normalized preferences are computed. Upper right: *P*-values of the difference of preferences. Lower left: *P*-values of the enclosed areas

three different fixation positions. Thus, in a coordinated eye–arm movement condition, we look to the target we selected to grasp.

Secondly, targets in central peripersonal space were chosen more frequently than peripheral targets, irrespective of the effector used for selection.

The first result implicates that the saccadic system is no longer autonomous during a coordinated, goal-directed movement of eye and arm. The visual information provided (with foveal resolution) is valuable to the manual system and therefore must not be lost or perturbed for the duration of the goal-directed movement. The work of Sarlegna et al. (2003) demonstrates the impact of visual target information on coordinated eye and arm movements. They provided their subjects with either erroneous information about the position of the hand or intrasaccadic target shifts in two series of experiments. Due to saccadic suppression, subjects could not perceive the shift of the target during the execution of the saccade. The correcting arm movement was clearly greater and was induced earlier (about 150 ms) when the target was shifted. Thus, the visual information is used primarily to localize the target and only secondarily to provide the actual position of the hand for error computation.

Two retinofugal pathways exist for the generation and control of saccades. One projects from the retina to the SC of the midbrain and is called the extrageniculate pathway. The other pathway projects from the retina via the lateral geniculate nucleus (LGN) to the occipital cortex and involves the PPC and the frontal eye field (FEF). It is commonly accepted that the extrageniculate pathway is involved in mediating reflexive eye movements (Frens and Erkelens 1991; Pashler et al. 1993; Wurtz and Goldberg 1971), whereas the geniculo-cortical pathway is active in situations when more response-preparation processes are needed, e.g. when a saccade shall be directed in response to a symbol or an antisaccade is required (Guitton et al. 1985). The occipital cortex and the SC are interconnected with area LIP in the PPC whose function relates to spatial attention and saccade planning (Snyder et al. 1998; Andersen et al. 1990; Asanuma et al. 1985; Fries 1984; Barbas and Mesulam 1981). New data suggest that the SC itself can also focus attention on a distinct position in space (Cavanaugh and Wurtz 2004, Muller et al. 2005) and lower psychophysical thresholds in that particular position. Hence the SC might be sufficient to ‘choose’ a

target when considered in isolation but is under physiological conditions governed by the aforementioned cortical areas. Together, these sites probably form a synergistic network. Neggers and Bekkering (2002) proposed a model for the implementation of coupling ocular gaze and arm movements which focuses on the saccadic and reach-related neurons of the SC. They assume that not only the saccadic neurons but also the reach-related neurons are aligned in a kind of topographic map so that movement fields do overlap. This model proposes that the intention to carry out an arm movement puts extra activity on the SC which results in a coupling of eye and arm movements. Thus, the SC might play a constructive role in the coupling of eye and arm movements to the same target. For preliminary target selection and establishing space related preferences other sites are likely to be involved, which are connected to the SC. Many studies emphasize the central role of the parietal cortex in space representation for visuo-motor actions (for instance Goodale and Haffenden 1998; Goodale and Milner 1992). The transformation of spatial information for limb movements is also located in the PPC (Snyder et al. 1997; Lacquaniti et al. 1995; Crammond and Kalaska 1989). The spatial proximity between these areas and area LIP could facilitate a concertation of eye and arm movement planning. Pouget and coworkers proposed a model—the ‘basis function framework’—which is able to explain coordinate transformations, provide different frames of reference, and predict the sensory consequences of a movement. This model consists of a multilayer network which can perform bidirectional coordinate transformations and uses basis function units. They claim that the common integrating layer for reaching towards stimuli *independently* of sensory modality works with a combination of eye/head-centred and head/body-centred frames of reference.

When all these considerations are taken into account, both of our main findings are coherent: (1) Our results provide further evidence that such a common spatial framework for eye–hand coordination does exist and is applied in visually guided reaching. (2) In this context the result that the central targets were preferred over the peripheral ones could originate from the common head-centred reference frame of the integrating layer of the model network.

For movements of the eye or the left/right arm a strong influence of the horizontal fixation position was observed already by Scherberger et al. (2003). They tested two macaque monkeys (*Macaca mulatta*) with a paradigm comparable to the one used in this study and found through variation of eye, head and trunk position that target selection preference was embedded in a head-centred frame of reference. Our results not only support this finding but indicate that the same frame of reference holds true for coordinated movements of eyes and hand. The slight preference for the right target at the central fixation position is most likely a result of the right-handedness of the subjects tested. Wardak et al. (2002)

found a similar preference (50 ms animal A, 25 ms animal B) for the right saccadic target in two macaque monkeys.

However, it should be mentioned that the preference we measured is not as stable as a sensory threshold: preferences are more variable between consecutive sessions of one subject. The variance may be influenced by certain activities of the subject before the test session or the overall configurational state of the system. This influence will most likely affect all of the measured conditions uniformly, so that the basic relations between them remain static.

