Neural and Temporal Dynamics Underlying Visual Selection for Action

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1Donders Institute for Brain, Cognition and Behaviour and 2Behavioural Science Institute, Radboud University Nijmegen, Nijmegen; and 3Division of Neuroscience, Rudolf Magnus Institute of Neuroscience, University Medical Center Utrecht, Utrecht, The Netherlands

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van Elk M, van Schie HT, Neggers SFW, Bekkering H. Neural and temporal dynamics underlying visual selection for action. J Neurophysiol 104: 972–983, 2010. First published June 10, 2010; doi:10.1152/jn.01079.2009. The present study investigated the selection for action hypothesis, according to which a subject’s action intention to perform a movement influences the way in which visual information is being processed. Subjects were instructed in separate blocks either to grasp or to point to a three-dimensional target-object and event-related potentials were recorded relative to stimulus onset. It was found that grasping compared with pointing resulted in a stronger N1 component and a subsequent selection negativity, which were localized to the lateral occipital complex. These effects suggest that the intention to grasp influences the processing of action-relevant features in ventral stream areas already at an early stage (e.g., enhanced processing of object orientation for grasping). These findings provide new insight in the neural and temporal dynamics underlying perception–action coupling and provide neural evidence for a selection for action principle in early human visual processing.

INTRODUCTION

When we go about our daily business we are confronted with an enormous amount of information that continuously enters our senses. To deal with this stream of information, typically we selectively attend to information that is relevant to our current behavioral goals. For example, normally you perceive the bookshelves next to your desk as a colored array of visual information. Only when you intend to grasp a specific book, do you selectively search for the book with the right color and subsequently process the size and the orientation of the book to grasp it. An intriguing question is how and when our action intentions influence the way in which visual information is selected.

Studies in the domain of motor control have begun to uncover the neural mechanisms underlying reaching and grasping (e.g., Culham and Valyear 2006). The posterior parietal cortex plays an important role in reaching toward visual targets. Lesions in this area have been reported in patients with optic ataxia who display severe misreaching to visual targets (Karnath and Perenin 2005). Furthermore, visuomotor coordination required for grasping is probably mediated by the anterior intraparietal sulcus (e.g., Binkofski et al. 1998; Culham et al. 2003). Patients with lesions in the anterior part of the intraparietal sulcus have difficulty with preshaping the hand for grasping objects, whereas reaching to objects is relatively spared (Binkofski et al. 1998). Although these studies indicate that the parietal cortex plays an important role in the sensorimotor transformations required for reaching and grasping, relatively little is known about the influence of action intentions on the selection of information in the visual system. According to the hypothesis of “selection for action” put forth by Allport (1987) action-related attentional mechanisms determine the early selection and processing of action-relevant information. At a behavioral level visual search studies have reported early effects of action intentions on the selection of action-relevant information (Bekkering and Neggers 2002; Craighero et al. 1996, 1999; Hannus et al. 2005). For instance, Bekkering and Neggers (2002) instructed subjects to prepare a grasping or a pointing movement toward a target object, defined by a specific orientation and color. Fewer first saccadic eye movements were made to objects with a wrong orientation when subjects prepared to grasp the object compared with when they prepared to point toward the object, although the same number of color errors were made for both types of actions. These studies suggest that the intention to grasp facilitates the processing of action-relevant visual features, thereby providing behavioral support for selection for action (Allport 1987, 1989).

The selection for action hypothesis is closely related to the premotor theory of attention, which proposes a strong coupling between action and perception (Sheliga et al. 1994). More precisely, according to the premotor theory, movement preparation and attentional processing recruit common neural mechanisms whereby motor preparation results in shifts in spatial attention. Empirical evidence for the suggestion that response preparation results in shifts in spatial attention has been obtained by behavioral studies indicating superior recognition of visual stimuli at intended saccade target locations (Deubel and Schneider 1996). In addition, neuroimaging studies have reported comparable activation in frontoparietal brain areas during saccade preparation and covert shifts of spatial attention (Beauchamp et al. 2001; Corbetta et al. 1998). Importantly, evidence from single-cell recordings in monkeys and transcranial magnetic stimulation (TMS) in humans suggests that for eye movements, (pre)motor areas influence spatial processing in early occipital areas during saccade preparation through feedback projections (Gutteling et al. 2009; Moore and Armstrong 2003; Neggers et al. 2007; Ruff et al. 2006), which could explain the coupling between motor preparation and early visual processing enhancements. For example, TMS pulses applied to the contralateral frontal eye field (FEF) affected the recognition of target stimuli that appeared at the intended saccade locations, thereby providing functional evidence for the role of FEF in feedback connections to visual areas (Neggers et al. 2007).

In addition, it has been shown that manual response preparation is accompanied by attentional shifts as well, resulting in enhanced recognition of targets at intended reaching and grasp-
ing locations (Deubel et al. 1998; Schiegg et al. 2003). Preparing a finger-lifting response, for instance, was found to facilitate the processing of tactile stimuli presented at the effector of the prepared movement (Juravle and Deubel 2009). Furthermore, early visual brain responses as reflected in the N1 component were found enhanced when visual probes presented during response preparation appeared at the intended movement location (Baldauf and Deubel 2009; Eimer et al. 2006; Gherri et al. 2009). These findings are in line with studies on visual attention that have reported enhanced N1 amplitudes to stimuli appearing at covertly attended locations (Gomez Gonzalez et al. 1994; Hillyard and Anllo-Vento 1998; Martinez et al. 1999). Most likely, these attentional effects arise due to corticocortical feedback from manual (pre)motor areas to posterior visual areas, similar to the frontooccipital feedback mechanisms described for eye movements (Moore and Armstrong 2003). This idea is supported by electrophysiological and neuroimaging studies revealing a frontoparietal network that is activated during response preparation and the directing of attention in space (Praamstra et al. 2005).

