RESEARCH ARTICLE

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Intention-based and stimulus-based mechanisms in action selection

Abstract Human actions can be classified as being either more stimulus-based or more intention-based. According to the ideomotor framework of action control, intention-based actions primarily refer to anticipated action effects (in other words response-stimulus [R-S] bindings), whereas stimulus-based actions are commonly assumed to be more strongly determined by stimulus-response [S-R] bindings. We explored differences in the functional signatures of both modes of action control in a temporal bisection task. Participants either performed a choice response by pressing one out of two keys in response to a preceding stimulus (stimulus-based action), or pressed one out of two keys to produce the next stimulus (intention-based action). In line with the ideomotor framework, we found intention-based actions to be shifted in time towards their anticipated effects (the next stimulus), whereas stimulus-based actions were shifted towards their preceding stimulus. Event-related potentials (ERPs) in the EEG revealed marked differences in action preparation for the two tasks. The data as a whole provide converging evidence for functional differences in the selection of motor actions as a function of their triggering conditions, and support the notion of two different modes of action selection, one being exogenous or mainly stimulus-driven, the other being endogenous or mainly intention-driven.

Keywords Action · Reaction · Event-related potential · Readiness potential · P300 component

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Introduction

Human action can be studied in two paradigmatic situations. In one, people act in a particular way to achieve certain desired effects in their environment. In the other, people act in response to external events, trying to accommodate to environmental demands. The difference between the two situations is typically addressed using varying terminology. The first type of action is usually referred to as "voluntary", "operant", or "intentional". Here, the action is selected on the basis of the agent's prior intentions. The second type of action is often considered with respect to notions like response or reaction. Here, the selection of a particular action is performed on the basis of prior stimulus events. Although the movements performed can be the same in both cases, there is reason to believe that the mechanisms underlying intention-based actions and stimulus-based actions may be different. In this article we seek to characterize the functional signatures of these two types of actions.

Before we introduce our experimental paradigm, we first give a brief characterization of intention-based versus stimulus-based actions and outline some recent theoretical approaches to the underlying mechanisms of selection and control. Then we introduce an experimental paradigm that allows us to contrast the two types of actions directly and characterize their functional signatures in terms of both behavioral and EEG data.

Intention-based and stimulus-based action

One of the main characteristics of the flexibility of human agents is their capability to perform actions according to intention and, thereby, act in a way that is internally-driven rather than externally- or stimulus-driven. The common-sense concept of such intentional, or voluntary, actions (see Jahanshahi and Frith 1998) typically refers to the idea that such actions serve to fulfill long-term *wishes* or *desires*. Accordingly, the key feature of the common-sense notion of intention-based actions is their *goal-directed-*

ness. Basically, most scientific definitions of voluntary action agree with this definition. A movement is considered a voluntary action if it is performed in order to produce some internally pre-specified, desired effect. What is more, according to some theories, action goals are also believed to play a core role in the acquisition, control, and planning of intention-based actions (see Hommel 2003; Hommel et al. 2001; Prinz 1997). In fact, according to the ideomotor theory of action control, representations of intended action *effects* are considered to be *causally responsible* for the selection of appropriate actions (Greenwald 1970). The ideomotor framework has recently gained empirical support from different domains, such as action-effect anticipation and response-effect compatibility (Elsner and Hommel 2001; Koch and Kunde 2002; Kunde 2001; Müsseler and Wühr 2002), sequence learning (Zießler and Nattkemper 2002), action perception (Knoblich and Flach 2001), bimanual coordination (Drewing and Aschersleben 2003; Mechsner et al. 2001) and infant action control (Hauf et al. 2004; Elsner and Aschersleben 2003).

Stimulus-based action, on the other hand, has been extensively studied in reaction-time experiments. In these experiments, participants respond to certain stimuli with certain responses, usually according to a particular mapping rule that has been prescribed in the instructions. For example, instructions might call for responding to a red stimulus by pressing a left-hand key and responding to a green stimulus by pressing a right-hand key.

Two modes of action selection

The distinction between intention-based and stimulus-based actions should not be overdrawn. Intention-based actions always require some stimulus guidance and stimulus-based actions always require some intentional guidance. It may be true that intention-based actions come into being through intentions, but in realizing those intentions the planning process cannot rely on intentional information alone; it also needs to take into account stimulus information from the actual environment. Similarly, while it may be true that stimulus-based actions are triggered by stimulus information from the environment, in the planning of appropriate responses, certain intentional states need to be in place. Unlike reflexes, for which stimulus information is both a necessary and sufficient condition, stimulus-based actions always derive from two functional sources of which stimulus information is but one. The other is an intentional set to respond to that information in a particular way (which, in experimental settings, is usually specified through instructions; see Prinz 1997).

Obviously, then, intentional information and stimulus information seem to be involved in both intention-based and stimulus-based actions. However, the two types of action differ in the relative contributions of stimulus- and intention-based information. Accordingly, it has been proposed that they differ in the functional architecture of the decision mechanisms involved in action selection. This proposal has been advanced in different frameworks, two of which are summarized below.

