RESEARCH ARTICLE

To eat or not to eat? Kinematics and muscle activity of reach-to-grasp movements are influenced by the action goal, but observers do not detect these differences

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Abstract Recent evidence suggests that the mirror neuron system responds to the goals of actions, even when the end of the movement is hidden from view. To investigate whether this predictive ability might be based on the detection of early differences between actions with different outcomes, we used electromyography (EMG) and motion tracking to assess whether two actions with different goals (grasp to eat and grasp to place) differed from each other in their initial reaching phases. In a second experiment, we then tested whether observers could detect early differences and predict the outcome of these movements, based on seeing only part of the actions. Experiment 1 revealed early kinematic differences between the two movements, with grasp-to-eat movements characterised by an earlier peak acceleration, and different grasp position, compared to grasp-to-place movements. There were also significant differences in forearm muscle activity in the reaching phase of the two actions. The behavioural data arising from Experiments 2a and 2b indicated that observers are not able to predict whether an object is going to be brought to the mouth or placed until after the grasp has been completed. This suggests that the early kinematic differences are either not visible to observers, or that they are not used to predict the end-goals of actions. These data are discussed in the context of the mirror neuron system.

Keywords Reach to grasp · Kinematics · Electromyography · Action prediction · Movement planning · Pre-grasp

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Introduction

Reaching towards a fruit bowl to retrieve a shiny red apple is an action that requires little thought. In performing this movement, it is likely that the acting individual knows exactly what they are going to do with the apple once it has been grasped. But, to an observer, the goal of the action might not be so clear. Will the fruit be brought directly from the bowl to the mouth of the grasper, handed to the child who is standing nearby, or moved aside so that a different piece of fruit can be reached? Being able to predict the post-grasp action might be useful to a hungry onlooker, and it appears that humans are able, from an early age, to anticipate actions after viewing only the initial stages of movement (Sebanz and Shiffrar 2007; Southgate et al. 2010).

Some researchers have attributed our ability to predict actions to the mirror neuron system (MNS; Fogassi et al. 2005). Discovered in monkeys, mirror neurons are cells in the premotor cortex which respond during both action execution and action observation (di Pellegrino et al. 1992). Studies using techniques such as transcranial magnetic stimulation (e.g. Fadiga et al. 1995) and functional imaging (e.g. Iacoboni et al. 1999) provide evidence for a

similar system in humans. Such studies indicate that activity in the human motor system is similar when a person observes a goal-directed action and when they perform the same action. According to recent reports, the MNS is activated even when part of an action is hidden from view (e.g. Villiger et al. 2011), suggesting that this system has the ability to predict the outcomes or goals of actions after seeing only the beginning. It is theorised that the appropriate 'motor chain' is activated in the observer at the beginning of the action; thus, an internal representation of the viewed movement is activated regardless of whether the entire action is seen (Fogassi et al. 2005). As the MNS is said to 'transform visual information into knowledge' (Rizzolatti and Craighero 2004), an important question to ask is: what visual information allows an observer to predict the outcome of an action? Previous studies suggest that observers can infer a great deal from viewing the kinematics of movements alone (e.g. Runeson and Frykholm 1983; Manera et al. 2011). So, do differences in the movements themselves allow us to predict whether an object will be, for example, brought to the mouth or thrown away?

To answer this question, we first need to know whether the initial stages of movement do in fact differ according to the goal of an action. Indeed, it has been shown that reach kinematics are influenced by what is going to be done with an object once it has been grasped. Marteniuk et al. (1987), for example, found that a reach-to-grasp movement that was followed by fitting an object into a 'tight fitting well' was characterised by a longer overall movement time, lower peak velocity and a longer deceleration phase, compared to a reach-to-grasp movement followed by throwing the object into a relatively large box. Similarly, Ansuini et al. (2006) found that reaching movements were slower and were characterised by a more gradual shaping of the hand to the object when the post-grasp movement required greater precision. Another study found that reaching movements towards a bottle were longer in duration when the subsequent action was pouring liquid from the bottle before placing it down, compared to when the post-grasp movement was simply placing (Schuboe et al. 2008). Grasp position is also affected by the end-goal of a movement, with objects being grasped lower down when they are to be moved upwards, and higher up when they are to be moved downwards (Cohen and Rosenbaum 2004; Schuboe et al. 2008). In addition, the initial stages of reach-to-grasp movements vary according to the size (e.g. Marteniuk et al. 1987; Pryde et al. 1998; Armbrüster and Spijkers 2006), texture (e.g. Fikes et al. 1994) and weight (e.g. Eastough and Edwards 2007) of the object being grasped.