Most studies that have investigated attentional effects of motor preparation focused on shifts of spatial attention toward the target location of an upcoming movement. However, in addition to directing our reach to the correct goal location, to correctly grasp an object we need to process the orientation and size of the object as well. For example, intending to grasp a book from a shelf requires information about the position, orientation, and size of the book. Effects of visual attention on the processing of nonspatial stimulus features, such as color or orientation, have been reported for both early event-related potential (ERP) components and slow-wave ERP effects (e.g., Baas et al. 2002; Eimer 1995; Proverbio et al. 2002; Slagter et al. 2005; Wijers et al. 1989). For example, attending to the orientation of a visual stimulus has been associated with an increased amplitude of both the N1 and the P1 components (Karayanidis and Michie 1997; O’Donnell et al. 1997; Proverbio et al. 2002). In addition, the selection of nonspatial stimulus features is further reflected in slow-wave effects, showing up as a stronger negative wave for the attended feature located above occipital sites (selection negativity [SN]) and as a stronger positive wave for the attended feature above frontal sites (frontal selection positivity [FSP]; Baas et al. 2002; Eimer 1995). These findings suggest that attending to nonspatial stimulus features, such as orientation, is reflected by enhanced early visual brain responses to the attended feature and the continuous selection of this information as reflected by SN effects over posterior areas. In line with the suggested functional and neural overlap between the processes controlling attention and action, one would predict similar early (N1, P1) and sustained (SN, FSP) ERP effects when the orientation of stimuli needs to be selected for action (e.g., grasping).

Consistent with this idea, the selection processes underlying the visual control of action are assumed to take place already at an early stage, within the first hundreds of milliseconds after stimulus onset (Bekkering and Neggars 2002). In the present study we directly investigated the hypothesis that selection for action (i.e., the intention to grasp or to point to an object) implicitly influences the processing of action-relevant nonspatial stimulus features (e.g., object orientation), comparable with previous studies that explicitly cued subjects to attend to orientation. In our experiment participants were instructed either to grasp or to point to a stimulus object, as soon as it was illuminated (object remained illuminated during the subject’s movement). Effects of action intention were explored by measuring ERPs to detect differences in visual processing of the stimuli between grasping and pointing conditions. Due to their high temporal resolution ERPs provide the opportunity to capture the time course of visuomotor processing. Because of our interest in early visual effects of action intention, ERPs provide an excellent tool to study the top-down effect of action intention on visual processing.

More specifically, it was hypothesized that both location and orientation are relevant to guiding and preshaping the hand for grasping a stimulus bar, whereas only location is relevant for pointing. Based on previous studies that investigated the effects of attention to nonspatial stimulus features, we expected to find differences in the amplitude of the early visual components and a subsequent SN and FSP between grasping and pointing conditions (e.g., Harter and Guido 1980; Kenemans et al. 1993).

To exclude the possibility that differences between grasping and pointing actually reflect differences in action initiation, no-go trials were included that consisted of a brief (100 ms) presentation of a target object. Subjects were instructed to ignore the brief stimulus flashes and to withhold from responding during the no-go trials. Similar to the go trials it was hypothesized that in the no-go trials the action intention of the subject (to grasp or to point) would implicitly influence the way in which information is processed in visual areas, independent of the requirement to execute the action. Accordingly, comparable effects of action intention at visual sites were expected for both the go and the no-go trials. Differences in visual processing between both grasping and pointing conditions would provide an electrophysiological argument for the effect of action intentions on the selective processing of visual stimuli that are relevant for action and thus new neurophysiological support for the hypothesis of selection for action and the commonality of the mechanisms supporting attention and action.

ME THOD S

Participants

Twenty-two participants (13 women) between 19 and 30 yr of age (mean age = 21.8 yr) participated in the experiment and were either offered an experimental remuneration or course credits for participation. All participants described themselves through informal verbal inquiry as being right-handed and had normal or corrected-to-normal vision. Prior to the experiment, informed consent was obtained for all subjects.

Experimental setup

The experimental setup is schematically represented in Fig. 1. Stimuli consisted of two rectangular Plexiglas three-dimensional (3D) objects (42 × 15 × 31 mm) that could be rear-lighted by an underlying array of red light-emitting diodes (LEDs). Both stimuli were placed at a stimulus board (915 × 565 × 150 mm) that was vertically arranged at a table. Small electromotors enabled rotation of the objects in different positions (45° clockwise [cw] and 45° counterclockwise [ccw]). The objects were placed on the left and right sides of a central fixation point (90 mm lateral to the vertical meridian and 70 mm below the horizontal median; see Fig. 1). The fixation
point consisted of a dimly lit red LED (2 mm). A small plastic pin (h = 10 mm, r = 10 mm) attached to the table, 420 mm below the fixation point, functioned as the “starting point” from which the participant started moving his or her hand every trial. The stimulus board was controlled by a computer, running Presentation 9.13 (Neurobehavioral Systems, Albany, CA).

Hand movements were recorded using an electromagnetic position tracking system, consisting of two MiniBird consoles (Ascension Technology, Burlington, VT). Two sensors were placed on the index finger and thumb of the participant. Position data were recorded at a frequency of 103.3 Hz on a disk operating system computer running custom-made software. On-line calculations were used to detect the movement onset and offset of grasping and pointing actions and the different postures of the hand (e.g., grasping the left or right object and pointing to the left or right object). All events (stimulus onset, movement onset, movement offset, and the different hand positions) were sent in parallel to a separate computer for electromyographic (EMG) recording and to the Presentation computer. On-line markers were set aligned with the sampling of the raw EEG signal, based on the incoming events.

Procedure

During the experiment participants were seated in a dark, sound-attenuated, and electrically shielded room, behind a table and facing the stimulus board. For each subject the distance to the stimulus board was adjusted to three fourths of the subject’s maximum arm extension, to enable comfortable reaching, grasping, and pointing to the target objects, without moving body parts other than the arm and the hand. The experiment was conducted in complete darkness and only a starting position, functioned as the “starting point” from which the participant started moving his or her hand every trial. The stimulus board was controlled by a computer, running Presentation 9.13 (Neurobehavioral Systems, Albany, CA).

