N400-like negativities in action perception reflect the activation of two components of an action representation

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The understanding of actions of tool use depends on the motor act that is performed and on the function of the objects involved in the action. We used event-related potentials (ERPs) to investigate the processes that derive both kinds of information in a task in which inserting actions had to be judged. The actions were presented as two consecutive frames, one showing an effector/instrument and the other showing a potential target object of the action. Two mismatches were possible. An orientation mismatch occurred when the spatial object properties were not consistent with a motor act of insertion being performed (i.e., different orientations of insert and slot). A functional mismatch happened when the instrument (e.g., screwdriver) would usually not be applied to the target object (e.g., keyhole). The order in which instrument and target object were presented was also varied. The two kinds of mismatch gave rise to similar but not identical negativities in the latency range of the N400 followed by a positive modulation. The results indicate that the motor act and the function of the objects are derived by two at least partially different subprocesses and become integrated into a common representation of the observed action.

Keywords: Event-related potentials; Action observation; Tool use; Mirror neurons; Language comprehension.

INTRODUCTION

Current accounts of action understanding rely on the idea that humans map observed actions on the representations they would use to perform the actions themselves. This process allows them to internalize the actions of others so that these actions can activate the same internal states that

would precede or follow them when actually performed (cf. Bach & Tipper, 2007; Barsalou, Niedenthal, Barbey, & Ruppert, 2003; Wilson & Knoblich, 2005).

Behavioral evidence for such a link between action and action perception comes from findings that humans have a tendency to imitate the actions of others, even when the actions are task-irrelevant (e.g., Bach, Peatfield, & Tipper, 2007; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Hommel, Müsseler, Aschersleben, & Prinz, 2001). On the neurophysiological level, neurons with so-called mirror properties have been discovered in the premotor and parietal cortices of the macaque monkey. Mirror neurons fire not only when the monkey performs a particular action, but also when it observes the action being performed by another creature (DiPellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; for similar data on humans, see Grèzes, Armony, Rowe, & Passingham, 2003; Manthey, Schubotz, & von Cramon, 2003; Buccino et al., 2001; Constantini et al., 2005).

The mirror neurons seem to represent actions in terms of viewpoint-independent features that are common to observed as well as produced actions, such as sounds (Kohler et al., 2002), action goals (Bekkering, Wohlschläger, & Gattis, 2002; Johnson-Frey et al., 2003), or the spatial relationship that is required for the actions to succeed (cf. Oztop and Arbib, 2002; see also Gallese, 2003). For example, for grasping, the hand's finger configuration, its orientation and grip aperture should match the corresponding features of the target object. These viewpoint-independent relational action features can be used to guide action production, but also allow an observed action to be identified (for a computational demonstration, see Oztop & Arbib, 2002).

These common representations for perception and action can explain how observers differentiate between the different motor acts they observe. However, mirror neurons are blind to the identity and function of the objects involved in the action (Jacob & Jeannerod, 2005; Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005), and fire even when actions on "meaningless" 3D-solids are observed. They therefore cannot account for how object use shapes action understanding. This limitation is crucial, because the outcomes of many actions depend heavily on the objects used, even when the motor acts involved are the same. Compare, for instance, inserting a credit card into a cash machine with inserting a ticket into a ticket canceller.

Evidence that humans have a dedicated system that links objects to possible functions comes mostly from lesion studies. Patients with damage to the temporal lobe and prefrontal cortex may perform the appropriate motor acts of everyday tasks, but use inappropriate instruments (e.g., brushing teeth with a comb; Ochipa, Rothi, & Heilman, 1989). They also exhibit impairments in selecting a typical target object for a given tool, or selecting tools with a similar function (Hodges, Spatt, & Patterson, 1999). The reverse pattern has also been observed. There are patients that can describe the function of a tool but cannot pantomime its usage (Buxbaum & Saffran, 1998). As of yet, imaging studies have failed to reveal a similar dissociation (e.g., Kellenbach, Brett, & Patterson, 2003; Boronat et al., 2005).

Recent studies have confirmed the use of functional information during action observation. When judging the appropriateness of motor acts, observers cannot ignore the function of the objects involved, even when the identity of the objects has no bearing on how the motor act is performed (Bach, Knoblich, Gunter, Friederici, & Prinz, 2005). Similarly, patients suffering from visual extinction can see an action instead of two objects in isolation, only if the objects are at the same time spatially and functionally appropriate for an action to be carried out with them (Riddoch, Humphreys, Edwards, Baker, & Wilson, 2003; for a similar result in healthy participants, see Green & Hummel, 2006).

Finally, the use of functional information in action perception has been demonstrated by studies using event-related potentials (ERPs). N400-like negativities are elicited when an object (or a gesture) with an inappropriate function is chosen for an everyday task (e.g., for shaving, a rolling pin was used instead of a razor, Sitnikova, Kuperberg, & Holcomb, 2003; see also Gunter & Bach, 2004). The N400-component is widely accepted as a measure of the difficulty of integrating a new stimulus into the surrounding semantic context (for a review, see Kutas & Federmeier, 2000), which suggests that knowledge about object function also provides a context during action observation.

The present study investigated the ERP-correlates of the processes that integrate the motor act and object function into a coherent representation of an observed action. We presented the

participants with static images frames of inserting actions and asked them whether the observed action was appropriate or not. The stimuli showed actions in mid-flight before they were fully executed. Such stimuli should be particularly effective in activating the mirror neurons because these neurons stop firing when an action's goal is reached (Rizzolatti, Fogassi, & Gallese, 2001). Static frames were used because, other than for movies, there is a clear onset for the stimuli. Yet they are processed just like full action displays (Stürmer, Aschersleben, & Prinz, 2000; Kourtzi & Kanwisher, 2000) and activate the mirror system (Johnson-Frey et al., 2003). A rating task in a prior study showed that our stimuli indeed strongly evoke the goal of the presented actions (Bach et al., 2005).

For each of the actions, the appropriateness of the motor act and the appropriateness of the object function were varied independently (see Figure 1 for examples). The appropriateness of the motor act was varied by manipulating the spatial relationship between the insert and the slot of the target object. For a motor act of insertion to succeed, both the insert and the slot must have identical orientations. With orthogonal orientations, the motor act is not successful (orientation mismatch). The appropriateness of object function was varied by manipulating the functional relationship between instruments and target objects. Some combinations of inserts and target objects were functionally related because the objects are usually used together to realize a prototypical action goal (e.g., key, keyhole), while others were not functionally related (functional mismatch; e.g., key, screw). Therefore, all in all, the actions could either be fully matching or they could contain one of three mismatches: functional mismatch, orientation mismatch, or double mismatch (orientation and functional mismatch). The participants pressed one key if the actions were fully matching and another key if the actions contained any mismatch.

This experimental design allowed us to dissociate the processing of the function of the objects from the processing of the motor act. Behavioral experiments using the same task and the same stimuli (Bach et al., 2005; Bach, Knoblich, Gunter, Friederici & Prinz, 2008) have shown that the difficulties of detecting orientation and functional mismatches are highly comparable (as measured by response times and
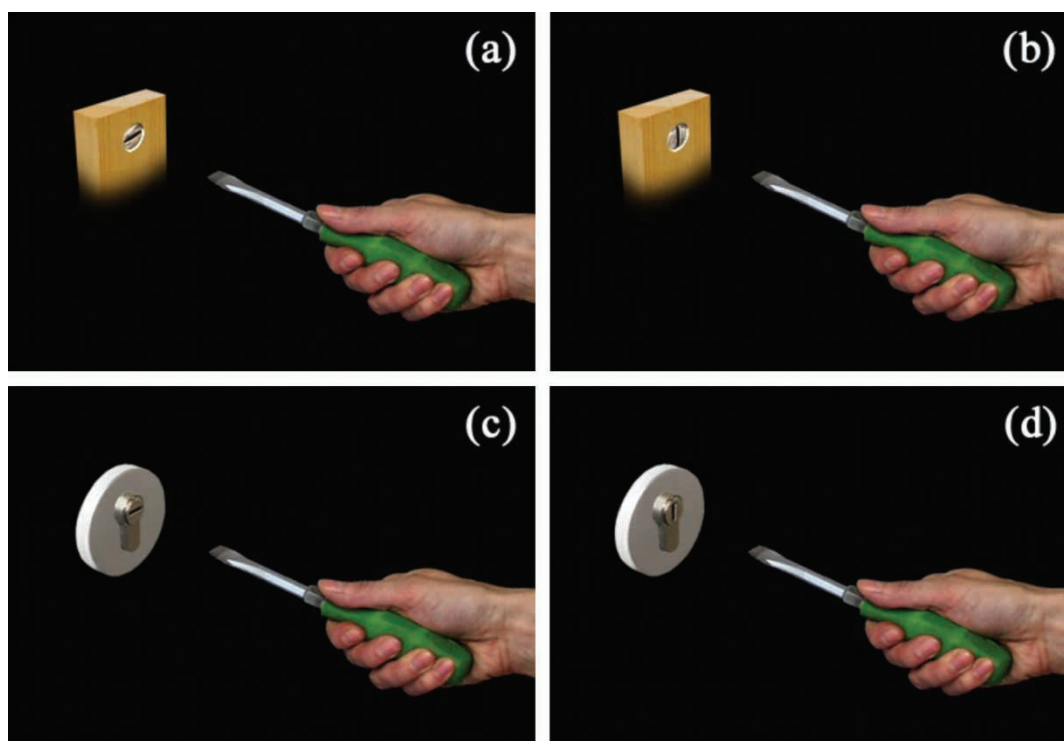
Figure 1. Examples for the stimuli used in the experiments: The two panels on the left (a, c) show actions in which the motor act was performed correctly, whereas the two panels on the right (b, d) contain orientation mismatches. The upper two panels (a, b) show functionally matching actions whereas the two lower panels (c, d) show functional mismatches.

error rates). Therefore, any differences between the ERPs elicited by the two mismatches are likely due to differences in the underlying processes, rather than to the general processing difficulty of the stimuli or the task.