Neurophysiological studies

Converging evidence for the two modes of action being controlled differently has come from recent neuroscientific studies. On the basis of these studies, it has been suggested that intention-based actions are mediated by fronto-striatal circuits, including the dorso-lateral prefrontal cortex, anterior cingulate, and SMA (medial premotor cortex). This system is considered to be engaged in context-dependent selection, linkage, initiation, and anticipatory control of motor subroutines. Externally triggered, stimulus-based actions, by contrast, are supposed to be controlled by circuits involving PMA (lateral premotor cortex) and parietal areas. The functional anatomy subserving spatially congruent visuomotor transformations, as used in the present study, has been extensively characterized in macaques (Jeannerod et al. 1995). This category of actions relies on a cerebral circuit with contributions from portions of the inferior parietal cortex (Fogassi et al. 2001; Gallese et al. 1994; Luppino et al. 1999; Rizzolatti et al. 1988; anterior intraparietal area, AIP; Sakata et al. 1995) and ventral premotor cortex (Rizzolatti et al. 1988). This system is assumed to operate in a "responsive mode", in which movements are selected on the basis of external stimuli (see Goldberg 1985; Passingham 1985). Support for this "two routes to action hypothesis" comes from brain-imaging studies (fMRI, PET, TMS, ERP) and from studies of patients with frontal damage, Parkinson's disease, and schizophrenia. For example, Jahanshahi and Frith (1998) proposed that akinesia in Parkinson's disease (PD) may be a manifestation of a dysfunction of the "willed action system". Accordingly, patients with PD are more dependent on visual cues than are their normal counterparts for the control or initiation of movements (Georgiou et al. 1993, 1994). The latter results, like the others summarized in this section, support the idea of two different movement control systems, one that is mainly intention-based and another that is mainly stimulus-based.

Psychological studies

Psychological studies have also supported the distinction between intention-based and stimulus-based action. The logic is as follows. According to the ideomotor principle, an actor acquires bi-directional associative links between the code of a particular action and the codes of the action's sensory consequences. These representations of the actions' environmental consequences serve as "perceptual intentions" capable of triggering their corresponding actions (Greenwald 1970; Hommel et al. 2001; Hommel 2003; Prinz 1997). In the case of stimulus-based actions, bindings refer to stimuli and ensuing responses. A simple

association process mediates the build-up of S-R rules: selecting an action in response to a given stimulus binds the codes of the action-relevant stimulus attributes and the corresponding action codes (Allport 1987, 1989; Logan 1988). Recently, Haggard et al. (2002) explored these two bindings in an experiment that used Libet's clock procedure (Libet et al. 1983; Libet 1985). This procedure focuses on participants' estimation of the time when they perceive certain sensory or motor events. Participants had to judge the time when they pressed a key or when a tone was presented by indicating the position of a clock hand. Results showed clear evidence for temporal attraction effects: as compared to control conditions, in which only key presses were performed or only tones were presented, tones and subsequent actions in response to them attracted each other in time. These findings suggest that actions and their antecedents or consequences may be reflected in the perceived times of the pertinent events. Haggard et al. (2002) suggested that these bindings may be of particular significance in the case of intention-based actions. For agents in the everyday environment, it may be important to distinguish between events in the world that follow from their own actions as opposed to events that occur independently. According to Frith (1992), agents distinguish between self-generated and external events by monitoring the stream of sensory events and comparing this stream to the anticipated consequences of ongoing actions. Haggard et al. (2002) suggested that action-binding effects (and perceptual attraction between the two events) occur whenever the center monitoring sensory events and predicted action effects detects a match between external events and predicted action consequences. Note that in the study of Haggard et al. (2002), the stimulus-based condition required no response. Consequently, the basis for inferences about the distinction between the two routes to action may not be as firm as one would like. One aim of the present study was to address this limitation.

Aims of the study

In the present study we sought to characterize in a new way the functional signatures of intention-based and stimulus-based actions, particularly with respect to their underlying bindings. We examined the two types of action in greater detail, studying them within a single experimental paradigm, and characterizing their functional signatures in terms of both behavioral and EEG measures.

To this end, we devised a paradigm in which participants were asked to perform a motor action that bisected a fixed and predictable temporal interval (temporal bisection task). Thus, a sequence of actions was interweaved with a sequence of stimuli. Actions and stimuli could be linked to each other in two different ways. In one condition, stimuli determined ensuing actions. In the other condition, actions determined ensuing stimuli. Thus, action selection was stimulus-based in one condition and was intention-based in the other. Under the stimulus-based condition, the spatial position of a stimulus determined the required response, whereas under the intention-based condition the selected action determined the spatial position of the following stimulus. To keep the degree of movement alteration in both conditions identical, we yoked the subjects' movements under the stimulus-based conditions to the movements that the subjects produced before under the intention-based condition. For exploratory purposes, we manipulated the number of stimulus and action alternatives (two versus four).

As mentioned earlier, we examined both behavioral and EEG data. In the behavioral data, we expected to see temporal attraction effects between stimuli and ensuing actions in the case of stimulus-based actions, and between actions and ensuing effects in the case of intention-based actions. This outcome, if obtained, would extend the finding of attraction effects (Haggard et al. 2002) in two ways: first, it would show that attraction effects also occur in a paradigm using continuous sequences of events. Second, it would demonstrate that attraction effects can also be found in the actual timing (an objective measure) of movements, not only in the perceived timing of them (a subjective measure).

In the EEG data, we expected to see patterns of event-related activity reflecting different proportions of stimulus- and action-related processing. For this purpose, we focused on stimulus-locked and response-locked EEG components. For non-lateralized stimulus-locked ERPs, we expected the P3 (a positive peak that occurs around 300 ms following stimulus onset) to be more pronounced for stimulus-based actions than for intention-based actions. The P3 is of special interest in the present context because, although the P3 has been primarily assumed to reflect stimulus processing (for reviews see Donchin and Coles 1988; Kok 1997; Verleger 1988), subcomponents of the P3 complex have been considered to be related to the stimulus-based selection of one among a number of action alternatives (Falkenstein et al. 1994; Koivisto and Revonsuo 2003).

In the response-locked ERPs, we expected to find a complementary pattern of activity: a more pronounced negative shift before movements in intention-based conditions than in stimulus-based conditions. This negativity is the so-called "Bereitschaftspotential" or "readiness potential" (referred to herewith as BP), which was first reported by Kornhuber and Deecke (1965). Our assumption is based on the finding that the BP is affected by whether decisions about the nature (Dirnberger et al. 1998; Praamstra et al. 1995) or timing of movements (Fuller et al. 1997; Jahanshahi et al. 1995) are made by the subject or triggered by external stimuli. Usually, higher amplitudes are observed prior to self-selected movements than prior to external-stimulus-triggered movements.