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At the start of each trial subjects placed their right hand on the starting position, with their index finger and thumb holding the metal pin. In the so-called go trials they were instructed to perform a grasping or pointing action with their right hand toward the 3D target object when it was illuminated and to respond as quickly and accurately as possible. During the “go trials” the 3D target object was illuminated during the entire trial. Half of the trials in each block consisted of so-called no-go trials, in which the object was only briefly illuminated for 100 ms. Subjects were instructed to ignore the brief stimuli and to withhold from responding. Each block consisted of 96 trials: 48 trials during which the participant had to grasp or point to the target object (go trials) and 48 trials with a brief flash of the stimulus (no-go trials). Go and no-go trials were presented in a randomized order throughout each block.

In half of all blocks subjects were required to grasp the object and hold it shortly between their index finger and thumb along the long axis of the Plexiglas bar before returning to the starting position. In the other half of all blocks they were required to point at the target object, touching it briefly at the center with their index finger and then return to the starting position. Grasping and pointing conditions were presented in separate blocks in an alternating fashion. At the start of each block participants performed one practice run, consisting of four trials, to familiarize all participants with the task (grasping or pointing).

A total number of eight blocks was administered: four blocks with the instruction to grasp the object and four with the instruction to point to the object. The position and orientation of the stimulus objects were randomized throughout each block: left bar ccw, left bar cw, right bar ccw, and right bar cw. After each block there was a short break, during which the participant rested.

Each trial started with the subject having his or her hand at the starting position. During a 2.5-s interval, both objects first rotated to a vertical orientation and then to the orientation (cw or ccw) for the next trial. Both objects always rotated in opposite directions, to prevent the participant from inferring the sounds of the rotating motors in which position stimulus objects were oriented. Even when the orientation of the stimuli was repeated between trials, objects rotated. Subsequent to the rotation interval one of both stimulus objects was rear-lighted by the onset of an underlying array of red LEDs. In the go-trials the subject performed a grasping or a pointing movement toward the object. Movement onset, grasping posture (left, right, cw, ccw), and pointing (left object, right object) were detected on-line during execution of the movement. After participants returned their hand to the starting position, the light under the stimulus object switched off. In the no-go trials the stimulus object switched off after 100 ms, followed by a 1-s interval.

Electrophysiological recordings

The electroencephalogram (EEG) was recorded using an electrocap (EasyCap, Herrsching-Breitbrunn, Germany) with 61 adaptors for electrode placement. Electrode positions were based on the M-10 Equidistant 61-channel arrangement, with an interelectrode distance of 37 ± 3 mm (given a head circumference of 58 cm). This montage was constructed out of triangles, which were measured on the 3D head surface and arranged around central electrode Cz. All Ag/AgCl electrodes were referenced to the electronically calculated average of the reference electrodes, placed at both earlobes. Horizontal and vertical electrooculograms (EOGs) were measured with Ag/AgCl electrodes placed on the outer canthi and above and below the subject’s left eye. The ground electrode was on the left clavicle. Impedance of the electrodes was kept to <10 kΩ. EEG and EOG signals were amplified using two 32-channel BrainAmp DC EEG amplifiers and sampled at 500 Hz. The signal was filtered on-line with an 80 Hz high cutoff filter. Data were recorded on-line using Brain Vision Recorder 1.02 (BrainProducts, Munich, Germany). Data analysis was performed off-line, with Brain Vision Analyzer 1.05, BESA 5.1.8 (Brain Electrical Source Analysis, MEGIS Software, Gräfelfing, Germany) and SPSS statistical software (Chicago, IL).
Behavioral analysis

Position data of the hand at the different positions were calculated on-line, using a simple distance criterion. An area (12.7 × 12.7 × 10.2 mm) was defined around each marker position. This was done separately for the starting position, the different grasping postures (left cw, left ccw, right cw, right ccw) and the different pointing postures (pointing to left object, pointing to right object). Events were generated based on on-line detection of the thumb and index finger inside the previously defined marker areas. Reaction times (RTs) were calculated off-line from the events recorded by the movement-tracking system. Based on stimulus onset, movement onset, and detection of the finger position at the target location, the RT (time between stimulus onset and movement onset) and movement time (MT; time between movement onset and detection of the finger at the target position) were calculated.

RTs and MTs that exceeded the subjects’ mean by >2SDs were excluded from data analysis. Subjects’ average RTs and MTs were subjected to a repeated-measures ANOVA with the factors Condition (Grasp vs. Point), Position of stimulus (Left vs. Right), and Orientation of stimulus (CW vs. CCW).

Electrophysiological data analysis

Electrophysiological data were analyzed and averaged in alignment with stimulus onset. Trials with amplifier or movement artifacts were excluded from analysis on the basis of a semiautomated visual inspection procedure on the raw data. Ocular artifacts were corrected using a semiautomatic correction procedure (Gratton et al. 1983). Grand-average data were calculated for each individual participant per electrode and per condition (grasping, pointing), pooled over left, right, cw, and ccw oriented stimulus objects.

Data analysis focused on the interval from −200 to 800 ms relative to stimulus onset (baseline from −100 to 0 ms). Main analysis of the grand-average data focused on differences between grasping and pointing conditions. Mean averages of electrodes located above the sites of interest were exported and tested for significance, using repeated-measures ANOVA analysis. On the basis of the literature on visual attention (Hillyard and Anllo-Vento 1998; Karayanidis and Michie 1997; Kenemans et al. 1993; O’Donnell et al. 1997), the strongest effects of grasping versus pointing were expected at bilateral occipital and frontal sites around the peak amplitudes of the visual components (i.e., N1) and in the subsequent interval in which typically the selection negativity and selection positivity are reported. Accordingly, for statistical analysis of the N1 component a 40-ms interval around the peak latency of the N1 was selected (180–220 ms), for the later selection negativity the interval from 220 to 500 ms was selected, and for the frontal selection positivity the interval from 200 to 500 ms was selected. In addition, differences in motor execution between grasping and pointing are likely reflected in slow-wave movement-related components (cf. van Schie and Bekkering 2007).