On the basis of the prior research on action observation, we predicted that, relative to full matches, functional mismatches would evoke an N400-like negativity, and possibly a later positive modulation (e.g., Sitnikova et al., 2003; Gunter & Bach, 2004). To our knowledge, no prior studies have investigated orientation mismatches in action perception tasks. The main aim of the present study was to characterize the ERPs evoked by these mismatches, and to establish whether they reflect processes that are independent of those detecting functional mismatches.

Some predictions can be derived from the idea that the detection of orientation mismatches relies on the same parietal and motor structures that would also be recruited for the actual (or imagined) rotation of the observed objects. Tasks that require orientation judgments of external objects usually rely strongly on right hemisphere regions (e.g., Inoue, Yoshino, Suzuki, Ogasawara, & Nomura, 1998; Keehner, Guerin, Turk, Miller, & Hegarty, in press; Pegna et al., 1997; Turnbull, Beschin, & Della Sala, 1997). When, however, the same tasks are performed on observed body parts or tools, parietal and motor regions of the left hemisphere are involved to a greater extent (Amorim, Isableu, & Jarraya, 2006; Gerardine et al., 2000; Goldenberg, 2001; Petit, Pegna, Harris, & Michel, 2006; Overney, Michel, Harris, & Pegna, 2005). This double dissociation has been confirmed in lesion and imaging studies (Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Tomasino, Toraldo, & Rumiati, 2003).

These findings suggest that the left and right lateralized brain areas should also be involved when, in the present experiments, the motor act has to be derived from the orientations of the effectors/instruments and the target objects. To test this hypothesis, effector/instrument and target object were presented sequentially and the order of presentation was varied across experiments (Experiment 1: instrument before target object; Experiment 2: target object before instrument). As ERPs were time-locked to the presentation of the second stimulus, they reflected the processing of target objects in the first experiment, and the processing of effectors/instruments in the second experiment. If deriving the motor act relies on the same neuronal structures that are also used for (mental) object rotation, the analysis of the orientation of target objects should evoke a right lateralized response, whereas the spatial analysis of effectors/instruments should evoke a stronger left hemisphere response.

EXPERIMENT 1: EFFECTORS/ INSTRUMENTS PRECEDE TARGET OBJECTS

In the first experiment, the effector/instrument was presented before the target object. ERPs were time-locked to the presentation of the second stimulus. Therefore, they reflect the processing of the target object relative to the instrument/effector presented in the first frame. We expected that functional mismatches would elicit an N400-like negativity relative to full matches. For orientation mismatches relative to full matches, a right lateralized effect was expected, because the ERPs measured the processing of external objects. If the motor act and the function of objects are processed separately, the ERPs elicited by functional and orientation mismatches should differ in their scalp distributions, time course, or polarity.

Method

Participants

Thirty-two students (16 female) ranging in age from 22 to 39 years participated in the study and received approximately €25 for their participation. One participant was excluded due to excessive drifts and oculomotor artifacts. All participants were right-handed and had normal or corrected-to-normal vision. The key assignment was counterbalanced across participants.

Material

Thirty-two photographs made up the stimulus set. They subtended visual 3° vertically and 4° horizontally, given the viewing distance of 100 cm. Sixteen pictures showed a hand holding one of the eight different objects to be inserted (screwdriver, coin, key, trolley-pin, safety belt, knife, ticket, credit card) in two different orientations each (vertically or horizontally). The other half of the pictures showed the corresponding eight target objects with the respective openings (screw,

slot for the coin, lock, trolley, credit card reader, ticket canceller, knife holder, slot for safety belt), again in both orientations.

Out of these photographs, two-frame sequences were assembled. In total there were 64 different two-frame sequences. For each stimulus depicting a target object, there were four combinations with different objects to be inserted (see Figure 1 for examples). One combination created a match on both dimensions, so that the insert and the target opening matched functionally and with regard to their orientation. One combination created an orientation mismatch only, while the functional match was preserved. One combination created a functional mismatch only, while the match of the orientations remained intact. The last combination created a mismatch on both dimensions (double mismatch). The resulting stimulus matrix was completely balanced (see Table 1 for an example). Any target object or insert that created a mismatch in combination with a given stimulus was completely appropriate when combined with another one. Therefore, in both the first and the second frame, exactly the same stimuli were presented in each condition. Visual between-stimulus differences cannot affect the results.

Procedure and design

Participants were seated in a dimly lit room facing a color monitor at a distance of 100 cm. They received a short computer-driven instruction and some examples were given. After a short training phase of 24 trials the experiment proper started. It lasted for about 20 min and consisted of two blocks of 96 trials each. The blocks were separated by a short pause. The order of sequences in each block was randomized. Correct sequences were presented three times as often as each of the mismatches, to avoid response bias. Therefore, there were 96 correct sequences and 96 sequences containing a mismatch. Of these 96 mismatching sequences, 32 contained a functional mismatch, 32 contained an orientation mismatch, and 32 contained both mismatches.

The course of each trial was as follows: The first frame was displayed for 1000 ms, showing one of the eight instruments in one of the two orientations. After a blank of 300 ms, the second frame was presented for another 1000 ms, showing one of the eight target objects, again in one of the two orientations. Participants were instructed not to react as long as this frame was presented. Afterwards the question "Correct? Incorrect?" was displayed and participants gave their judgment of the sequence at leisure by pressing a key. If their judgment was correct, the next trial started after an intertrial interval of 200 ms. If they made an error or did not react within the given time interval of 1500 ms, an error-message was displayed.

Recordings and data analyses

The EEG was recorded using 56 Ag–AgCl electrodes embedded in an elastic cap (electro-cap) and was referred to the left mastoid. Offline, the ERPs were re-referenced to the mean of the left and right mastoids. Bipolar horizontal and vertical EOG was recorded. Electrode resistance was kept under 5 kΩ. The signals were recorded continuously with a band pass between DC and 70 Hz and digitized at 250 Hz. Average ERPs, starting 200 ms before and lasting 1000 ms after the start of each trial, were computed for each electrode position for each of the four conditions. Trials were only included in the average when the

TABLE 1
Example stimulus matrix for the different combinations of a ticket, a ticket canceller, a credit card, and a credit card reader.

Insert	Target object Orientation	Screwdriver Horizontal	Screwdriver Vertical	Key Horizontal	Key Vertical
Screwdriver	Horizontal	Full match	Orientation-only mismatch	Functional mismatch	Double mismatch
Screwdriver	Vertical	Orientation-only mismatch	Full match	Double mismatch	Functional mismatch
Key	Horizontal	Functional mismatch	Double mismatch	Full match	Orientation-only mismatch
Key	Vertical	Double mismatch	Functional mismatch	Orientation-only mismatch	Full match

The lines show the different instruments and the columns show the target objects with which they are combined. Each stimulus occurs once in all four conditions.

action was correctly judged. Approximately 8% of the trials were excluded from the averages due to ocular artifacts (EOG rejection ± 40 μV). The efficacy of the eye activity correction was checked by visual inspection, and trials still containing artifacts were rejected. Averages were aligned to a 200 ms pre-stimulus baseline.

To compare the effects elicited by the different conditions, latency windows were assigned to the evoked potentials on the basis of visual inspection of the grand averages, according to the following procedure. First, for each of the mismatching conditions latency windows were assigned separately. The start of a latency window was assigned when one of the electrodes FC5, FC6, CP5 and CP6 (nomenclature follows American Electroencephalographic Society, 1991) showed a difference of more than 1 μV between the fully matching and the respective mismatching condition (and continued to increase). The end of a latency window was assigned if at the four electrodes the difference was lower than 1 μV and continued to decrease. Statistical analyses were then carried out on the latency window with the maximum overlap between the three latency windows of the mismatching conditions. If there was no overlap, or the overlap did not include the interval in which the ERP effects of all three mismatching conditions reached their maximum, separate but identical statistical analyses were performed on each of the latency windows assigned to the three mismatching conditions.