Deciding which target to choose is an important task for the framework described above. Numerous studies suggest that the actual decision is a distributed process in which several areas participate (see for instance Horwitz and Newsome 1999; Platt and Glimcher 1998). Selection of targets for saccades seems to occur at multiple sites in the brain, for instance in the SC (Basso and Wurtz 1997; McPeck and Keller 2004) and in prefrontal and parietal cortices (Iba and Sawaguchi 2003; Wardak et al. 2002). If FEF or LIP are inactivated, saccade target selection is severely impaired (Schiller and Chou 1998; Wardak et al. 2002). The activity of neurons in SC and LIP is modulated if the number of possible movement targets is varied or the statistical probability of becoming a saccade target is altered (Basso and Wurtz 1997; Platt and Glimcher 1999). If a monkey has to decide in which direction a coherent motion signal of a random dot display moves, the activity in LIP correlates with his decision before a movement is generated. This correlation is existent even when the stimulus contains no directional information (Shadlen and Newsome 1996). Modulating the activity of decision-related areas in advance of a new stimulus presentation could be a means of incorporating prior probabilities. Similar mechanisms may be applied to establish preferences like those observed in our experiments.

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References

- Andersen RA, Bracewell RM, Barash S, Gnadt JW, Fogassi L (1990) Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J Neurosci* 10(4):1176–1196
- Asanuma C, Andersen RA, Cowan WM (1985) The thalamic relations of the caudal inferior parietal lobule and the lateral prefrontal cortex in monkeys: divergent cortical projections from cell clusters in the medial pulvinar nucleus. *J Comp Neurol* 241(3):357–381
- Barbas H, Mesulam MM (1981) Organization of afferent input to subdivisions of area 8 in the rhesus monkey. *J Comp Neurol* 200(3):407–431