We expected two major outcomes with the lateralized EEG. The first one bore on the response-locked LRP (Lateralized Readiness Potential) over motor areas. The LRP takes the form of increased cortical activity contra-lateral to a forthcoming response. It is thought to reflect

specific motor preparation (Gratton et al. 1988; De Jong et al. 1988). Since we assume that the two routes to action have a final common pathway (Passingham 1985; see also Sherrington 1906), we do not expect intention-based and stimulus-based actions to differ with regard to the amplitude or onset latency of the LRP. However, we do expect that intention-based and stimulus-based actions will be associated with different patterns of stimulus-related EEG lateralization. For example, the N2pc and the N2cc (negative deflections over parietal and central electrodes, respectively, contralateral to the target hemifield in the time range of the N2 complex) are considered to reflect the processing of spatial parameters in both the visual and the motor domains, respectively (see Wascher and Wausch-kuhn 1996). We assume that these components show that the motor system is more strongly affected when the stimuli determine the subsequent response (stimulus-based) than when intentions determine the subsequent response (intention-based).

Method

Subjects

Ten subjects (eight female, two male) participated in a single session lasting about 1.5 hours. All subjects were right-handed adults with a mean age of 24 years. None had a history of neurological disease or trauma. All subjects were naive with respect to the purpose of the experiment. The data from one subject were discarded due to serious EEG artifacts.

Apparatus and stimuli

Participants sat at a table facing a computer screen. On the table, between the front edge and the screen, was a keyboard with four keys arranged in a square. The stimulus on the screen consisted of an × symbol (1.2°×1.2° degrees of visual angle). In the two-choice condition, it was presented about 2.2° to the left or to the right of a central fixation point. In the four-choice condition, it was presented at a distance of about 2.2° from the fixation point in one of the four corners of a virtual square centered on the fixation point. The × was presented in yellow on a black background. Additionally, an auditory pacing signal composed of sine tones (600 Hz; 100 ms in duration) was presented at the start of each data collection run (see below) through the headphones at a comfortable loudness level (60 dBA). Stimulus presentation was controlled by a VSG 2/5 graphic card, installed on a personal computer (IBM-compatible). The computer controlled the experimental procedure and registered the key presses with a temporal resolution of 1 ms.

EEGs were recorded from 60 scalp positions covering the entire scalp using Ag/AgCl electrodes with an electrode affixed at Cz as reference. To control for ocular artifacts, the electro-oculogram (EOG) was recorded both vertically from above and below the left eye (vEOG) and horizontally from the outer canthi of both eyes (hEOG). EEG and EOG were amplified and filtered by two Synamps (Neuroscan) DC-amplifiers (0–100 Hz band-pass). EEG and EOG were digitized at 500 Hz and stored on a second PC (IBM-compatible) continuously. EEG was off-line re-referenced to linked mastoids and was corrected for eye movements (Gratton et al. 1983) and other artifacts.

Task

Each subject took part in four experimental conditions based on the crossing of two experimental factors: (1) *Action Condition*: stimulus-based versus intention-based action, and (2) *Choice Condition*: two- versus four-choice. There were 20 runs per condition, each consisting of 35 actions and 35 stimuli (SASASAS...). The stimuli were presented at a constant inter-stimulus interval (ISI) of 1200 ms. Each run began with ten pacing signals, with which participants had to synchronize their keypresses. Visual stimuli were presented 600 ms before and 600 ms after the pacing signal, respectively. Participants then continued pressing the keys without the pacing tones, attempting to maintain the target interval as accurately as possible for 25 further keypresses (continuation phase). Thus, in the continuation phase, the subject had to bisect the interval between two visual stimuli.

In the four-choice condition, subjects used all four keys, whereas in the two-choice condition subjects used only the lower two keys. Under the intention-based condition, the subject's action (which key was pressed) determined the position of the subsequent stimulus, whereas under the stimulus-based condition, subjects were instructed to react to the position of the previous stimulus with the appropriate keypress. The stimulus-response mapping was compatible in all conditions. That is, under inten-tion-based conditions a left/right keypress resulted in a stimulus appearing to the left or right of the fixation cross, and under stimulus-based conditions a stimulus presented at a given position had to be followed by a reaction on the spatially congruent key (for example, upper left key following an upper left stimulus). Under the intention-based condition, subjects were instructed to produce a random sequence of stimuli "as if they tossed a coin before each action". Figure 1 illustrates the two action conditions.

Overall, subjects performed 80 runs (each consisting of 35 actions and 35 stimuli). The two choice conditions were presented in blocks of 20 runs, which were presented in alternating order: four-choice alternating with two-choice. Half the subjects started with the four-choice condition, whereas the other half of the subjects started with the two-choice condition. Within each of these 20-run blocks, subjects alternated between ten runs under the intention-based condition and ten runs under the stimulus-based condition (intention-based, stimulus-based, inten-tion-based, stimulus-based, and so on). In the stimulus-based runs, the sequence of stimuli to which a given
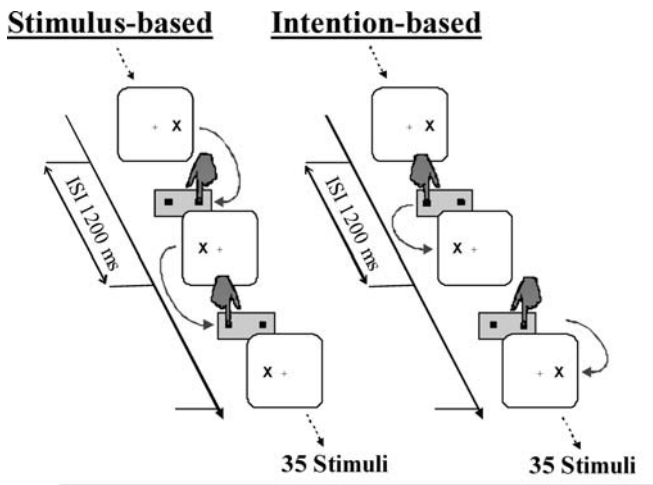
Stimulus-based   Intention-based