The main analysis included the within-subject factors Function (functional mismatch present/not present) and Orientation (orientation mismatch present/not present). For the assessment of effects of scalp distribution, we differentiated between six anterior and six posterior regions of interest, each reflecting the collapsed data of two electrodes (ROIs, see Figure 2).[1] Three additional factors were entered into the analysis to account for differences between these ROIs. The first two of these factors were AntPos (anterior electrode sites/ posterior electrode sites, indicated by the first three

letters of the ROIs) and Hemisphere (left/right hemisphere, indicated by the fourth letter of the ROIs). The third factor was Eccentricity (outer, middle, inner electrodes, indicated by the final digit of the ROIs) to assess differences between broad and more central scalp distributions.

For significant effects of scalp distribution, we report the results of tests run on the data normalized according to McCarthy and Wood (1985). The Geisser-Greenhouse correction (Geisser & Greenhouse, 1959; Vasey & Thayer, 1987) was applied when evaluating effects with more than one degree of freedom. Unless otherwise stated, the significances reported for post-hoc analyses remained significant when corrected for multiple comparisons according to the Bonferroni-Holm procedure (Holm, 1979).
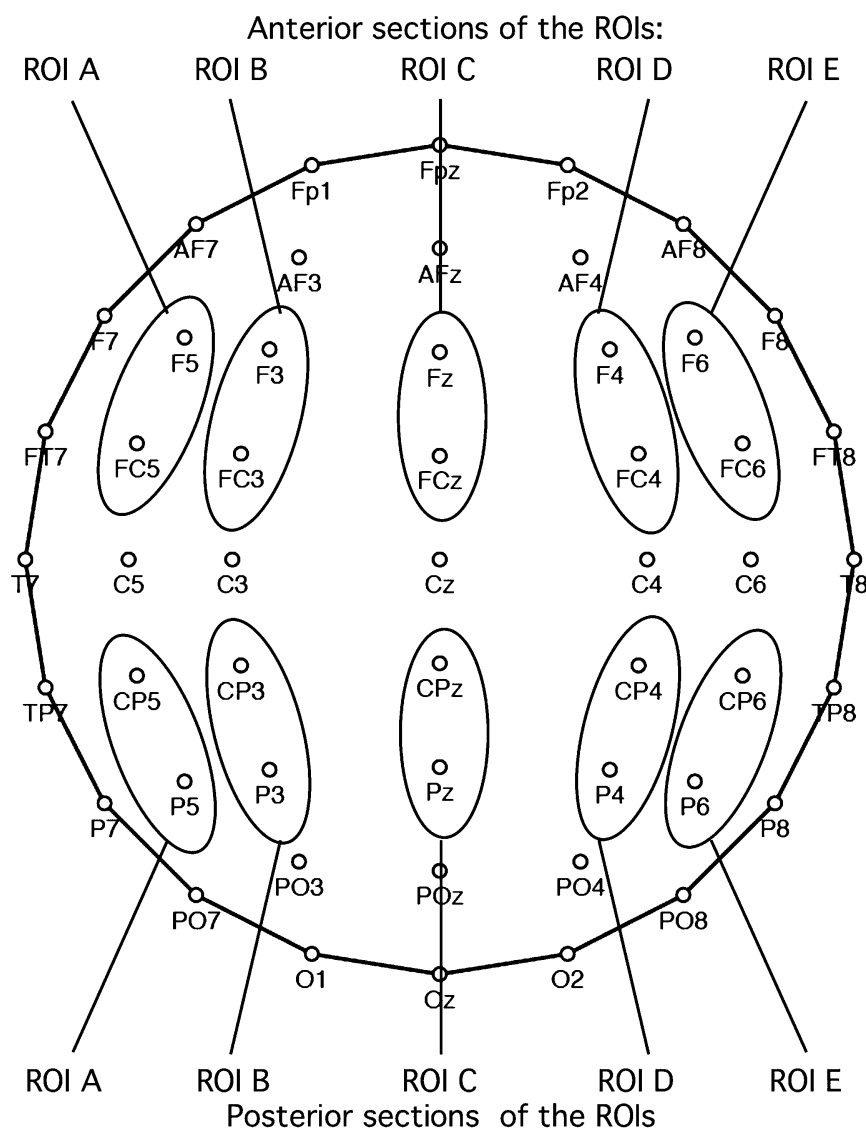
Results

Participants made almost no (0.2%) errors judging the fully matching condition. Orientation mismatches were incorrectly judged in 3% of the trials, functional mismatches were incorrectly judged in 0.6% of the trials and double mismatches were incorrectly judged in 2% of the trials. The differences between the conditions were not significant.

All three mismatches gave rise to a negativity followed by a positive modulation (see Figure 3 for the evoked potentials). To investigate the ERPs statistically, three latency windows were assigned to the evoked potentials on the basis of the visual inspection procedure described above.[2] This resulted in one latency window for the negative inflection (360–480 ms), capturing the negative effect evoked by orientation mismatches and also the interval in which the negativities following functional and double mismatches reached their maximum. Two latency windows

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[1] The ROIs were similar to our previous study on N400-effects in action/gesture perception (Gunter & Bach, 2004). Because our hypothesis primarily concerned laterality differences, there was no ROI for midline electrodes, but four ROIs capturing the most lateral electrodes were added (F7/F8, FT7/FT8, TP7/TP8, P7/P8). Note that the 10 chosen ROIs also include the electrode sites at which there were significant differences in the N400 time window in the other prior ERP-study on action observation (Sitnikova et al., 2003).

[2] To further validate the selection of latency windows, we split the analysis window into 40 ms intervals. For each of these intervals and for each of the ROIs, we investigated whether full matches and either of the single mismatches differed significantly (after correcting for multiple comparisons with respect to number of ROIs and latency windows). This showed that significant deviations of either single mismatching condition from the full matches indeed started to appear in the interval of 360 to 400 ms and remained significant throughout the selected latency window. One exception was the interval between 480 and 520 ms, which corresponded to the end of our first latency window (capturing the negative inflections) and the start of latency window 2 (start of the positive modulation).

Figure 2. The six anterior and posterior ROIs used for the analyses in each experiment.

were chosen to describe the positive modulations, one for the positivity evoked by orientation mismatches (500–700 ms), and one for the functional mismatches, which occurred around 100 ms later (600–800 ms). Identical repeated measurements ANOVAs were run for each of these intervals, as described above. Table 2 shows the results of this analysis. See Figure 4 for the scalp distributions of the differences between the fully matching and each mismatching condition in the three latency windows.

Latency window 1 (360–480 ms)

The ANOVA revealed main effects of Orientation and Function, confirming that both types of

mismatch elicit negative inflections. As indicated by the interactions of Orientation and Hemisphere and of Orientation and Eccentricity, the negativity elicited by orientation mismatches was right lateralized and was more pronounced over central electrodes.

The negativity elicited by functional mismatches had different scalp distributions on anterior and posterior ROIs (interactions of Function, Hemisphere and AntPos, and of Function, Eccentricity and AntPos). On posterior ROIs, a right lateralization, $F(1, 30) = 5.8$, $MSE = 0.4$, $p < .05$, with a central maximum was evident, $F(2, 60) = 7.6$, $MSE = 0.1$, $p < .005$, $\varepsilon = .672$, but neither effect was present on anterior ROIs (both, $F < 1$).
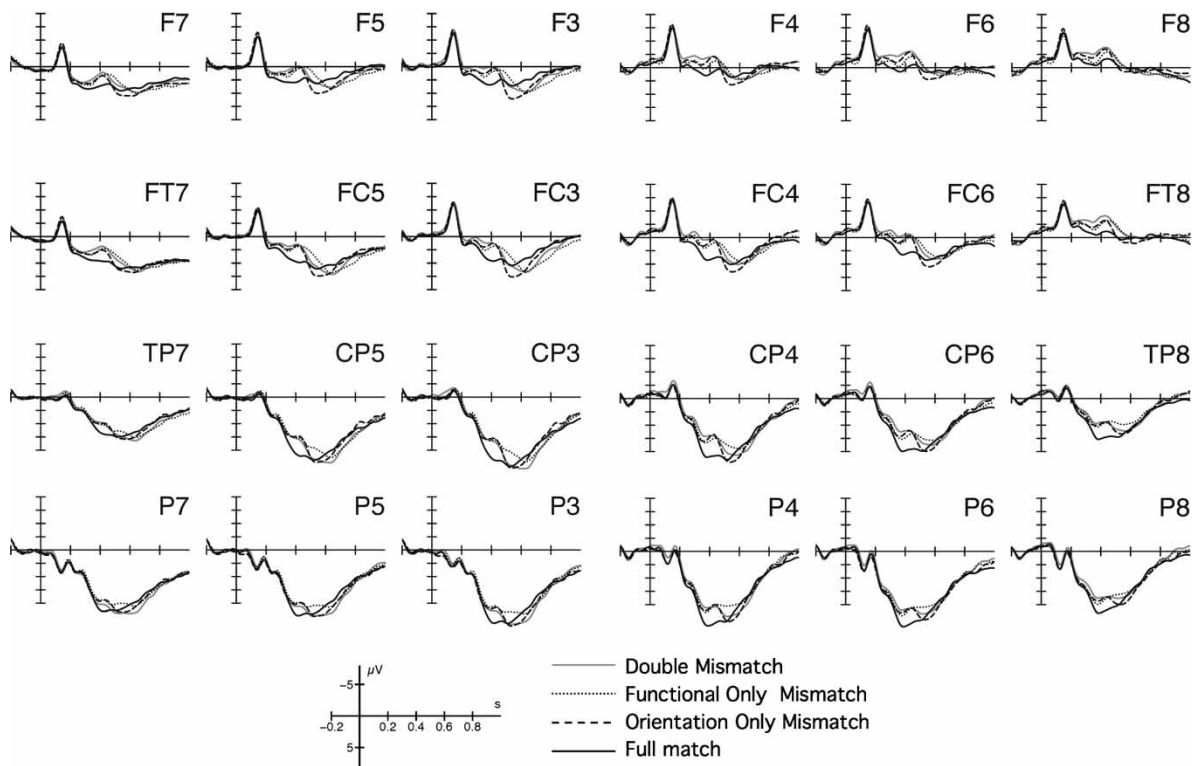
Figure 3. Evoked potentials for the three mismatching conditions plotted against the fully matching condition (Experiment 1).