To investigate differences between grasping and pointing during subjects’ reaching for the object, an additional analysis was conducted from 680 to 800 ms relative to stimulus onset. Main analysis of ERPs focused on differences between grasping and pointing conditions, with Condition (grasping vs. pointing) and Electrode (left vs. right) as within-subject factors.

Source analysis

A minimum norm analysis was applied to the grand-averaged ERPs, for both grasping and pointing and on the difference between grasping and pointing. The minimum norm technique was applied from 0 to 800 ms relative to the onset of the stimulus. Source estimation was conducted using approximately 2,500–4,500 locations on an individual, Talaraich-transformed brain surface mesh fitted to the boundary between gray and white matter. The minimum norm was computed with spatiotemporal weighting according to Dale and Sereno (1993).

RESULTS

Behavioral results

Overall, subjects were quite proficient in the performance of the task, as evidenced by the low number of false alarms (responses faster than 100 ms occurred <1% of all trials). For both reaction times and movement times <1% of all trials was excluded because the RT or MT exceeded the participant’s mean by >2SDs, indicating that participants were fairly constant and accurate in their movements. The mean reaction and movement times for grasping and pointing conditions are represented in Table 1 and were analyzed using a repeated-measures ANOVA with the factors Condition (Grasp vs. Point), Position of stimulus (Left vs. Right), and Orientation of stimulus (CW vs. CCW).

Analysis of reaction times revealed a significant main effect of Condition, reflecting faster reaction times for pointing (516 ms) than for grasping (527 ms) \( F(1,21) = 8.9, P < 0.01 \). A main effect of Position reflected faster reaction times toward objects on the right side (513 ms) compared with objects on the left side (530 ms) \( F(1,21) = 28.1, P < 0.001 \). Finally, a main effect of Orientation reflected faster reaction times to objects oriented in a clockwise fashion (518 ms) compared with objects oriented in a counterclockwise fashion (524 ms) \( F(1,21) = 19.7, P < 0.001 \). No significant interaction effects were found (all values of \( P > 0.15 \)).

Analysis of the movement times revealed a pattern that was comparable to that of the reaction times. A main effect of Condition reflected faster movement times for pointing (527 ms) than for grasping (582 ms) \( F(1,21) = 44.4, P < 0.001 \). A main effect of Position reflected faster movements toward objects at the right side (532 ms) than toward objects at the left side (578 ms) \( F(1,21) = 48.4, P < 0.001 \). A main effect of Orientation reflected faster movements to clockwise-oriented objects (547 ms) compared with counterclockwise-oriented objects.

<table>
<thead>
<tr>
<th>Action Condition</th>
<th>Left Object</th>
<th>Right Object</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasp</td>
<td>CCW</td>
<td>CW</td>
</tr>
<tr>
<td>Reaction time</td>
<td>527 (16)</td>
<td>534 (15)</td>
</tr>
<tr>
<td>Movement time</td>
<td>620 (28)</td>
<td>588 (26)</td>
</tr>
<tr>
<td>Point</td>
<td>CCW</td>
<td>CW</td>
</tr>
<tr>
<td>Reaction time</td>
<td>526 (14)</td>
<td>522 (15)</td>
</tr>
<tr>
<td>Movement time</td>
<td>550 (23)</td>
<td>553 (26)</td>
</tr>
</tbody>
</table>

Values are means with SE in parentheses (in milliseconds). Action condition includes Grasp and Point; Position of stimulus includes Left Object and Right Object; and object orientation is either clockwise (CW) or counterclockwise (CCW).

1 Note that reaction times were calculated relative to stimulus onset, rather than to the time point at which it became apparent whether the subject needed to respond (stimulus onset + 100 ms). If subjects had been given the opportunity to directly respond as soon as the object was illuminated, we may have expected faster reaction times. Still, this confound does not affect the analysis of reaction and movement times because the go/no-go delay was constant for both grasping and pointing and the different stimulus conditions.
objects (562 ms) \[F(1,21) = 9.4, P < 0.01\]. A significant interaction was found between Condition, Position, and Orientation \[F(1,21) = 4.6, P < 0.05\]. Post hoc \(t\)-test revealed that this interaction reflected the orientation of the object affected movement times only when subjects grasped left objects \(t(22) = 2.5, P < 0.05\), but for the right object and for pointing conditions no differences were found in movement times between clockwise- and counterclockwise-oriented objects (all values of \(P > 0.09\)).

**Event-related potentials: go trials**

The stimulus onset and the initiation of the reaching movement resulted in a pattern of visual components and slow waves. In both the grasping and the pointing conditions P1 (peak at 120 ms) and N1 (peak at 200 ms) components were found at bilateral occipital sites. From 180 to 500 ms a positive slow wave developed that was found maximal above parietal cortex. A comparable parietal positive slow wave was found in previous studies (cf. van Schie and Bekkering 2007) and likely reflects the involvement of parietal areas in the preparation and on-line control of movements. From 350 ms after stimulus onset a readiness potential developed, slightly lateralized to the left hemisphere, that developed into a frontocentral motor-related potential. In association with the onset of the motor-related potential, the parietal slow wave lateralized bilaterally and shifted to the left and right temporal lobes.