Fig. 1 Illustration of the two conditions

subject was required to respond in run *n*, was yoked to the sequences produced by the same subject in run *n*−2 of the intention-based runs. To prevent subjects from recognizing this yoking of runs, the sequence was presented in reverse order. Moreover, the position of the stimuli was "mirrored" such that a left stimulus produced in the intention-based run was presented on the right side in the stimulus-based run, and vice versa. Runs were cancelled and repeated when the timing of a keypress deviated by more than ±350 ms from the exact bisection point.

In 1% of all cases, catch trials were used to ensure that subjects attended to the stimuli in both conditions. Here stimuli were presented at an odd location. In the two-choice condition, the catch stimuli were presented slightly more (about 0.3°) to the left (in the case of a left stimulus) or slightly more to the right (in the case of a right stimulus). In the four-choice condition, catch stimuli were presented slightly more distant from the fixation point (about 0.3°). Subjects were instructed to stop tapping immediately when a catch stimulus was presented.

Behavioral data analysis

The first 15 intervals were discarded from the analysis (ten intervals in which the pacing signal was presented and the first five intervals in the continuation phase). Thus, the data analysis was based on the remaining 20 intervals of each run. The difference between the onset of each keypress and the required bisection time (600 ms before/after the onset of a stimulus) was computed for each keypress and averaged over the sequences. From these data, the average deviation (mean asynchrony) for each participant was computed per condition.

Electrophysiological data analysis

ERPs were calculated time-locked to both the onset of the stimulus and the onset of the response (the keypress). In

both cases, ERPs were computed relative to a 100 ms pre-stimulus baseline voltage level. P3 amplitude was measured as the mean amplitude at the electrodes CPz and Pz between 250 and 400 ms in the stimulus-locked averages. The amplitudes were entered into an ANOVA with the factors Action Condition (intention based versus stimulus based), Choice (two-choice versus four-choice) and electrode (CPz, Pz).

Response-locked ERP amplitudes (R-ERPs) were measured between 200 and 100 ms before movement onset at the electrodes Fz and FCz. An ANOVA including the factors Electrode (Fz, FCz), Action Condition (intention based versus stimulus based) and Choice (two-choice versus four-choice) was carried out.

Stimulus-locked event-related lateralizations (ERLs) of the EEG were calculated for two epochs by subtracting the EEG activity ipsilateral to an event from the activity recorded contralateral to the event:

$$
\begin{aligned}
\text{ERL(right event)} &= \text{ERP(left hemisphere)} \\
&\quad -\text{ERP(right hemisphere)} \\
\text{ERL(left event)} &= \text{ERP(right hemisphere)} \\
&\quad -\text{ERP(left hemisphere)} \\
\text{ERL} &= \text{ERL(right event)} \\
&\quad +\text{ERL(left event)}2
\end{aligned}
$$

(see Gratton et al. 1988). First, at electrode pairs P7/8, P3/4, and C1/2, early lateralization in the range of the N1 was measured as the most negative peak in the stimulus-coded lateralizations between 120 and 220 ms after stimulus onset. An ANOVA including the factors Electrode (P7/8, P3/4, and C1/2), Action Condition (intention-based versus stimulus-based), and Choice (two-choice versus four-choice) was carried out. Second, SLRP (stimulus-locked lateralized readiness potential) amplitudes were measured for the electrode pair FC3/FC4 between 230 ms and 360 ms after stimulus onset. An ANOVA including the factors Action Condition (intention based versus stimulus based) and Choice (two-choice versus four-choice) was also implemented.

The LRP proper was tested in the response-locked activity as the mean amplitude within the last 150 ms preceding the response at the electrode pair FC3/4.

Results and discussion

Behavioral results

The asynchronies (the temporal displacements of the actions relative to the target interval bisection values) were computed separately for the two action conditions and for the two choice conditions. Results consistently showed negative asynchronies, indicating that the keypresses systematically preceded the bisection point. A repeated measures analysis of variance (ANOVA) with the factors Action Condition (stimulus-based versus intention-based), and Choice (two-choice versus four-choice) revealed only

one significant effect, the main effect of Action Condition; $F_{(1,8)}=11.48$, $p<0.01$. Mean asynchronies were larger under the stimulus-based condition (−117 ms, se=18) than under the intention-based condition (−53 ms, se=15). Neither a main effect of choice nor an interaction of action condition by choice was observed.