It was important to investigate whether the scalp distribution of the negativity differed between orientation and functional mismatches.

Planned, pairwise comparisons with the factors Condition (orientation mismatches, functional mismatches), AntPos, Hemisphere and

TABLE 2
The results of the main analysis of Experiment 1 for the three latency windows (360–480, 500–700, 600–800).

Source	Df	*360–480*			*500–700*			*600–800*		
		F	*MSE*	*ε*	*F*	*MSE*	*ε*	*F*	*MSE*	*ε*
Orient	1, 30	13.0***	66.4		9.0**	73.0		4.9	71.3	
Orient*Hemi	1, 30	6.8*	0.7		0.6	1.7		0.1	3.1	
Orient*Hemi*AntPos	1, 30	1.0	0.2		0.1	0.7		0.1	1.8	
Orient*Eccen	2, 60	4.2*	0.3	.60	3.6*	0.6	.62	0.0	0.8	.66
Orient*Eccen*AntPos	2, 60	0.2	0.0	.83	1.7	0.7	.91	0.4	0.3	.98
Funct	1, 30	11.8***	80.9		0.2	80.4		10.7**	96.1	
Funct*Hemi	1, 30	1.5	0.6		3.1*	1.3		7.9**	2.8	
Funct*Hemi*AntPos	1, 30	8.4**	0.2		3.0*	0.5		1.3	1.2	
Funct*Eccen	2, 60	3.2*	0.4	.68	2.3	0.3	.75	10.6***	0.8	.76
Funct*Eccen*AntPos	2, 60	3.8*	0.1	.80	2.2	0.2	.80	2.8*	0.4	.82
Orient*Funct	1, 30	28.4***	39.2		0.1	67.0		1.1	67.6	
Orient*Funct*Hemi	1, 30	0.3	1.0		0.0	1.1		0.5	2.5	
Ori*Fun*Hemi*AntPos	1, 30	0.1	0.2		0.9	0.5		0.1	1.4	
Ori*Fun*Eccen	2, 60	4.5*	0.2	.70	0.3	0.4	.74	0.7	0.9	.76
Ori*Fun*Eccen*AntPos	2, 60	0.1	0.1	.76	2.0	0.1	.79	1.4	0.3	.78

Only those effects are listed that reached significances in at least one of the latency windows in one of the experiments and included either the factor Orientation or Function or both (*p <.1, **p <.01, ***p <.001). For effects concerning scalp distributions, the results are based on the correction of McCarthy & Wood (1985).
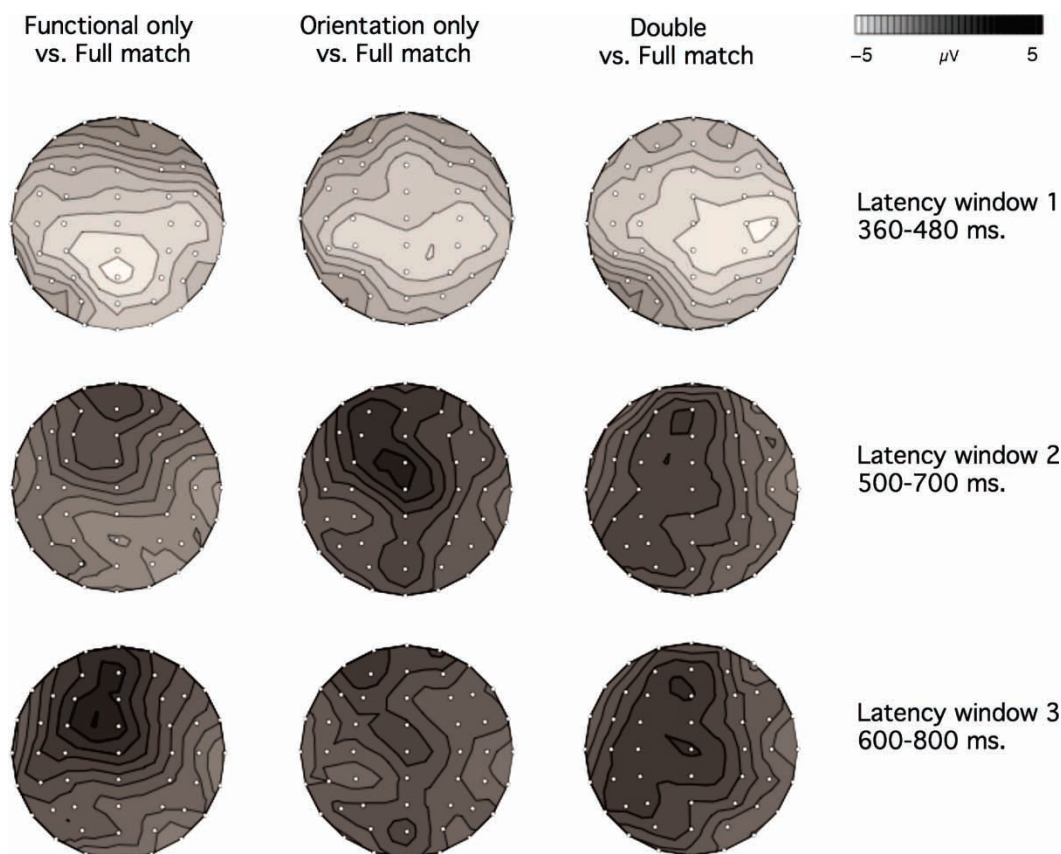
Figure 4. Scalp distributions of the voltage differences between the fully matching condition and the three types of mismatching conditions (from left to right: functional only mismatches, orientation only mismatches, double mismatches) in the three latency windows (from top to bottom: 360–480 ms, 500–700 ms, 600–800 ms) in Experiment 1.

Eccentricity did not reveal differences between orientation and functional mismatches, on either the anterior or posterior ROIs.

Finally, there was an interaction of Orientation and Function. This means that the negativity elicited by double mismatches was not an additive function of the two single mismatches. In particular, although both orientation and functional mismatches were more negative than the correct condition (orientation: $F(2, 30) = 32.0$, $MSE = 57.4$, $p < .001$; function, $F(2, 30) = 29.2$, $MSE = 73.9$, $p < .001$), double mismatches did not elicit a larger negativity than either of these single mismatches (both, $F < 1$).

A similar interaction was also present in the scalp distributions (interaction of Orientation, Function and Eccentricity). Again, even though both single mismatches showed a more central scalp distribution than full matches (orientation: $F(2, 60) = 9.0$, $MSE = 0.2$, $p < .005$; function, $F(2, 60) = 6.8$, $MSE = 0.2$, $p < .005$), the centrality of the

scalp distribution of double mismatches was not more pronounced than the scalp distribution of either of the two single mismatches (both, $F < 1$).

Latency window 2 (500–700 ms)

The main effect of Orientation confirmed that orientation mismatches evoked an overall positive modulation in this interval. Consistent with visual inspection, the positivity was centrally distributed (interaction of Orientation with Eccentricity). Neither effects of lateralization nor different scalp distributions on anterior or posterior ROIs were statistically detectable.

There was no similar overall main effect of function. Although also for functional mismatches a positivity started to emerge in this interval, a remainder of the preceding negativity was still present in the right hemisphere, as indicated by the interaction of Function and Hemisphere. As was the case for the negativity

in the first latency window, the amount of lateralization differed on anterior and posterior ROIs (interactions of Function, Hemisphere and AntPos). On posterior ROIs, the positivity was more negative on the right than on the left, $F(1, 30) = 12.0$, $MSE = 0.7$, $p < .005$. On anterior ROIs no effect of lateralization was detectable, $F(1, 30) = 1.19$.