**N1 effect.** Early differences in visual processing in response to stimuli presented in grasping and pointing conditions were found on the N1 component, over bilateral occipital electrodes, and are represented in Fig. 2 (left). Statistical analysis was conducted using a 2 (Condition: Grasp vs. Point) \(\times\) 2 (Electrode: Left hemisphere vs. Right hemisphere) repeated-measures ANOVA on the N1 interval (180–220 ms) on the electrodes that, with respect to the standard 10/20 system, lie between PO8 and P8 and between PO7 and P7. A main effect of Condition was reflected in a stronger negative N1 amplitude for grasping compared with pointing \(F(1,21) = 5.1, P < 0.05\). An interaction effect between Condition and Electrode indicated that these differences were stronger over the left occipital hemisphere \(F(1,21) = 6.4, P < 0.05\).

**Selection negativity.** Following the initial effect on the N1, the occipital difference continued in the form of a bilateral selection negativity that showed a more negative wave for grasping compared with pointing, which is represented in the right side of Fig. 2. This occipital selection negativity persisted until movement onset and continued during the first part of the action. The occipital slow-wave effect was found significant from 220 to 500 ms after stimulus onset \(F(1,21) = 4.7, P < 0.05\) at the same electrodes used for analyzing the N1 effect. No interaction with hemisphere was found (\(F < 1\)).

In sum, effects of action intention in the go trials became apparent in a stronger N1 effect and a subsequent selection negativity.
negativity for grasping compared with pointing. It could well be that both effects reflect the same functional mechanism (i.e., enhanced processing of orientation information for grasping compared with pointing). To provide further evidence for the notion that both the N1 effect and the selection negativity reflect a comparable functional process, the commonalities in the scalp distribution of the N1 effect and the selection negativity were investigated. To this end, first a correlation analysis was conducted. The N1 effect and the selection negativity were compared across the entire set of 61 electrodes using the average value per electrode calculated from the interval in which the effects were found significant, as entries to calculate Pearson’s correlation. A highly significant correlation was found between both effects, $r = 0.937, P < 0.001$, indicating that the N1 effect and the selection negativity had a comparable scalp topography.

To further test the overlap between both effects, two rectangular $3 \times 3$ electrode grids were selected overlaying the left and right occipital hemispheres (cf. Praamstra et al. 2005). A repeated-measures analysis was conducted on the mean amplitudes of the N1 effect and the selection negativity with the factors ERP effect (N1 vs. SN), Hemisphere (Left vs. Right), Anterior–Posterior axis (3 levels), and Medial–Lateral axis (3 levels). No significant interactions were found between ERP effects and any of the other factors (all values of $F < 1.4$; all values of $P > 0.27$), suggesting that both the N1 effect and the SN had a comparable distribution.

**FRONTAL SELECTION POSITIVITY.** Over frontal areas, stimuli presented in the grasping condition generated a selection positivity, compared with stimuli presented in the pointing condition. The selection positivity was found broadly distributed over frontal areas, as can be seen in the right side of Fig. 2. Statistical analysis of the selection positivity was conducted on the electrodes that with respect to the standard 10/20 system correspond with AF4 and AF3. The selection positivity was found significant from 200 to 500 ms after stimulus onset, as reflected in a main effect of Condition at frontal sites [$F(1,21) = 16.6, P < 0.001$]. No significant interaction with hemisphere was found ($F < 1$). The frontal selection positivity was found accompanied by a stronger positive slow-wave difference for grasping compared with pointing centered above the vertex, which is represented in Fig. 2 (central electrode at middle panel). This central effect was found significant between 220 and 500 ms after stimulus onset at central sites [$F(1,21) = 4.8, P < 0.05$], at electrodes in between C1 and CP1 and C2 and CP2, with respect to the standard 10/20 system. An interaction with hemisphere indicated that this effect was slightly lateralized to the right side of the scalp [$F(1,21) = 6.6, P < 0.05$].

**MOVEMENT-RELATED POTENTIAL.** From about 680 ms onward a stronger bilateral negativity was observed over central sites for grasping compared with pointing, reflecting a stronger motor-related potential for grasping compared with pointing (see Fig. 2). This motor-related potential was found significant between 680 and 800 ms after stimulus onset at electrodes CP3 and CP4 with respect to the standard 10/20 system [$F(1,21) = 4.6, P < 0.05$]. No interaction with hemisphere was found.

**Control for ocular confounds**

Previous studies have indicated that the location at which visual information is projected onto the retina influences the amplitude and distribution of visual components at occipital sites (e.g., Andersson et al. 2004; Gunter et al. 1994). In general, the more foveal the stimulus position projects onto the retina, the stronger the visual effect, as measured in both electrophysiological primate studies and human visual ERP studies. Eye movements toward the left or the right stimulus determine the retinal position of the stimulus and thereby influence the strength of the visual effect. To control for the possible confound that differences in visual processing between grasping and pointing might be attributable to differences in eye movements between both action conditions, analyses on the EOGs were performed. Because the fixation point was located centrally between and slightly above both stimulus objects, both horizontal and vertical eye movements are indicative of making saccades toward the stimulus object. Therefore inspection of both horizontal and vertical EOGs was deemed necessary to control for this possible confound. Visual inspection of the EOGs indicated that subjects successfully maintained fixation until movement onset (~500 ms after stimulus onset). From that point onward, the vertical ocularogram indicated that subjects sometimes made saccades toward the target objects, probably to guide their subsequent hand movements (Bekkering et al. 1994, 1995; Neggers and Bekkering 2000).

Importantly, analysis of the horizontal EOG in the intervals used for the main analysis (0–500 ms) revealed no significant interaction effect between Condition (grasp, point) and Position of the stimulus object (left, right) (all values of $F < 1$), indicating that subject’s horizontal eye movement to the right and the left object was comparable in both action conditions. Furthermore, analysis of the vertical EOG revealed no significant interaction effect between Condition and Position of the stimulus object (all values of $F < 1$), indicating that the subject’s vertical eye-movement behavior was comparable in both action conditions.