Negative asynchronies are commonly found in synchronization experiments (Aschersleben and Prinz 1995). More importantly, our data are consistent with the perceptual attraction effect of Haggard et al. (2002).
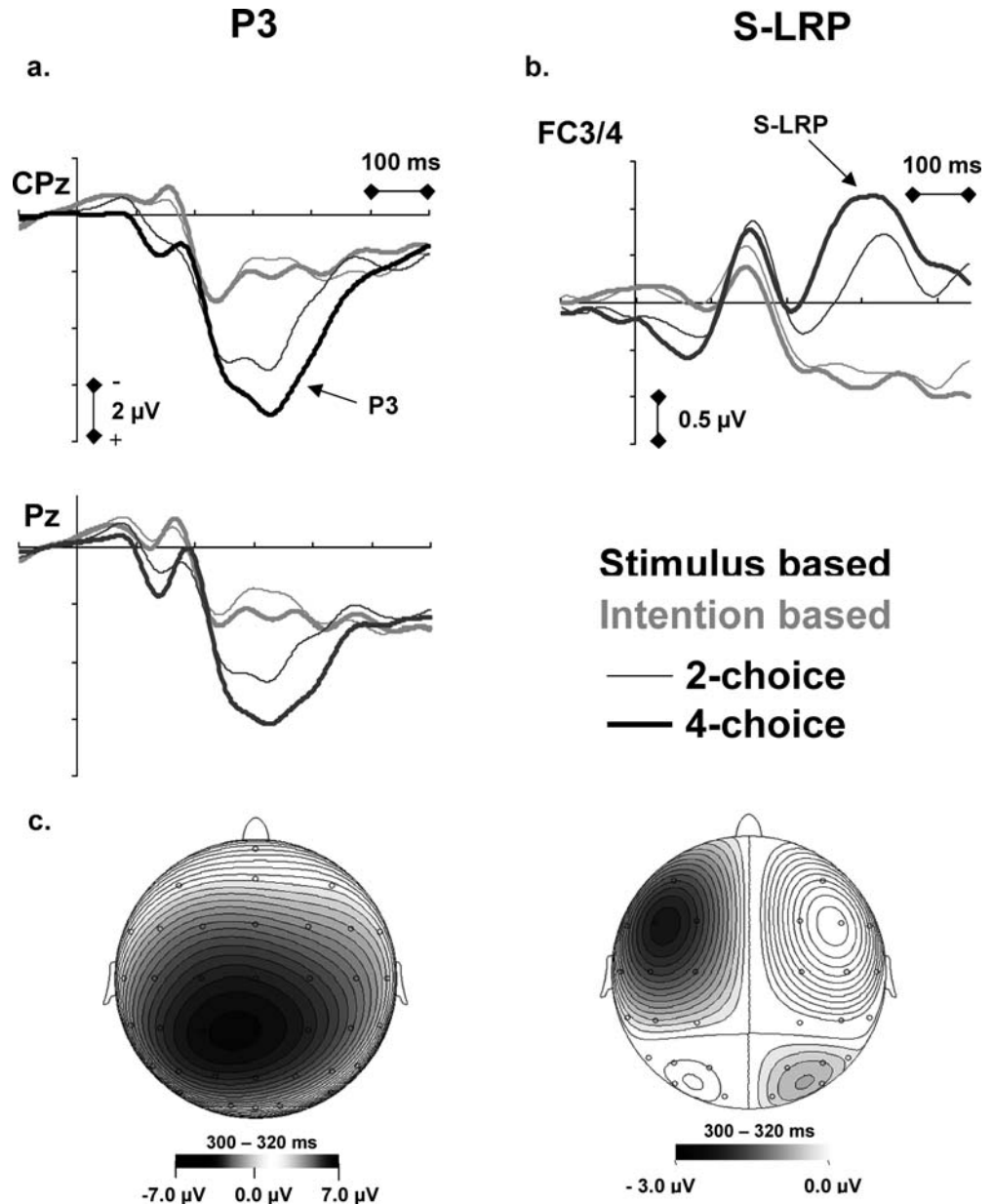
Electrophysiological results

In the analysis of the EEG data, we focused primarily on activations in the interval between stimuli and ensuing responses. Of course, our paradigm does not provide pure activations reflecting stimulus processing or response preparation in isolation. Rather, the electrophysiological activity recorded in the time window between S and R will always be a combination of activations due to stimulus- and response-related sources. The question we asked was: what are relative contributions of the stimulus- and response-related components for the stimulus- and intention-based actions?

Stimulus-locked and response-locked ERP components (S-ERPs and R-ERPs, respectively) were considered separately. With regard to the P3 complex (see Fig. 2, left panel), the main effects of Action Condition ($F_{(1,8)}=13.92$, $p=0.001$) and Choice (two-choice versus four-choice; $F_{(1,8)}=6.74$, $p<0.05$) were qualified by an interaction of Action Condition×Choice ($F_{(1,8)}=5.935$, $P<0.05$). These effects were associated with much larger P3 amplitudes for the stimulus-based conditions than for

Fig. 2a–c Stimulus-locked ERPs (P3, panel **a**) and stimulus-locked lateralized readiness potential (S-LRP, increased negativity at electrode sites contralateral to the side of stimulus presentation, panel **b**) in the two action and two choice conditions depicted for representative electrodes. A clearly pronounced centro-parietal P3 and a fronto-central lateralization are visible with stimulus-based actions only. Panel **c** shows topographic maps of the P3 (*left*) and the S-LRP (*right*)

the intention-based conditions. Moreover, only under the stimulus-based conditions did the selection difficulty affect P3 amplitudes (one-tailed t-tests four-choice versus two-choice: CPz: $t=3.39$, $df=8$, $p<0.01$; Pz: $t=2.88$, $df=8$, $p<0.01$). In fact, under the intention-based conditions, the P3 complex was virtually absent.

The P3 is the most prominent cortical potential that is sensitive to cognitive processing (Verleger 1988). In recent years, it has been argued that the P3 is composed of two subcomponents. For example, Falkenstein et al. (1994, see also Brookhuis et al. 1983; and Naylor et al. 1987) found two P3 subcomponents in a choice reaction task: an early P-SR and a late P-CR. In contrast to the P-SR (simple reaction), the P-CR (choice reaction), which has a parietal topography, is present in choice reaction tasks only. Falkenstein et al. consider the P-CR to be related to the response selection stage (to the assignment of specific response to specific stimuli). We believe that the P3 observed in the experiment reported above can also be interpreted along these lines; namely that it reflects the formation of the link between stimulus processing and response (see also Verleger et al. 2003). This view is supported by several findings. First, the P3 is present only under the stimulus-based conditions. Second, the topography of the P3 found in the present study fits very well with the topography of the P-CR. Third, both Naylor et al. (1987) and Falkenstein et al. (1994) reported an effect of response complexity on the latency of the "late P3" (two-choice versus four-choice in case of Falkenstein et al.). They considered this to corroborate the notion that the late positive complex is related to response selection. We did not find an effect of response complexity on the P3 latency. This is probably because the specific procedure of the present study (temporal bisection task) offset any latency difference between four-choice and two-choice runs. (Note that there is no effect of choice complexity on the bisection points.) However, our results show a clear effect of choice complexity on the amplitude of the P3. We suggest that this effect reflects higher processing demands on the reaction system that forms the link between stimulus processing and responding.