As before, we investigated whether these lateralization effects at posterior ROIs differed between conditions. Functional mismatches, $F(1, 30) = 5.2$, $MSE = 1.0$, $p < .05$, and double mismatches, $F(1, 30) = 8.9$, $MSE = 0.7$, $p < .01$, showed this lateralization when compared to full matches, but orientation mismatches did not ($F < 1$). Double mismatches showed a stronger lateralization than orientation mismatches, $F(1, 30) = 8.1$, $MSE = 0.4$, $p < .01$, but for functional mismatches this difference to orientation mismatches was not significant, $F(1, 30) = 2.2$, $MSE = 1.1$, $p < .15$.

Latency window 3 (600–800 ms)

This latency window captures the positive modulation elicited by functional mismatches, but the positivity elicited by orientation mismatches had already started to disappear. Consistently, no effect of orientation mismatches was detectable in this interval: There was no main effect of Orientation, and Orientation did not interact with Function or with any factor describing the scalp distribution.

There was, of course, a main effect of Function, confirming the positivity elicited by functional mismatches. It had a different scalp distribution on anterior and posterior ROIs (interactions of Function and Eccentricity and of Function, Eccentricity and AntPos). Post-hoc analyses showed that the effect had a central scalp distribution on anterior ROIs, $F(2, 60) = 11.2$, $MSE = 0.7$, $p < .001$, $\varepsilon = .74$, but less so on posterior electrode sites, $F(2, 60) = 3.0$, $MSE = 0.5$, $p < .08$, $\varepsilon = .69$; not significant when corrected for multiple comparisons.

As before, the functional positivity was more negative on the right than on the left (interaction of Function and Hemisphere), indicating that a remainder of the preceding negativity was still present. This right lateralization was present when functional mismatches were compared to full matches, $F(1, 30) = 7.8$, $MSE = 3.5$, $p < .01$, and to orientation mismatches, $F(1, 30) = 4.3$, $MSE = 3.2$, $p < .05$, but not for the comparison

of orientation and full matches, $F(1, 30) = 1.1$. It was also marginally significant for the comparison of double mismatches and full matches, $F(1, 30) = 3.4$, $MSE = 2.7$, $p < .08$. Thus, even in this latest latency window a remainder of the preceding negativity was present for functional and double mismatches, but not orientation mismatches.

Discussion

Both functional and orientation mismatches gave rise to a negativity followed by a positive modulation. The negativity elicited by functional mismatches was similar to the N400 component usually observed for semantic mismatches (Van Petten, 1995; Kutas & Federmeier, 2000), with regard to both latency and scalp distribution of pictorial stimuli (West & Holcomb, 2002). In particular, a slight right lateralized distribution has often been observed before (Kutas & Hillyard, 1984). An N400-like negativity for functional mismatches was predicted from prior research. It indicates that the functional mismatches in the action snapshots of the present study evoked very similar brain responses as mismatches in actions that were fully executed and presented as movies (Sitnikova et al., 2003).

Interestingly, a very similar negativity–positivity pattern was also observed for orientation (and double) mismatches. This similarity might indicate a similarity of the underlying processes, or that both kinds of mismatches are detected on the basis of the same action representation. Consistent with this view, the negativities in the two conditions were not independent of one another. In contrast to what would have been expected if both negativities reflected independent processes, the negativity elicited by double mismatches was not larger than the negativities elicited by the single mismatches. Although it is premature to provide a specific interpretation for this interaction, it indicates that the processes detecting both kinds of mismatch operate on overlapping representations.

Other aspects of the findings indicated that the processes were at least partially different. First, the observed right lateralization of orientation mismatches relative to full matches was predicted from previous findings, demonstrating that spatial judgments of objects are predominantly carried out in the right hemisphere (e.g., Inoue et al., 1998, Pegna et al., 1997, Turnbull et al., 1997). For

functional mismatches, the right lateralization was less pronounced and restricted to posterior electrode sites. However, these differences must be interpreted with caution because they were not significant when the negativities elicited by functional and orientation mismatches were directly compared.

Second, the two mismatch effects also followed different time courses. The negativity following functional mismatches lasted longer than the negativity elicited by orientation mismatches. In the second latency window (500–700 ms), the negativity elicited by orientation mismatches had already disappeared and was replaced by a positive modulation. For functional mismatches, a remainder of the negativity was still present in the right hemisphere, where the negative modulation was also the strongest in the first latency window (360–480 ms). Even in the last latency window (600–800 ms), the positive modulation evoked by functional mismatches was still more negative in the right than in the left hemisphere. Because the effects of orientation and functional mismatches were of equal peak amplitude in the first latency window, and because the detection times and difficulties were comparable (e.g., Bach et al., 2005), the difference in time course suggests that the underlying processes are at least partially different.

Interestingly, this right lateralization could also be confirmed for double mismatches, indicating that a remainder of the right lateralized negativity elicited by functional mismatches was also present for double mismatches.

EXPERIMENT 2: TARGET OBJECTS PRECEDE EFFECTORS/INSTRUMENTS

In this experiment, the target object was presented before the effector/instrument. ERPs were time-locked to the presentation of the second stimulus. Therefore, they now reflect orientation and functional processing of the effector/instrument relative to the target object presented in the first frame. For functional mismatches, we expect an effect similar to Experiment 1. However, now, a left lateralization for orientation mismatches was predicted for orientation mismatches. The reason is that studies on the spatial manipulation of body parts have revealed a stronger involvement of the left

hemisphere than the spatial manipulation of external objects.

Method

Participants

Thirty-two German students (16 female) ranging in age from 20 to 30 years participated in the study and received approximately €25 for their participation. None of them had participated in Experiment 1. One participant was excluded for excessive drifts. All participants were right-handed and had normal or corrected-to-normal vision. The key assignment was counterbalanced across participants.

Material

The material was identical to that of the previous experiment.

Procedure and design

The experimental setup was identical to that of the previous experiment. The course of each trial was also identical to the previous experiment, with the exception that the target objects were now shown in the first frame and the effectors/instruments in the second.

Recordings and data analyses

The recordings were carried out as in the previous experiment. Latency windows were assigned according to the procedure described in Experiment 1.

Results

Participants committed 3% errors judging the matching condition. Orientation mismatches were incorrectly judged in 5% of the trials, functional mismatches were incorrectly judged in 4% of the trials and double mismatches were incorrectly judged in 3% of the trials. There were no significant differences between the conditions.

As can be seen from Figure 5, all three mismatches again gave rise to a negativity followed by a positive modulation. To investigate the ERPs statistically, three latency windows
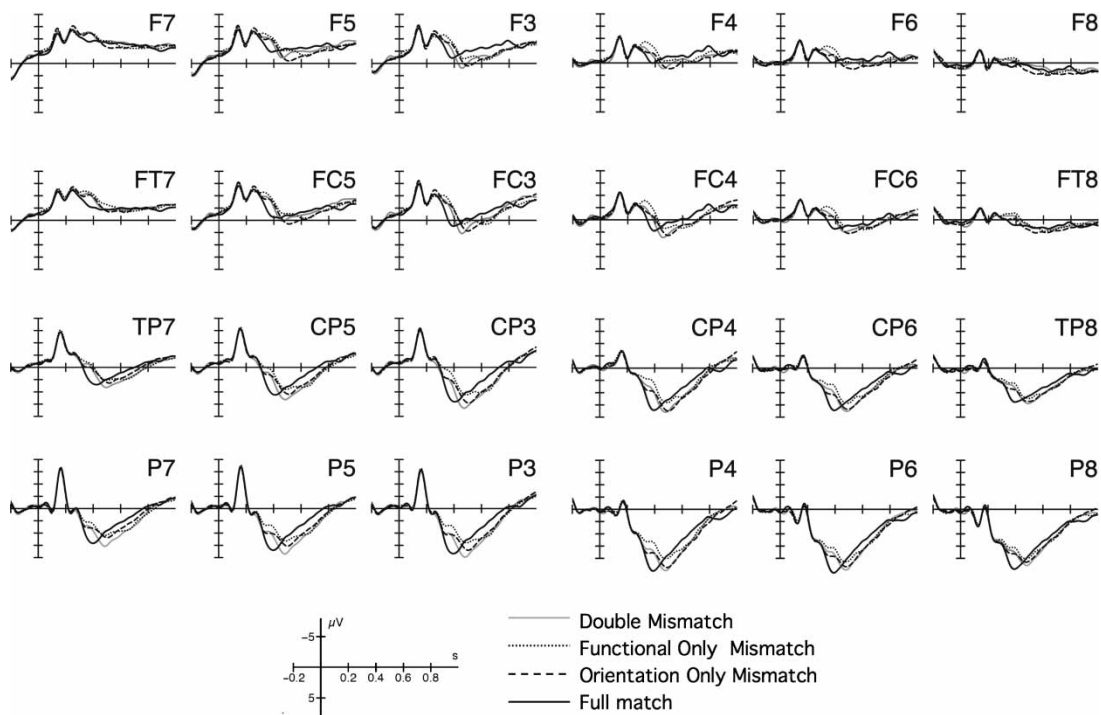
Figure 5. Evoked potentials for the three mismatching conditions plotted against the fully matching condition (Experiment 2).

were assigned to the evoked potentials according to the procedure described above.[3] There was again one latency window that captured the negativities elicited by orientation, functional and double mismatches (320–440 ms). In the present experiment it was not strictly necessary to have two latency windows to describe the positive effects, because there was considerable overlap of the latency ranges in which the effects in the mismatching conditions reached their maximum. Still, two separate latency windows with identical relative timings and durations as in Experiment 1 were used in order to obtain comparable results between the experiments (450–650 ms, 550–750 ms). Table 3 shows the results of these ANOVAs carried out for each of the latency windows. Figure 6 shows the scalp distributions of the differences between the fully matching and each mismatching condition in the three latency windows.