**Source analysis**

Grand-average ERPs for grasping and pointing in the go trials were selected for source analysis using minimum-norm localization in BESA 5.1.8 (MEGIS Software). First, a source analysis was conducted on the grand-average ERPs for both grasping and pointing to identify brain areas recruited during both grasping and pointing conditions. Following the ERP effects at the sensor level, the parietal positive slow wave for both grasping and pointing was localized to the parietooccipital sulcus (Brodmann area [BA] 19) from about 200 to 500 ms (see Fig. 3). The motor-related potential was localized to the supplementary motor area (BA 6) from about 500 to 800 ms (Fig. 3). Second, a source analysis was conducted on the difference between grasping and pointing conditions. The N1 effect and the stronger selection negativity for grasping compared with pointing were localized to ventral occipital areas (BA 18/19; lingual gyrus and fusiform gyrus) from about 200 to 800 ms (Fig. 3, bottom). Furthermore, the difference in motor-related potentials between grasping and pointing was reflected in a stronger source activation in premotor areas (BA 6) from 600 to 800 ms and in the inferior parietal lobule from 600 to 800 ms (BA 40; see Fig. 3, bottom).
Event-related potentials: no-go trials

In the no-go trials in both grasping and pointing conditions, P1 (peak at 120 ms) and N1 (peak at 190 ms) components were found, in response to the presentation of the stimulus object. A positive slow wave developed above parietal cortex (no-go P3) from about 220 ms that shifted to central electrodes and persisted until 550 ms after stimulus onset. As expected, no movement-related potential was found.

In contrast to the go trials, as can be seen in Fig. 4 (left), in the no-go trials no significant difference was found in the N1 amplitude between grasping and pointing \( [F(1,21) = 1.8, P > 0.19] \). Main differences between grasping and pointing conditions in the no-go trials were reflected in a stronger selection negativity for grasping compared with pointing over bilateral occipital sites, which is represented in Fig. 4 (right). The stronger negative slow-wave effect over occipital electrodes in the grasping condition was found from 220 to 370 ms after stimulus onset \( [F(1,21) = 5.0, P < 0.05] \). No significant interaction with hemisphere was found \( (F < 1) \).

The distribution of the selection negativity was compared between the go trials and the no-go trials, using a repeated-measures analysis on the mean amplitudes of the selection negativity with the factors ERP effect (SN go vs. SN no-go), Hemisphere (Left vs. Right), Anterior–Posterior axis (3 levels), and Medial–Lateral axis (3 levels). First, a main effect of ERP effect indicated that the selection negativity was stronger in the go trials than that in the no-go trials \( [F(1,21) = 6.4, P < 0.05] \). A significant interaction was found between ERP effect and Anterior–Posterior \( [F(2,20) = 10.9, P < 0.001] \), indicating that the selection negativity in the no-go trials was more broadly distributed over posterior and anterior occipital areas compared with the selection negativity in the go trials, which was found more focally distributed at bilateral central occipital areas. No other significant interactions were found with ERP effect.

Similar to the go trials a positive slow-wave difference centered above the vertex was found in the no-go trials for grasping compared with pointing, which is represented in Fig. 4 (right). This central effect was found significant between 220 and 400 ms after stimulus onset \( [F(1,21) = 5.6, P < 0.05] \). No interaction with hemisphere was found \( (F < 1) \).

In contrast to the go trials, in the no-go trials no selection positivity was observed between grasping and pointing \( (F < 1.8, P > 0.20) \); see Fig. 4, right).

Comparison of the N1 amplitude between the go and no-go trials

Contrary to our initial expectations, the effects of action intention on visual processing did not completely overlap between the go trials and no-go trials. That is, for the go trials...
a stronger N1 component and a subsequent selection negativity were observed for grasping compared with pointing, whereas for the no-go trials only the later selection negativity was found. One explanation for this apparent inconsistency is that the N1 effect in the go trials reflects the combined effects of both top-down processing (intention to grasp or point) and bottom-up incoming visual information. In contrast, in the no-go trials the stimulus switched off after 100 ms and accordingly in the N1 interval, bottom-up visual information was no longer available (taking into account the conduction speed from stimulus onset to V2; cf. Foxe and Simpson 2002). If the N1 amplitude is indeed sensitive to bottom-up visual information, we should expect an overall reduction of the N1 amplitude for no-go trials compared with that for go trials.

To directly test this hypothesis an additional analysis was conducted using a 2 (Condition: Go, No-go) × 2 (Action: Grasp, Point) × 2 (Hemisphere: left, right) repeated-measures ANOVA on the N1 interval (180–220 ms). First a main effect of Condition [F(1,21) = 5.7, P < 0.05] reflected a stronger overall N1 amplitude in the go trials compared with that in the no-go trials. An interaction between Condition and Action [F(1,21) = 5.5, P < 0.05] reflected that the N1 amplitude was modulated by the intention to grasp or point only in the go trials. Finally, a marginally significant interaction between Action and Hemisphere [F(1,21) = 5.5, P < 0.05] reflected that the strongest effects of action intention were observed over the left hemisphere.

DISCUSSION

In the present study we investigated the effects of a subjects’ intention to grasp or point toward an object on the processing of visual information. It was found that grasping compared with pointing enhanced the amplitude of the N1 component and resulted in a subsequent occipital selection negativity and a frontal selection positivity. The possible neural and functional mechanisms underlying these effects will be discussed in more detail in the following text.