The support of the present data for the notion of two routes for action selection can be checked further by relating the stimulus-related activity to event-related lateralizations of the EEG. The right panel of Fig. 2 shows that, after early lateralizations (which we will discuss later), there is an increase of lateralization that begins about 200 ms after stimulus onset. This lateralization has a frontal topography (SLRP, stimulus-locked lateralized readiness potential). As for the P3, it is present only under the stimulus-based conditions and is affected by selection difficulty. That is, in the epoch between 200 ms and 400 ms after stimulus presentation, we observed two EEG components: a centro-parietal P3 and a fronto-central SLRP. Intriguingly both components occurred at about the same time, both were present only under the reaction conditions, and both showed a clear effect of choice complexity. The latter conclusions were supported by the relevant ANOVA, which showed a main effect of

Action Condition ($F_{(1,8)}=25.01$; $P<0.001$) which was qualified by an interaction of Action Condition×Choice ($F_{(1,8)}=6.26$, $P<0.05$). One-tailed t-tests (four-choice versus two-choice) confirm this pattern of results: stimulus-based condition: $t=2.38$, $df=8$, $p<0.05$; intention-based condition: $t=0.49$, $df=8$, $p>0.3$. We suggest that these two components reflect stimulus-driven processes that take effect whenever specific movements are to be carried out in response to specific stimuli. One might argue that they work hand in hand, with the parietal positivity being related to stimulus-related processing (for example stimulus evaluation) and the fronto-central LRP being associated with response-related processing (for instance, implementation of an appropriate response). However, the parietal positivity does not appear to be associated with specific response programming or recruitment of muscle groups, as discussed next.

EEG lateralizations over motor areas have often been considered to reflect processes, probably located in the primary motor cortex, which are closely linked to response activation and execution (Osman and Moore 1993; Praamstra et al. 1999; for a review see Eimer 1998). However, our paradigm differs in a critical respect from usual paradigms investigating the SLRP. Usually, subjects are required to respond as quickly as possible, such that overt response and SLRP occur at about the same time, which, in turn, accentuates its possible importance for motor activation and execution. In our tasks, by contrast, subjects were required to act 600 ms after stimulus presentation. Under the stimulus-based conditions, subjects performed the movements with an average negative asynchrony of about 115 ms (they responded about 485 ms after stimulus onset). However, the SLRP observed in the present experiment occurred between 200 and 400 ms after stimulus onset. Thus, the SLRP cannot be said to be closely related to response execution. Instead, it must reflect a preparatory process that is removed from the final build-up and release of motor activation. One might argue that this functional description does not fit with the usual notion that the LRP is generated by the primary motor cortex (Osman and Moore 1993; Praamstra et al. 1999). However, there is already some evidence that other cortical areas are involved in generation of the LRP. For example, Praamstra et al. (1996) suggested that the lateral premotor area contributes to the LRP in Parkinson's disease patients. It is tempting to speculate that activation of the lateral premotor system is also responsible for the stimulus-locked LRP observed here only under the stimulus-based conditions. This would fit with the two routes hypothesis outlined above. The LRP might reflect activation in lateral premotor areas, whereas the P3 might reflect the activity of parietal areas.

If we assume that the LRP observed in our study is indeed due to activation of the lateral premotor system, it is reasonable to ask why other experiments show lateralizations due to M1 activity while we claim that our experiment does not. One possible answer is that part of the lateralizations that we observed could be attributed to M1 activity, but this part occurs later and is time-locked

to the subjects' movements (response-locked LRP, see below).

Another aspect of the stimulus-locked lateralizations supports the idea of two routes for action selection. Figure 3 shows that increased negativity contralateral to the side of the stimulus presentation was observed simultaneously over sensory, parietal, and motor areas in the N1 range. All main effects were significant: Electrode ($F_{(2,16)}$=19.80, $p<0.001$), Action Condition ($F_{(1,8)}$=9.02, $p<0.05$), and Choice (not shown in the figure, $F_{(1,8)}$=9.84, $p<0.05$, with four-choice actions yielding larger amplitudes than two-choice actions). The main effects were accompanied by an interaction of Electrode×Action Condition that did not reach significance ($F_{(2,16)}$=2.37, $p=0.12$). However, t-tests confirmed the pattern of results shown in Fig. 3. The contrast stimulus-based versus intention-based actions was significant at electrode pairs C1/C2 (t=4.36, df=8, $p=0.001$) and P3/P4 (t=4.35, df=8, $p=0.002$), but failed to reach significance at electrode pair P7/P8 (t=0.53, df=8, $p=0.3$). Although this lateralized activity seems to be homogenous, there are good reasons to assume that asymmetries over sensory (P7/P8), parietal (P3/P4), and motor areas (C1/C2) reflect different functions within a network: Early lateralizations over sensory areas can be considered to reflect visual selection (N2pc, Praamstra and Oostenveld 2003). Early lateralizations over parietal areas can be considered to reflect activity of the superior parietal lobule that subserves the mapping of the visuo-spatial attributes onto motor responses (Iacoboni et al. 1996; see also Wascher et al. 1999). Asymmetries over motor areas (such as N2cc, Praamstra and Oostenveld 2003]) are considered to reflect visuo-spatial processing for response selection. Both the N2pc and the N2cc can be assumed to appear earlier, that is, in the N1 range (N1pc, N1cc), if unilateral stimuli are used, as in the present study (Shedden and Nordgaard 2001; see also Eimer 1996). According to Praamstra and Oostenveld, the dorsal premotor cortex is the most likely source of the N2 cc, being a motor area that is close to the executional level,