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[3] The selection of the latency windows was again validated with the procedure described in footnote 1. After adjusting for multiple comparisons, significant differences started to appear after 320 ms and remained present in all 40 ms intervals with the exception of the interval between 440 and 480 ms, which again corresponded to the end of our first latency window and the start of latency window 2.

Latency window 1 (320–440 ms)

Functional mismatches again gave rise to a negative inflection, as indicated by the main effect of Function. Its scalp distribution differed between anterior and posterior ROIs (interaction of Function, Eccentricity and AntPos), being centrally distributed on posterior ROIs, $F(2, 60) = 4.3$, $MSE = 0.2$, $p < .06$, $\varepsilon = .585$, but not on anterior ROIs ($F < 1$).

There was no main effect of Orientation, but an interaction of Function and Orientation. To further investigate this interaction, we compared full matches with each of the mismatching conditions. All mismatches gave rise to a negative inflection (all, $p < .001$) compared to full matches. It was larger for functional mismatches than for orientation mismatches, $F(1, 30) = 8.5$, $MSE = 72.8$, $p < .05$, and double mismatches, $F(1, 30) = 9.8$, $MSE = 67.3$, $p < .005$. Orientation and double mismatches did not differ statistically.

The interaction of Orientation, Function and Eccentricity indicated that the conditions differed in how pronounced the central scalp distribution was. To investigate these differences, separate pairwise comparisons between the three mismatching conditions and the fully matching condition were run. The factors were Condition

TABLE 3
The results of the main analysis of Experiment 2 for the three latency windows (320–440, 450–650, 550–750).

Source	Df	320–440			450–650			550–750		
		F	*MSE*	*ε*	*F*	*MSE*	*ε*	*F*	*MSE*	*ε*
Orient	1, 30	1.5	95.9		18.8***	80.1		10.1*	73.4	
Orient*Hemi	1, 30	2.7	0.4		0.7	0.8		0.0	2.0	
Orient*Hemi*AntPos	1, 30	2.5	0.2		0.2	0.4		0.0	1.2	
Orient*Eccen	2, 60	2.2	0.2	.61	12.9***	0.5	.61	10.1***	0.6	.64
Orient*Eccen*AntPos	2, 60	0.0	0.1	.80	0.4	0.1	.76	0.0	0.2	.78
Funct	1, 30	22.7***	97.9		0.5	111.9		4.1*	111.3	
Funct*Hemi	1, 30	0.1	0.6		2.7	0.8		5.3*	1.6	
Funct*Hemi*AntPos	1, 30	.01	0.2		3.1*	0.4		5.2*	0.7	
Funct*Eccen	2, 60	0.4	0.5	.56	3.6*	0.5	.59	4.8*	0.6	.64
Funct*Eccen*AntPos	2, 60	6.3**	0.1	.93	13.2***	0.1	.85	9.4***	0.2	.88
Orient*Funct	1, 30	45.1***	51.6		1.1	75.4		5.8*	77.6	
Orient*Funct*Hemi	1, 30	2.1	0.9		0.7	1.0		0.0	1.7	
Ori*Fun*Hemi*AntPos	1, 30	0.0	0.1		0.5	0.3		0.0	0.6	
Ori*Fun*Eccen	2, 60	24.8***	0.3	.67	2.8*	0.4	.66	3.5*	0.8	.65
Ori*Fun*Eccen*AntPos	2, 60	1.4	0.1	.85	0.1	0.1	.92	0.1	0.2	.93

Only those effects are listed that reached significance in at least one of the latency windows in one of the experiments and included either the factor Orientation or Function or both (*$p < .1$, **$p < .01$, ***$p < .001$). For effects concerning scalp distributions, the results are based on the correction of McCarthy & Wood (1985).

(full matches, orientation mismatches, functional mismatches, or double mismatches) and Eccentricity. Compared to full matches, both orientation mismatches, $F(2, 60) = 5.6$, $MSE = 0.3$, $p < .05$, $ε = .60$, and functional mismatches, $F(2, 60) = 19.3$, $MSE = 0.3$, $p < .001$, $ε = .60$, had a more pronounced central scalp distribution, but double mismatches did not ($F < 1$). Importantly, the central scalp distribution was more pronounced for functional than for orientation mismatches, $F(2, 60) = 6.5$, $MSE = 0.2$, $p < .01$, $ε = .64$.

Analogous pairwise comparisons were also run to investigate the interaction of Function, Orientation and Hemisphere that was significant after the normalization procedure of McCarthy and Wood (1985) was applied, $F(1, 30) = 5.2$, $MSE = 0.6$, $p < .05$. Orientation mismatches and full matches differed in their lateralization, $F(1, 30) = 9.1$, $MSE = 0.5$, $p < .005$. This was consistent with visual inspection, according to which orientation mismatches gave rise to a left lateralized negativity. No hemispheric asymmetries were apparent for the comparison of functional or double mismatches with the fully matching condition (both, $F < 1$). The direct comparison of orientation mismatches with functional mismatches revealed hemispheric asymmetries for the uncorrected tests, $F(1, 30) = 4.8$, $MSE = 6.9$,
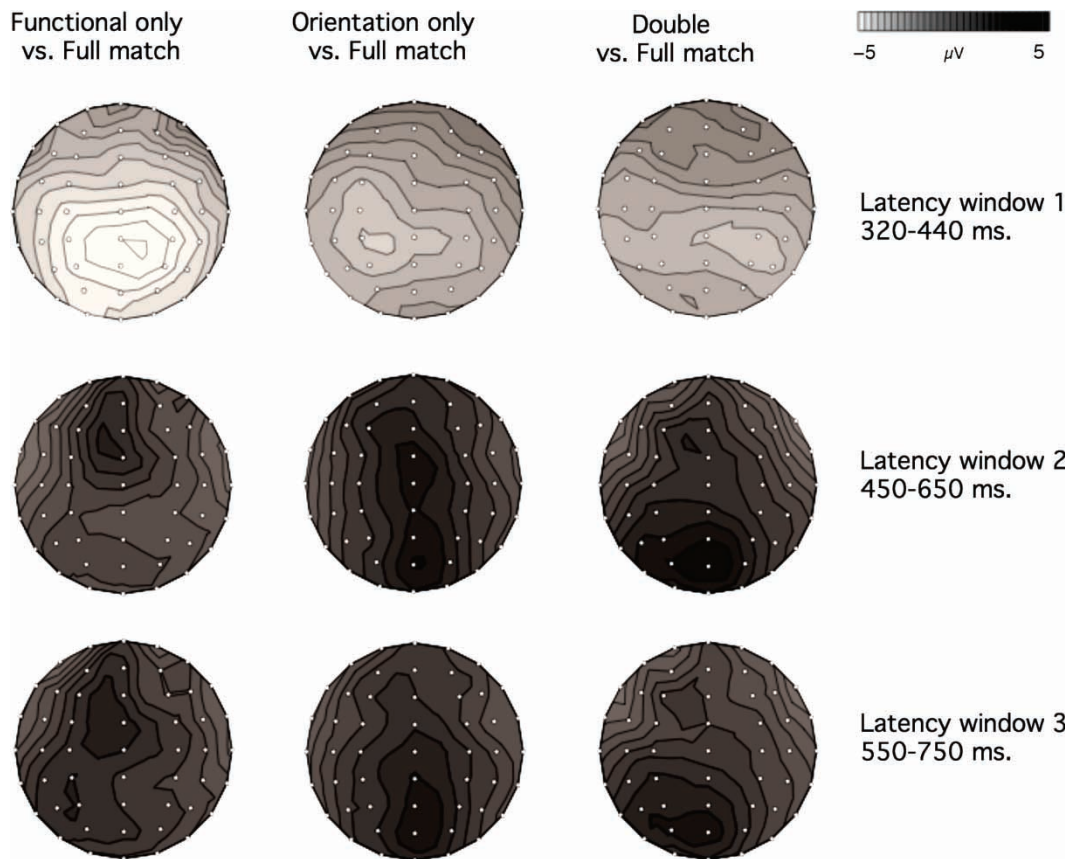
$p < .05$, but not for the correction of McCarthy and Wood, $F(1, 30) = 1.99$.

Latency window 2 (450–650 ms)

As in Experiment 1, there was a main effect for Orientation confirming the positive modulation elicited by orientation mismatches. As before, it was centrally distributed (interaction of Orientation and Eccentricity), and showed neither differences between anterior and posterior ROIs nor a lateralization.