- Basso MA, Wurtz RH (1997) Modulation of neuronal activity by target uncertainty. *Nature* 389(6646):66–69
- Batista AP, Buneo CA, Snyder LH, Andersen RA (1999) Reach plans in eye-centered coordinates. *Science* 285(5425):257–260
- Carey DP (2000) Eye-hand coordination: eye to hand or hand to eye? *Curr Biol* 10(11):R416–R419
- Carey DP, Coleman RJ, Della Sala S (1997) Magnetic misreaching. *Cortex* 33(4):639–652
- Cavanaugh J, Wurtz RH (2004) Subcortical modulation of attention counters change blindness. *J Neurosci* 24(50):11236–11243
- Cohen YE, Andersen RA (2000) Reaches to sounds encoded in an eye-centered reference frame. *Neuron* 27(3):647–652
- Crammond DJ, Kalaska JF (1989) Neuronal activity in primate parietal cortex area 5 varies with intended movement direction during an instructed-delay period. *Exp Brain Res* 76(2):458–462
- Findlay JM (1980) The visual stimulus for saccadic eye movements in human observers. *Perception* 9(1):7–21
- Fisk JD, Goodale MA (1985) The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Exp Brain Res* 60(1):159–178
- Frens MA, Erkelens CJ (1991) Coordination of hand movements and saccades: evidence for a common and a separate pathway. *Exp Brain Res* 85(3):682–690
- Fries W (1984) Cortical projections to the superior colliculus in the macaque monkey: a retrograde study using horseradish peroxidase. *J Comp Neurol* 230(1):55–76
- Fries W (1985) Inputs from motor and premotor cortex to the superior colliculus of the macaque monkey. *Behav Brain Res* 18(2):95–105
- Gescheider GA (1997) *Psychophysics: the fundamentals*, 3rd edn. Lawrence Erlbaum Associates, Mahwah
- Gielen CC, van den Heuvel PJ, van Gisbergen JA (1984) Coordination of fast eye and arm movements in a tracking task. *Exp Brain Res* 56(1):154–161
- Goodale MA, Haffenden A (1998) Frames of reference for perception and action in the human visual system. *Neurosci Biobehav Rev* 22(2):161–172
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15(1):20–25
- Goodale MA, Pelisson D, Prablanc C (1986) Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature* 320(6064):748–750
- Grunewald A, Linden JF, Andersen RA (1999) Responses to auditory stimuli in macaque lateral intraparietal area. I. Effects of training. *J Neurophysiol* 82(1):330–342
- Guitton D, Bachtel HA, Douglas RM (1985) Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. *Exp Brain Res* 58(3):455–472
- Horwitz GD, Newsome WT (1999) Separate signals for target selection and movement specification in the superior colliculus. *Science* 284(5417):1158–1161
- Iba M, Sawaguchi T (2003) Involvement of the dorsolateral prefrontal cortex of monkeys in visuospatial target selection. *J Neurophysiol* 89:587–599
- Lacquaniti F, Guigon E, Bianchi L, Ferraina S, Caminiti R (1995) Representing spatial information for limb movement: role of area 5 in the monkey. *Cereb Cortex* 5(5):391–409
- Lévy-Schoen A (1969) Détermination et latence de la réponse oculomotrice à deux stimulus simultanés ou successifs selon leur excentricité relative. *Année Psychol* 69:373–392
- Lévy-Schoen A (1974) Le champ d'activité du regard: données expérimentales. *Année Psychol* 74:43–66
- Linden JF, Grunewald A, Andersen RA (1999) Responses to auditory stimuli in macaque lateral intraparietal area. II. Behavioral modulation. *J Neurophysiol* 82(1):343–358
- Lunenburger L, Kutz DF, Hoffmann KP (2000) Influence of arm movements on saccades in humans. *Eur J Neurosci* 12(11):4107–4116
- Mazzoni P, Bracewell RM, Barash S, Andersen RA (1996) Spatially tuned auditory responses in area LIP of macaques performing delayed memory saccades to acoustic targets. *J Neurophysiol* 75(3):1233–1241
- McPeck RM, Keller EL (2004) Deficits in saccade target selection after inactivation of superior colliculus. *Nat Neurosci* 7(7):757–763
- Muller JR, Philiastides MG, Newsome WT (2005) Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proc Natl Acad Sci USA* 102(3):524–529
- Murata A, Gallese V, Kaseda M, Sakata H (1996) Parietal neurons related to memory-guided hand manipulation. *J Neurophysiol* 75(5):2180–2186
- Neggers SF, Bekkering H (2000) Ocular gaze is anchored to the target of an ongoing pointing movement. *J Neurophysiol* 83(2):639–651
- Neggers SF, Bekkering H (2002) Coordinated control of eye and hand movements in dynamic reaching. *Hum Mov Sci* 21(3):349–376
- Pashler H, Carrier M, Hoffman J (1993) Saccadic eye movements and dual-task interference. *Q J Exp Psychol A* 46(1):51–82
- Platt ML, Glimcher PW (1998) Response fields of intraparietal neurons quantified with multiple saccadic targets. *Exp Brain Res* 121(1):65–75
- Platt ML, Glimcher PW (1999) Neural correlates of decision variables in parietal cortex. *Nature* 400(6741):233–238
- Pouget A, Deneve S, Duhamel JR (2002) A computational perspective on the neural basis of multisensory spatial representations. *Nat Rev Neurosci* 3(9):741–747
- Prablanc C, Martin O (1992) Automatic control during hand reaching at undetected two-dimensional target displacements. *J Neurophysiol* 67(2):455–469
- Sarlegna F, Blouin J, Bresciani JP, Bourdin C, Vercher JL, Gauthier GM (2003) Target and hand position information in the online control of goal-directed arm movements. *Exp Brain Res* 151(4):524–535
- Scherberger H, Goodale MA, Andersen RA (2003) Target selection for reaching and saccades share a similar behavioral reference frame in the macaque. *J Neurophysiol* 89(3):1456–1466
- Schiller PH, Chou IH (1998) The effects of frontal eye field and dorsomedial frontal cortex lesions on visually guided eye movements. *Nat Neurosci* 1(3):248–253
- Seal J, Commenges D (1985) A quantitative analysis of stimulus- and movement-related responses in the posterior parietal cortex of the monkey. *Exp Brain Res* 58(1):144–153
- Shadlen MN, Newsome WT (1996) Motion perception: seeing and deciding. *Proc Natl Acad Sci USA* 93(2):628–633
- Snyder LH, Batista AP, Andersen RA (1997) Coding of intention in the posterior parietal cortex. *Nature* 386(6621):167–170
- Snyder LH, Batista AP, Andersen RA (1998) Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. *J Neurophysiol* 79:2814–2819
- Snyder LH, Calton JL, Dickinson AR, Lawrence BM (2002) Eye-hand coordination: saccades are faster when accompanied by a coordinated arm movement. *J Neurophysiol* 87(5):2279–2286
- Soechting JF, Engel KC, Flanders M (2001) The Duncker illusion and eye-hand coordination. *J Neurophysiol* 85(2):843–854
- Stricanne B, Andersen RA, Mazzoni P (1996) Eye-centered, head-centered, and intermediate coding of remembered sound locations in area LIP. *J Neurophysiol* 76(3):2071–2076
- Stuphorn V, Bauswein E, Hoffmann KP (2000) Neurons in the primate superior colliculus coding for arm movements in gaze-related coordinates. *J Neurophysiol* 83(3):1283–1299
- Wardak C, Olivier E, Duhamel JR (2002) Saccadic target selection deficits after lateral intraparietal area inactivation in monkeys. *J Neurosci* 22(22):9877–9884
- Werner W (1993) Neurons in the primate superior colliculus are active before and during arm movements to visual targets. *Eur J Neurosci* 5(4):335–340
- Werner W, Dannenberg S, Hoffmann KP (1997) Arm-movement-related neurons in the primate superior colliculus and underlying reticular formation: comparison of neuronal activity with EMGs of muscles of the shoulder, arm and trunk during reaching. *Exp Brain Res* 115(2):191–205
- Wurtz RH, Goldberg ME (1971) Superior colliculus cell responses related to eye movements in awake monkeys. *Science* 171(966):82–84