but is also known to exhibit visuospatial attention-related activity (Boussaoud 2001). In short, the widespread early asymmetries shown in Fig. 3 may reflect different aspects of automatic sensory-motor integration, viz visuo-spatial selection, S-R mapping processes, and response selection. The temporal coincidence of these components indicates that they evolve in parallel; that they operate on stimulus information that is accessed by all processes involved, rather than in a serial transmission from one stage to the other (see Praamstra and Oostenveld 2003). Importantly, in our results, early encoding of directional information, as indicated by asymmetries at the electrode pair P7/P8, did not differ between the two Action Conditions. This suggests that subjects attended to the stimulus in both conditions to an equal degree and that the system derives sensory directional codes automatically, independent of whether or not the stimulus is response-relevant. By contrast, asymmetries over parietal areas related to S-R mapping and response-related asymmetries over motor areas were pronounced for stimulus-based actions compared to intention-based actions, indicating that S-R mapping and response selection occurs only (or to a larger degree) if the stimuli are relevant for the upcoming movement. Thus, as with the P3 and the SLRP, the mode of movement seems to determine to what extent stimuli are processed right up until response activation. Moreover, as with the P3 and the SLRP, parietal and lateral premotor areas seem to be involved.

A clear difference between the two action conditions was also observed for the response-locked ERPs (R-ERPs) during the preparatory phase. The R-ERP was more negative for intention-based actions than for stimulus-based actions (see Fig. 4). The main effects of Action Condition ($F_{(1,8)}$=24.72, $p=0.001$) was qualified by an interaction of Action Condition×Choice ($F_{(1,8)}$=6.30, $P<0.05$). However, in contrast to the stimulus-locked ERPs, one-tailed t-tests contrasting four-choice versus two-choice in stimulus-based actions did not reach significance (Fz: t=1.38, df=8, $p>0.1$; FCz: t=1.07, df=8,
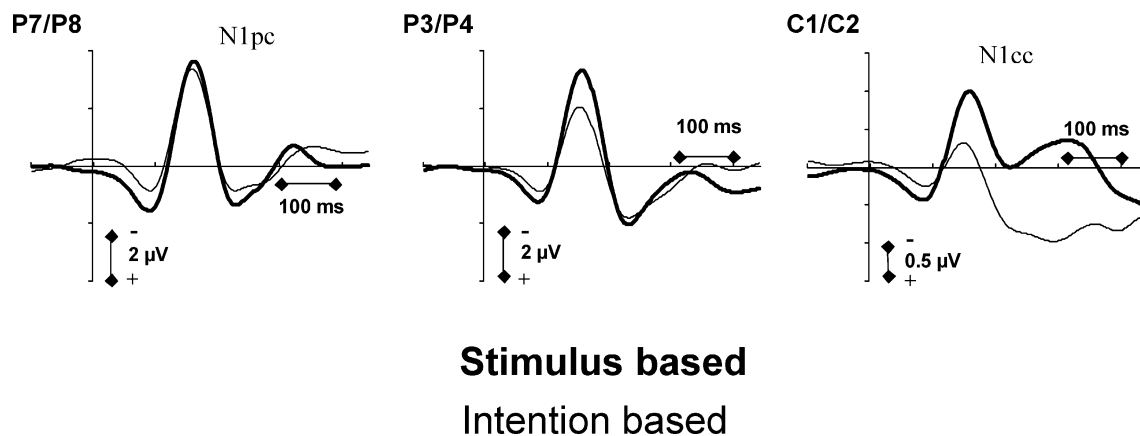

Stimulus based

Intention based

Fig. 3 Stimulus-locked event-related lateralizations of the EEG (increased negativity at electrode sites contralateral to the side of stimulus presentation) over the motor areas (C1/C2), parietal areas (P3/P4), and sensory areas (P7/P8). The early asymmetries reflect different aspects of automatic sensory-motor integration, viz visuo-spatial selection, S-R mapping processes and response selection. The results suggest that visuo-spatial selection takes place independent of whether or not the stimulus is response-relevant, whereas more response-related processes occur only if the stimuli are relevant for the upcoming movement
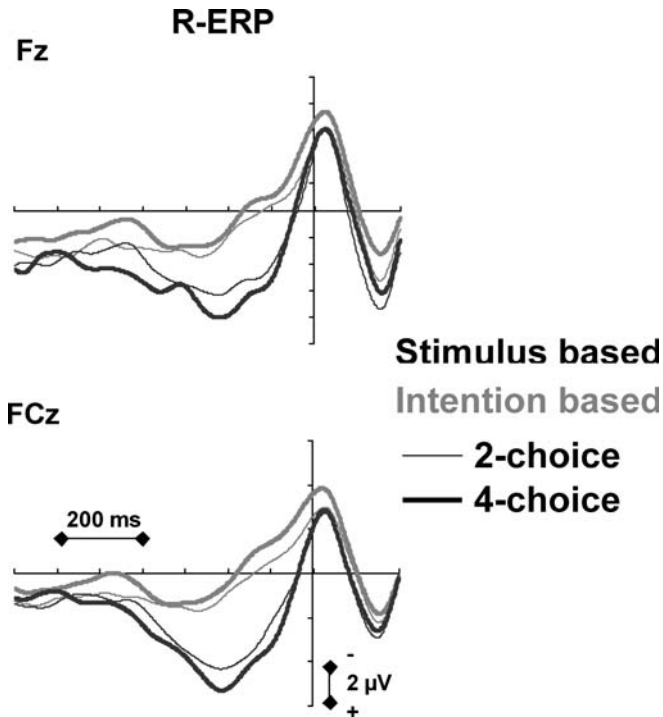
R-ERP

Fz

Stimulus based
Intention based

━━ **2-choice**
━━ **4-choice**

FCz

200 ms

2 µV

Fig. 4 Response-locked ERPs in the two action and two choice conditions depicted for representative electrodes. A slow negative shift is visible preceding the responses. This slow negative shift is larger with intention-based actions than with stimulus-based actions

$p>0.1$). Note that this component is not a readiness potential in the traditional sense, owing to the restricted pacing of the response and the short inter-response intervals used here. Nevertheless the R-ERP exhibits a slow negative shift preceding the response that might have some functional similarities to the traditional RP.