Although there was no main effect of Function, there were interactions of Function and Eccentricity, and of Function, AntPos and Eccentricity, indicating different scalp distributions over anterior and posterior ROIs. The conditions containing a functional mismatch elicited a positive modulation with a central scalp distribution on anterior ROIs, $F(1, 30) = 10.59$, $MSE = 0.3$, $p < .001$, $ε = .71$, but a flat distribution on posterior ROIs ($F < 1$). This was consistent with visual inspection according to which the positive modulation after functional mismatches emerged first over anterior central electrodes.

Finally, there was an interaction of Function, Orientation and Eccentricity. Although all mismatching conditions had a more pronounced central distribution than full matches (all, $p < .01$), they did not differ from each other.

Functional only
vs. Full match

Orientation only
vs. Full match

Double
vs. Full match

−5   μV   5

Latency window 1
320–440 ms.

Latency window 2
450–650 ms.

Latency window 3
550–750 ms.

Figure 6.   Scalp distributions of the voltage differences between the fully matching condition and the three types of mismatching conditions (from left to right: functional only mismatches, orientation only mismatches, double mismatches) in the three latency windows (from top to bottom: 320–440 ms, 450–650 ms, 550–650 ms) in Experiment 2.

Latency window 3 (550–750 ms)

As in the previous latency window, there was a main effect of orientation mismatches. The positive modulation elicited by orientation mismatches was again centrally distributed (interaction of Orientation and Eccentricity) without evidence of lateralization.

A main effect of Function was also obtained. This replicates the finding from Experiment 1 that the positivity elicited by functional mismatches was fully present only in the latest latency window. As always, its scalp distribution differed between anterior and posterior ROIs (interactions of Function and Hemisphere, of Function, AntPos and Hemisphere, of Function and Eccentricity, and of Function, AntPos and Eccentricity). On anterior ROIs, the positivity was centrally distributed, $F(2, 60) = 12.1$, $MSE = 0.4$, $p < .001$, $\varepsilon = .77$, without evidence of lateralization ($F < 1$). On posterior ROIs, the positivity had a flat distribution ($F < 1$)

that was more negative on the right than on the left, $F(1, 30) = 18.4$, $MSE = 0.8$, $p < .001$.

As before, we investigated whether the lateralization over posterior ROIs was detectable for both conditions containing function mismatches. It was present when the fully matching condition was compared to double mismatches, $F(1, 30) = 10.6$, $MSE = 1.1$, $p < .005$, and to functional mismatches, $F(1, 30) = 5.9$, $MSE = 1.1$, $p < .05$, but not when it was compared to orientation mismatches ($F < 1$). In addition, the lateralization of orientation mismatches differed significantly from the lateralization of functional mismatches, $F(1, 30) = 4.8$, $MSE = 0.8$, $p < .05$, and double mismatches, $F(1, 30) = 11.4$, $MSE = 0.7$, $p < .005$.

Finally, there were interactions of Orientation and Function and of Function, Orientation and Eccentricity. Even though all mismatching conditions showed an overall difference when compared to full matches (all, $p < .01$), their amplitudes did not differ from each other. Similarly, even

though all mismatching conditions had a more pronounced central scalp distribution than full matches (all, $p < .01$), there were no differences in Eccentricity between the mismatching conditions.

Discussion

Experiment 2 replicated the main findings of Experiment 1. Orientation and functional mismatches elicited a negative inflection followed by a positive modulation. Again, the two processes were not independent of one another. The negativity elicited by double mismatches was not an additive effect of the negativities elicited by the two single mismatches.

Importantly, in the present experiment, the negativities elicited by orientation and functional mismatches differed in their scalp distributions. The negativity evoked by functional mismatches had a more pronounced central scalp distribution than the negativity elicited by orientation mismatches. In addition, the negativity elicited by orientation mismatches showed a lateralization to the left, which was not obtained for functional mismatches. This lateralization was predicted from the finding that orientation processing of instruments/effectors would give rise to a left hemispheric response. It also confirms that the participants differentiated between two objects involved in the actions. Instead of solving the task by treating both stimuli as external objects, they seemed to be aware that one was an external target object and the other an instrument held by a hand.

Although less pronounced, the differences in time course were also similar to Experiment 1. The negativity elicited by functional mismatches was longer lasting than the negativity elicited by orientation mismatches and seemed to overlap with the following positive modulation. As in the previous experiment, the positivity elicited by functional mismatches appeared around 100 ms later than the positivity elicited by orientation mismatches. Moreover, at least for the last latency window, the positivity elicited by functional mismatches was lateralized to the left over posterior ROIs, which would be expected if – as in the previous experiment – a remainder of the functional negativity was still present in the right hemisphere. This lateralization could again be

demonstrated for functional and double but not orientation mismatches, consistent with the view that the processes evoked by functional processing also take place in double mismatches.

COMPARISON OF THE TWO EXPERIMENTS

A comparison of the results of Experiments 1 and 2 suggests that stimulus type (effector/instrument or target object) affects orientation processing, but not the processing of object function. Whereas the negativities elicited by functional mismatches were similar in the two experiments, a right lateralization was observed for the processing of the orientation of the target objects, and a left lateralization for the spatial processing of effectors/instruments. To confirm this differential effect of stimulus type statistically, the data from the two experiments was entered into one ANOVA with the between-subjects factor Type (ERPs reflect the processing of effector/instrument, or the target object) and the within-subject factors Orientation, Function, and Hemisphere. This was done for each of the three latency windows separately. For the sake of brevity, only the effects qualified by stimulus Type are discussed.

Results

Latency window 1 (Experiment 1, 360–480 ms; Experiment 2, 320–440 ms)

The ANOVA revealed a significant interaction of Orientation, Hemisphere and Type, $F(1, 60) = 9.65$, $MSE = 0.5$, $p < .005$, but no analogous interaction of Function, Hemisphere and Type, $F(1, 60) < 1$. Therefore, stimulus type affected the lateralization of orientation mismatches but not of functional mismatches. The direct comparison of orientation and functional mismatches further confirmed this notion. The marginally significant interaction of Hemisphere, Condition and Type, $F(1, 60) = 3.50$, $MSE = 0.4$, $p < .07$, indicated that the effect of stimulus type was stronger for orientation than for functional mismatches.

We investigated whether this pattern could be shown for each of the mismatching conditions when compared to the fully matching conditions.

Indeed, there was an interaction of Condition, Hemisphere and Type when orientation mismatches were compared to the fully matching condition, $F(1, 60) = 10.6$, $MSE = 0.6$, $p < .005$, but not when functional mismatches were compared to the fully matching condition, $F(1, 60) < 1$. In addition, the interaction of Hemisphere, Condition and Type was also present for double mismatches, $F(1, 60) = 5.5$, $MSE = 0.7$, $p < .05$. This is consistent with the view that double mismatches show contributions of the spatial and the functional process.

Latency windows 2 and 3 (Experiment 1, 500– 700 ms and 600–800 ms; Experiment 2, 450– 650 ms and 550–750 ms)

All effects mirror those of the analyses of Experiment 1 and 2. No effect was qualified by Type.

Summary

The comparison of the two experiments revealed two important findings. First, stimulus type only affected spatial processing, not functional processing. The negativity following functional mismatches was not affected by the manipulation of stimulus type. The spatial processing of target objects in Experiment 1 and effectors/instruments in Experiment 2 was associated with left and right lateralized negativities, respectively. Such a hemispheric asymmetry was predicted if the detection of orientation but not functional mismatches was based on the same processes that also occur when humans (mentally) rotate either body parts or external objects.

Second, Stimulus type only affected the negative modulations, not the positive modulations. This can be interpreted as the negative effects being specific to the type of mismatch (spatial, functional, double) and stimulus type (effectors vs. target objects), whereas the positive effects occurred for all stimulus and mismatch types.

GENERAL DISCUSSION

The understanding of actions of tool use depends not only on the motor act that is performed, but also on the objects that are used. We investigated the electrophysiological correlates of the pro-

cesses that integrate both aspects into a representation of the observed action.

ERPs were recorded while the participants watched inserting actions that could mismatch in two ways. Functional mismatches occurred when the function of the objects was not appropriate to achieve the given action outcome (e.g., credit card being applied to a ticket canceller). Orientation mismatches occurred when the orientations of insert and slot of the target object were not consistent with an inserting action being performed (different orientations of insert and slot). Because the two mismatches were independent of each other they could also occur simultaneously (double mismatch).

Both types of mismatch gave rise to a negative inflection in the latency range of the N400-component followed by a positive modulation. For functional mismatches, such a pattern was predicted on the basis of prior research on action and gesture perception (Gunter & Bach, 2004; Sitnikova et al., 2003). The new finding was that a very similar N400-like negativity and a later occurring positivity were also evoked by orientation mismatches. This similarity in the ERPs was surprising because the detection of orientation and functional mismatches could be based on very different kinds of information. Whereas the detection of functional mismatches required deriving ''semantic'' memory-based object representations, the detection of orientation mismatches depended on the objects' spatial properties. N400-effects have, however, been observed before when very different kinds of semantic information – even across sensory modalities – had to be integrated into a common representation (for a review, see Kutas & Federmeier, 2000; Kounios, 2002). As such, the present data suggest that the negativities were evoked when either an orientation or a functional mismatch precluded the integration of the new object into an action representation that specified which objects had to be used and which motor act had to be performed for the action to be successful (cf. Bach et al., 2005).