Both grasping and pointing were found to result in the typical perception and action ERP components. In the first 200 ms after the onset of the stimulus, classical visual ERP components could be identified, reflecting early visual processing. In association with the preparation of the action during the go trials, a parietal positive slow wave developed together with a motor-related potential (cf. van Schie and Bekkering 2007). In line with these ERP findings, source localization of both grasping and pointing revealed activation in visual areas followed by a subsequent activation of the parietooccipital sulcus (POS) from about 200 ms. The POS is known for its role in the visual guidance and on-line control of movements (Culham and Valyear 2006; Filimon et al. 2009). For example, damage to the POS results in optic ataxia, a disorder that is characterized by misreaching toward visual targets, often accompanied by an erroneous orientation of the hand before grasping the object (Battaglia-Mayer et al. 2001; Perenin and Vighetto 1988). In addition to its role in visually guided reaching toward central and peripheral visual targets (Filimon et al. 2009; Prado et al. 2005), the POS is involved in the planning of pointing movements as well, suggesting that it specifically codes visual target locations for subsequent actions (Connolly et al. 2003). In line with these findings, in the present study the parietal positive slow wave was localized to the POS for both grasping and pointing, which both require the coding of the target location to make an appropriate reaching movement.

However, in contrast to pointing only grasping requires the processing of information about the orientation of the target object. Accordingly, by comparing brain responses between grasping and pointing, the current experiment allowed us to identify how one’s intention to grasp or point influences the processing of nonspatial visual information. The first difference between grasping and pointing became apparent around 180 ms after stimulus onset during the go trials and was reflected in an enhanced N1 component and a subsequent selection negativity, which were stronger for grasping compared with pointing. The effect of spatial and nonspatial attention on the amplitudes of the P1 and N1 components has been well documented and likely reflects a mechanism of gain control or selective amplification of incoming sensory information in the 200-ms interval after stimulus onset (Gomez Gonzalez et al. 1994; Hillyard and Anllo-Vento 1998). For example, studies on visual attention have shown that attending...
to the orientation of an object results in an enhancement of both the P1 amplitude (Karayanidis and Michie 1997; Proverbio et al. 2002) and the N1 component (O’Donnell et al. 1997). Accordingly, modulation of the N1 amplitude found in the go trials likely reflects the top-down influence of action intention on incoming sensory signals in visual areas. In contrast, in the no-go trials no modulation of the N1 amplitude was observed and the overall N1 amplitude was found reduced in the no-go compared with that in the go trials. The N1 reflects a relatively early level of stimulus processing that is dependent on both bottom-up incoming sensory information (sustained stimulus duration in the go trials) and top-down effects of action intention (Mangun 1995). The absence of an effect of action intention on the N1 component and the smaller N1 amplitude in the no-go trials are likely due to the shorter stimulus presentation (100 ms) in the no-go compared with the go trials.

Interestingly, previous studies have shown a stronger occipital N1 component in conditions in which a discrimination is required (i.e., choice RT tasks) compared with conditions in which subjects merely detect the presence of a stimulus (simple RT tasks; Hopf et al. 2002; Vogel and Luck 2000). For instance, Vogel and Luck (2000) showed that, irrespective of differences in arousal, motor-response processes or perceptual load, a larger N1 was observed in conditions that required a discrimination. Accordingly, the amplitude of the occipital N1 is sensitive to discrimination-related processes as well. In the present study, the grasping condition required the implicit discrimination of orientation, whereas the pointing condition did not. Therefore the stronger N1 component for grasping compared with pointing in the go trials may also reflect processes related to discrimination of goal-related features. Although the present data do not allow us to disentangle whether the N1 effect reflects the enhanced processing of action-related features or processes related to implicit orientation discrimination, both accounts go well with the notion that relevant visual information is selected for subsequent action (Allport 1989).

In both the go trials and the no-go trials a stronger selection negativity was observed for grasping compared with pointing at bilateral occipital sites. Selection negativities from 200 ms onward have been found in association with attention to and processing of nonspatial stimulus features such as color or shape (e.g., Hillyard and Anllo-Vento 1998; Karayanidis and Michie 1997; Proverbio et al. 2002). Because the processing of nonspatial stimulus features is more important for grasping compared with pointing, the subsequent selection negativity likely reflects the enhanced processing of nonspatial action-relevant stimulus features (e.g., orientation and size). An open question is why in the no-go trials effects of action intention were reflected only in the later selection negativity, but not in the earlier N1 component. As discussed earlier, the N1 reflects the selective amplification of incoming stimulus information (Mangun 1995) and the absence of an N1 effect in the no-go trials is likely related to the shorter stimulus duration. In contrast, the selection negativity may reflect top-down effects of action intention, independent of the actual execution of the action. Although the precise functional significance of early and late effects of action intention on visual processing remains to be determined, still, the finding of a selection negativity for both the go and the no-go trials suggests that the visual system is in a different state when preparing to grasp compared with preparing to point, irrespective of the actual motor output.

In the present study the N1 effect and the subsequent selection negativity for grasping compared with pointing had a comparable scalp distribution over bilateral occipital sites, suggesting comparable neural sources. Several studies have identified sources of the N1 and the selection negativity to visual areas that are typically considered part of the ventral stream (Anllo-Vento et al. 1998; Baas et al. 2002; Di Russo et al. 2002; Gomez Gonzalez et al. 1994). In line with these findings, in the present study a stronger source activation was found for grasping compared with pointing over ventral occipital areas (BA 18/19; lingual gyrus and fusiform gyrus) from about 200 to 800 ms after stimulus onset. These ventral stream areas can be considered part of the lateral occipital complex (LOC) and are involved in the processing of visual and haptic object information (Saito et al. 2003; Still and Sathian 2008). More specifically, the LOC appears to be involved in the perception of both geometrical and volumetric object features (Amedi et al. 2001; Moore and Engel 2001) and may encode haptic object information in relation to the early perceptual processing of the shape of graspable objects (Amedi et al. 2002; Grill-Spector et al. 1999; Majdandzic et al. 2007). Accordingly, the stronger activation for grasping compared with pointing in ventral occipital areas likely reflects a more elaborated visual analysis required for preshaping the hand during the preparation of a grasping movement.