In summary, both stimulus- and response-locked ERP components showed a marked difference between preparing for an intention-based or a stimulus-based action. However, note that both ERP components were based on the very same EEG activity; it is only that this activity was analyzed in a stimulus-locked or response-locked fashion, respectively. Due to the similarity in ERP topography and amplitude for the two kinds of action, it is hard to assign the effect to either stimulus or response processing per se. However, there are good reasons to believe that both stimulus and response processing contribute to the observed activity. First, the more pronounced component structure in stimulus-locked averages (P3) is a clear sign of stimulus-related activity. Second, the central topography of the difference wave (not depicted) that is very similar to the topography of a regular readiness potential indicates that the need to intentionally plan the action under the intention-based condition is another cause of the ERP differences. Third, the finding that four-choice responses differed from two-choice responses only in the stimulus-locked activity (P3), not in the response-locked activity (R-ERP), clearly shows that the two components at least partly reflect different processes. Fourth, using a similar experimental paradigm, Keller and colleagues (submitted)

decoupled response- and stimulus-related activity by using both long (1600 ms) and short (1200 ms) ISIs (inter-stimulus intervals); in the experiment reported here, the ISI was 1200 ms. The reasoning for varying ISIs was as follows. For short ISIs, stimulus processing may still be very much in progress at the temporal bisection point (600 ms). In contrast, for long ISIs, stimulus processing should be less active for the last 200 ms before the bisection point (800 ms). Keller and colleagues found that the R-ERP difference between the intention-based and the stimulus-based condition was more pronounced at short than at long ISIs, indicating that stimulus-related processes contributed to the R-ERP differences in the 1200 ISI condition (and to a lesser degree in the 1600 ISI condition). However, they also found that, in the long ISI condition, activity occurring during the last 200 ms before movements was still larger for intention-based movements than for stimulus-based movements. Assuming that activity occurring during this time period is a relatively pure index of response-related processes, this can be taken as evidence for differences in response-related preparatory processes that lead to intention-based and stimulus-based actions. These arguments suggest that the observed activity in the present experiment reflects a mixture of both stimulus- and response-related processes.

In view of the differences between intention-based and stimulus-based activity, it is intriguing that specific motor preparation as reflected in the response-locked LRP remained essentially invariant under the stimulus-based and intention-based conditions. No differences were observed between the two action conditions over hand motor areas (see Fig. 5; effect of Action Condition: $F_{(1,8)}=0.58$). This suggests that different routes to action may result in the same motor processes, a conclusion
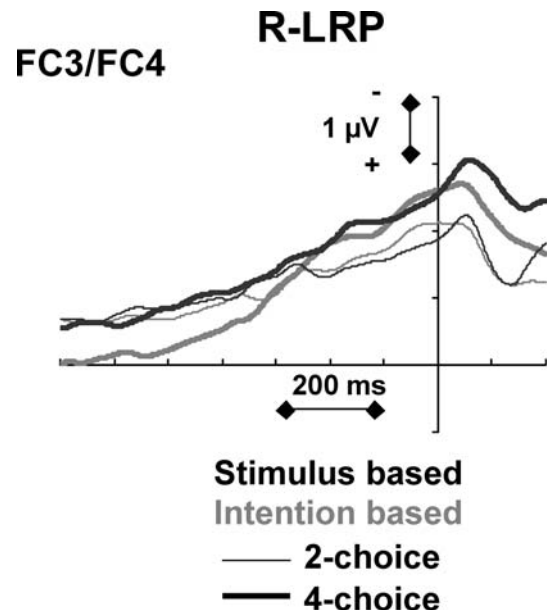
R-LRP

FC3/FC4

1 µV

200 ms

Stimulus based
Intention based

━━ **2-choice**
━━ **4-choice**

Fig. 5 Response-locked LRP (increased negativity at electrode site contralateral to the side of the response) in the two action and two choice conditions. There is apparently no difference in specific motor preparation between the tasks

reminiscent of Sherrington's (1906) well-known concept of the final common pathway and in accordance with the two routes hypothesis.

Conclusions

Taken together, the data from this study provide new insights into the functional signatures of intention-based and stimulus-based actions. These insights are most obvious if we relate our two dependent measures to each other. In the behavioral data, we found a temporal attraction effect, showing that the motor act was shifted toward the anticipated action-effect under the intention-based condition as compared to the stimulus-based action condition, where it was shifted towards the stimulus (see also Haggard et al. 2002 for a related finding). The EEGs confirmed two different modes of processing. In the reactive mode, processing worked in a stimulus-driven fashion, as demonstrated by various stimulus-locked EEG components. In this mode, stimulus- and attention-related processes (P3, N1pc) and response-related processes (S-LRP, N1cc) ensured that a given stimulus elicited an appropriate response. In the intention mode, response-locked ERPs (RP) showed that other cortical structures mediated the execution of voluntary or operant actions. Of course, the most tantalizing possibility is that the isolation of these other structures may point to the source of intentional control. Claiming that there is such a site or presuming its location would, of course, be premature, but the method introduced here might provide a way of pursuing this most elusive and, perhaps for cognitive neuroscience as a whole, most important question.

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