The interaction between the negativities confirmed that action knowledge provided a common context into which the spatial and functional object properties were integrated. The negativities elicited by double mismatches were not an additive function of the negativities elicited by spatial and functional mismatches. They were either of the same amplitude (Experiment 1) or only as large as the smaller of the two negativities

elicited by these mismatches (Experiment 2). This pattern suggested that whichever mismatch was detected more easily disrupted the action representation that had been established, so that an integration of the second dimension was not undertaken. A similar finding was provided by a behavioral study using the same stimuli (Bach et al., 2005). There, the presence of an orientation mismatch interfered with the judgment of functionally matching actions, but not with actions that already contained a functional mismatch. Thus, consistent with the present findings, the presence of a mismatch was irrelevant if no representation of the observed action could be established due to another mismatch.

Of course, the notion that a common action representation is established from the motor act and the function of the objects does not mean that the two processes deriving both kinds of information are identical. Indeed, there were reliable differences between the ERPs elicited by the two kinds of mismatches. Because the detection times and difficulties of the two mismatches are highly comparable (e.g., Bach et al., 2005) and participants saw exactly the same instruments and target objects in each condition, these differences indicate that the underlying processes or brain structures are at least partially different.

First of all, there were differences in time course and scalp distribution. Consistent with prior research on N400-like negativities evoked by pictorial stimuli (Sitnikova et al., 2003; West & Holcomb, 2002), the negativities elicited by functional mismatches had a central scalp distribution and were long lasting. In contrast, the negativity elicited by orientation mismatches was shorter lasting and also had a flatter scalp distribution, at least when the ERPs reflected the processing of effectors and instruments (Experiment 2). The differences in scalp distribution and time course were particularly apparent in the later latency windows in both experiments, where a remainder of the preceding negativity was still present in the right hemisphere for function (and double) mismatches, but not for orientation mismatches.

The negativities also seemed to be differentially affected by the manipulation of stimulus type. Orientation mismatches gave rise to left and right lateralized negativities for the processing of instruments/effectors (Experiment 2) and target objects (Experiment 1), respectively. In contrast, the negativities elicited by functional mismatches had an equally pronounced right-ward lateralization in both experiments. Such an asymmetry was predicted if the detection of orientation mismatches – but not functional mismatches – relied on the parietal and motor structures that are also involved in orientation judgments of objects and body parts (e.g., Kosslyn et al., 1998; Tomasino et al., 2003). The present findings are therefore consistent with the idea that the recognition of the motor act relies on structures in the parietal–premotor pathway, most notably the mirror neurons, and that the integration of object function into an action is supported by a separate pathway, possibly involving temporal and prefrontal structures (Hodges, Bozeat, Lambon Ralph, Patterson & Spatt, 2000). The parallel involvement of both of these systems in action perception has demonstrated before in a magnetoencephalography study on the perception of symbolic gestures (Nakamura et al., 2004).

Taken together, the negativities elicited by both mismatches did not only reflect a general process that established an action representation form the motor act and from the function of the objects. They also reflected distinct subprocesses that derive both kinds of information from an observed action. Such a hybrid view of the N400 is consistent with prior research that describes the role of the N400 as deriving meaning by bridging modality specific sensorimotor information and more general higher-level representations (Kutas & Federmeier, 2000; Holcomb & West; 2002; Kounios, 2002).

Further studies need to clarify the functional role of the positive modulation that followed the negativities elicited by both types of mismatch in our study and previous studies on action perception (Gunter, Knoblich, Bach, Prinz, & Friederici, 2002; Sitnikova et al., 2003). As noted by Sitnikova and colleagues (2003), this late positivity is reminiscent of the P600 effect obtained in language studies. The P600 is elicited by an anomalous sentence structure or by syntactic mismatches (Friederici, 1995; Hagoort & Brown, 2000; Osterhout, Holcomb, & Swinney, 1994; Osterhout & Mobley, 1995). Therefore, Sitnikova and colleagues (2003) argued that their functional mismatches might have contained structural mismatches as well, which were responsible for the P600-like modulation. In contrast to this hypothesis, the present findings suggest that the late positive effect can be elicited by any mismatch in the perceived action, irrespective of whether it is functional or structural.

This does not rule out that the late positivity is a P600. Recent research has started to challenge purely structural/syntactic interpretations of the P600. P600 effects have been reported for semantic anomalies in sentences when these anomalies were realized as a mismatch between a verb and the semantic/thematic features of its noun arguments (e.g., van Herten, Kolk, & Chwilla, 2005). In such cases the P600 might also follow N400 effects (e.g., Friederici & Frisch, 2000; Frisch & Schlesewsky, 2001), as was the case in the present study. It has therefore been proposed that the P600 reflects a more general checking mechanism. Accordingly, the P600 is elicited when there is a mismatch between the world knowledge of the listener and an unexpected sentence meaning (van Herten et al., 2005). Such a more general interpretation of P600 effects would also accommodate the present findings. According to this view, the late positive modulations in our study were elicited because orientation and functional mismatches required a ''reading'' of the perceived action that did not correspond to the world knowledge of the observers.

It is intriguing that mismatches in actions can give rise to similar ERPs as mismatches in sentences. This observation resonates well with the suggestion that the capacity for language has developed out of the capacity to produce and understand actions (Arbib, 2005; Rizzolatti & Arbib, 1998), or that the same types of conceptual knowledge are involved in both domains (Lindemann, Stenneken, van Schie, & Bekkering, 2006). Of particular interest might be that the negativity–positivity pattern in the present experiments matches the N400–P600 pattern elicited by verb–argument structure violations in language. It has been speculated that the language system could have developed naturally from action representations that were already organized in a prototypical verb–argument grammar, where the verb reflects the actions, and the nouns reflect the objects involved in it (Arbib, 2005; Rizzolatti & Arbib, 1998). Of course, although our data are certainly suggestive of such a view, future studies are needed that investigate more directly whether the similarity in the ERPs elicited mirrors a similarity in the underlying brain structures or processes.

Since the present study is one of the first investigating action observation with ERPs, open questions remain. First, because our instruction required participants to parse the scenes as actions, our study cannot say anything about the automaticity of the processes that establish the action representations. Two recent studies confirmed, however, that the spatial and functional processes that were manipulated explicitly in the present study do occur automatically without an instruction. Riddoch and colleagues (2003) showed that patients suffering from visual extinction were ''seeing an action'' instead of two objects in isolation if the objects were at the same time functionally and spatially appropriate for an action to be carried out with them (e.g., pen presented above paper). Green and Hummel (2006) replicated this effect in healthy participants and found again that action-like processing depended on the spatial and functional appropriateness of the presented objects.

A second question results from the observation that objects by themselves can elicit action tendencies in the observer, even when no action is presented (''affordances'', Gibson, 1979; Tucker & Ellis, 1998, 2001). This might be particularly true for functionally related objects. Patients exhibiting utilization behaviour unintentionally perform even complex actions of tool use when the objects involved in the action are placed in front of them (e.g., Lhermitte, 1983). Because we used static images that showed the actions in midflight before they were fully executed, it could therefore be the case that our ERP-effects reflect such complex action affordances being evoked, rather than the observation of actions of others.

One way to rule out this possibility would be to run the experiment again and remove the body parts from the stimuli. However, humans tend to infer actions even when no body parts are presented, as for instance demonstrated by the study of Riddoch and colleagues (2003), in which the patients were ''seeing an action'' in the absence of body parts. As such, even if such an experiment would yield the same results as the present study, we could not be sure whether the ERPs reflect object affordances or inferred actions. One could, however, also make the reverse prediction: If our effects reflect action observation and not just affordances evoked by the objects, then identical ERP effects should be evoked if the actions were shown as movies and fully executed. This indeed seems to be the case. The study of Sitnikova and colleauges (2003) presented movies in which even the functionally mismatching actions were fully executed (e.g., for shaving a rolling pin was used instead of a razor). Nevertheless, these mismatches evoked the same N400–P600 pattern, albeit with slightly different

scalp distributions, as the functional mismatches in the action snapshots in the present study. We are therefore confident that our results reflect action perception processes rather than mere action affordances.

CONCLUSIONS

The present study demonstrates that action comprehension needs to be conceptualized with regards to how both the motor act and the function of the objects shape the understanding of an action. Although at least partially different subprocesses seem to be involved in deriving these two aspects, they were integrated into one coherent representation of the observed action. N400-like negativities therefore seem to be a general marker of the difficulty of establishing a meaningful representation of the perceived action on the basis of motor and functional information. The present results may also serve as a starting point for studies that investigate more directly whether action and language understanding relies on overlapping brain structures or processes, as suggested by the negativitypositivity pattern evoked by mismatches in the two domains.

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