Studies on saccadic eye movements have implicated a special role for the frontal eye fields (FEFs) in modulating the activation in early occipital areas (Moore and Armstrong 2003; Neggers et al. 2007; Ruff et al. 2006; Super et al. 2004). For example, subthreshold stimulation of neurons in monkey’s FEF resulted in an enhanced visual response of V4 neurons, when a stimulus was presented in the neuron’s receptive field (Moore and Armstrong 2003). Several studies have now shown comparable corticocortical feedback mechanisms from the FEF to early visual areas in humans as well (Gutteling et al. 2009; Neggers et al. 2007; Van Ettinger-Veenstra et al. 2009). Interestingly, in a recent TMS–EEG study, when subjects were required to attend either to faces or to a moving grid, TMS-induced visual ERP responses provided direct evidence for FEF-feedback projections to occipital areas underlying human visual attention (Morishima et al. 2009). Whereas feedback projections to occipital areas have mainly been studied for the initiation of saccadic eye movements, the present findings suggest that a comparable feedback mechanism in which pre-motor areas modulate the activation in early visual areas may underlie the preparation of grasping and pointing movements.

In line with the idea that prefrontal regions contribute to the selection of object-specific information for action in posterior visual areas, Barceló et al. (2000), using a visual detection task, found an impaired behavioral performance and a reduced enhancement of the N1 amplitude in prefrontal lesion subjects compared with normal subjects. In addition, Yago et al. (2004) reported a reduced selection negativity in a spatial attention task for prefrontal lesion patients compared with control participants. These findings are consistent with primate studies, in which deactivation of lateral prefrontal cortex was found to result in an attenuation of activity in visual cortex to behaviorally relevant cues (Chafee and Goldman-Rakic 2000; Fuster et al. 1985). Together, these studies suggest that prefrontal
brain areas may modulate the activation of occipital areas, thereby facilitating the processing of task-relevant visual information (Desimone and Duncan 1995).

Importantly, the occipital ERP effects cannot be attributed to differences in the initiation of grasping and pointing movements because analysis of the visual ERP effects was restricted to the premovement interval. In addition, in the no-go trials an occipital selection negativity was found comparable to that in the go trials, suggesting that the stronger selection negativity for grasping reflects the automatic effect of action intention on visual processing, irrespective of movement execution. An intriguing question is how the present finding of a stronger involvement of ventral stream areas in grasping compared with pointing may relate to previous findings on this topic. That is, several studies have shown that grasping compared with reaching recruits dorsal stream areas, such as the anterior intraparietal cortex (AIP; Cohen et al. 2009; Culham et al. 2003, 2006). More specifically, the parietal lobe is especially involved in the visuomotor transformations required for grasping (Grefkes et al. 2004; Murata et al. 2000) and in the online control of grasping movements (e.g., Desmurget et al. 1999; Jeannerod et al. 1995). However, in the present study effects of action intention on visual processing were found in the premovement interval, before the grasping or pointing movement was initiated. Furthermore, in contrast to previous studies the present experiment was conducted in complete darkness and visual information of the moving hand was not available. Accordingly, whereas parietal areas support the online and visually guided control of grasping movements, selection of visual information for subsequent action may be supported by ventral stream areas, such as the LOC. In line with this suggestion, in a recent study TMS pulses applied to the LOC were found to selectively affect only delayed but not immediate grasping (Cohen et al. 2009). One intriguing possibility is that grasping objects requires integration of the output of visual selection processes (ventral stream areas) with the motor programs required to implement the grasping movement (area AIP; for a recent discussion, see Schenk and McIntosh 2010). In support of this suggestion, several studies have shown anatomical projections from ventral stream areas to the inferior parietal lobule (Borra et al. 2008; Rushworth et al. 2006; Webster et al. 1994; Zhong and Rockland 2003).

Moreover, frontal ERP differences were found between grasping and pointing conditions, as reflected in a frontal selection positivity (FSP) for grasping compared with pointing. The FSP likely reflects task-related visual processing (van der Stelt et al. 1998) and has been found in association with combined attention to different nonspatial stimulus features (Kenemans et al. 1993). Whereas early studies suggested that the FSP might reflect a polarity reversal at anterior scalp sites of the posterior selection negativity (SN), both originating from a common neural source (Harter and Guido 1980), other studies suggest that the FSP and the SN may actually reflect separate neural mechanisms, given that the onset latencies and the laterality of the scalp distribution can differ between effects (cf. Kenemans et al. 1993). One possibility is that the FSP reflects a selection-for-action process in prefrontal cortex (Smid et al. 1999), determining what information should be selected and maintained in active working memory for the upcoming action. A comparable frontal slow-wave effect was found in association with a working-memory task that increased in amplitude with the amount of visual object information to be retained (van Schie et al. 2005). Furthermore, numerous studies have shown the central role of prefrontal areas in object working memory (Courtney et al. 1997; D’Esposito et al. 1998). Accordingly, the stronger FSP for grasping compared with that for pointing may reflect the selection of object information (e.g., orientation and size) in working memory that is relevant for the upcoming action. This interpretation is in line with the absence of a frontal selection positivity in the no-go trials. Apparently, in the no-go trials action intentions had an effect on early visual processing, as reflected in the selection negativity, but this visual information needed no further processing and maintenance in frontal areas. Thereby different contributions of brain areas to the mechanism of selection for action can be distinguished, suggesting a special role for frontal areas in the maintenance of stimulus information in object-working memory.

Conclusions

Whereas many studies have focused on the brain mechanisms involved in the visuomotor transformations required for reaching and grasping (for review, see Culham and Valyear 2006), the mechanisms whereby the brain selects visual information that is relevant to one’s current action intentions have largely been ignored. In the present study it was found that a subject’s action intention modulates visual processing at an early stage. These findings can be interpreted as evidence that the motor system recruits visual processing resources in the occipital lobe. That is, the processing of object-related features that are relevant for the upcoming action, such as orientation, is facilitated to optimally perform the grasping movement. Thus the present findings suggest that action intentions influence the selection of nonspatial stimulus features and provide new insight in the neural and temporal dynamics of the selection for action process (Allport 1987).

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