In this study, we were specifically interested in how reach-to-grasp movements differ depending on whether the grasped object is going to be brought to the mouth or placed in another location, and whether the object is a food or a non-food item. Hand-to-mouth actions are one of the most-practiced movements performed by humans, emerging first at the foetal stage of development (for review see Rochat 1993; Bremner and Cowie in press), and remaining a large part of our daily movement repertoire throughout life. In monkeys, at least, there are mirror neurons which respond selectively to the observation of eating and food-related actions (Ferrari et al. 2003; Fogassi et al. 2005). In Fogassi et al. (2005) study, some neurons responded selectively to the observation of grasp-to-eat, or to grasp-to-place actions even when the final eating or placing action was hidden from view, indicating that the monkey MNS differentiates eating and placing actions from an early phase of the movement. To ascertain whether this differentiation was based on kinematic differences between the movements, Fogassi also analysed the hand trajectory, velocity and finger aperture of the monkeys' movements. To investigate whether the differences in mirror neuron responses could be explained by kinematic differences, Fogassi and colleagues included two different 'grasp-to-place' conditions, one in which the monkey placed the object in a container next to its mouth and another in which the monkey placed the object on a table in front of its body. The data showed similar mirror neuron responses to the observation of both grasp-to-place conditions, both of which were different to the response to observing the grasp-to-eat movement. Whilst these results indicate that kinematic differences do not explain the different neural responses to the observation of eating and placing actions, Fogassi et al. did indeed find that grasp-to-eat and grasp-to-place movements differed in terms of peak velocity and peak finger aperture.

As food-directed actions are also used as stimuli in human MNS research (e.g. Cheng et al. 2007; Sartori et al. 2011a, b; Villiger et al. 2011), we set out to build a profile of the kinematics and muscle activity underlying grasp-to-eat and grasp-to place movements in humans. Interestingly, Fogassi et al. (2005) also found that a subset of neurons that responded most strongly to grasp-to-eat actions were more responsive to grasp-to-place actions when the object was a food compared to a non-food item. We therefore also investigated the extent to which movements towards food and non-food objects differ, and whether there is an effect of object–action congruency (i.e. whether grasp-to-eat actions are performed differently when they are directed towards foods versus non-foods).

The first aim of this study was therefore to establish whether, and how, reach-to-grasp movements differ depending on whether the grasped object is going to be placed, or brought to the mouth. To this end, in Experiment 1, we tracked the positions of the wrist, index finger, and thumb and recorded muscle activity using electromyography (EMG), whilst participants performed grasp-to-place and grasp-to-eat actions towards either a plum or a ball. Based

on previous findings of the effect of the post-grasp action on pre-grasp kinematics, it was anticipated that the reaching phases of grasp-to-eat and grasp-to-place actions would differ from each other. A second aim was to establish whether observers can distinguish grasp-to-place and grasp-to-eat actions, after viewing only the early stages of movement. We carried out two behavioural studies (Experiments 2a and 2b) in which participants viewed portions of actions and were asked to predict the outcome of these actions.

Experiment 1

Methods

Participants

Ten participants aged 21–34 years ($M = 26.2$, $SD = 4.6$) were recruited from the School of Psychology and Clinical Language Sciences at the University of Reading. One participant was left-handed by self-report, and two of the authors (KN and NH) were participants. The experimental procedures were approved by the local ethics committee (refs: 2011/05/NH; UREC 11/11); participants gave written, informed consent; and the experiments were conducted in accordance with the Declaration of Helsinki.

Apparatus and stimuli

The position of the hand during movements was recorded using a Polhemus Fastrak (Polhemus Inc., Colchester, VT, USA) motion tracking system with six degrees of freedom (X, Y, Z, azimuth, elevation and roll). Three data points (thumb, index finger and wrist) were acquired, each at 40 Hz. EMG data were acquired with an AD Instruments Powerlab 16/30 and two dual bioamplifiers (ADI, Colorado Springs, CO, USA). EMG electrodes were attached to the skin to record activity over four muscles of the participants' dominant hand and forearm: the first dorsal interosseous (FDI) and the thenar eminence (i.e. abductor pollicis brevis, APB) in the hand, and the forearm flexor (i.e. flexor digitorum superficialis, FDS) and extensor muscles (i.e. extensor digitorum communis, EDC). Two circular electrodes were placed on the skin overlying each muscle, approximately 2 cm apart, in a belly-tendon fashion, and ground electrodes were attached to the styloid process of the wrist and the lateral epicondyle of the elbow. The experiment was controlled and data were acquired using custom software written in MATLAB 2010b (Mathworks, Inc.). All experimental and analysis scripts are available from the last author's website (http://neurobiography.info).

The food object was a (red) Victoria plum (an approximate spheroid ~3.5 cm high and ~4.0 cm wide and deep).

The non-food object was an orange table tennis ball (a sphere, 4.0 cm in diameter).

Design

The experiment followed a repeated measures design. The four experimental conditions were derived from crossing the two variables: action (grasp to eat and grasp to place) and object (plum and ball). The four conditions were run in blocks of 20 trials, with two blocks per condition, giving a total of eight blocks per participant. For each participant, the order of blocks 1–4 was pseudorandomised and the order of blocks 5–8 was the reverse of 1–4.

Procedure

The participants were seated in a chair in front of a table where the target object was placed (Fig. 1). Kinematic markers were placed on the fingernails of the thumb and index finger, and on the dorsal aspect of the wrist, and the self-adhesive EMG electrodes were attached to the skin. The markers and wires were secured and positioned so that they did not restrict the participants' movements. The actions were always performed with the dominant hand, and the participants were told that their movements, including the speed of their movements, should be 'as natural as possible'. In the grasp-to-place conditions, following an
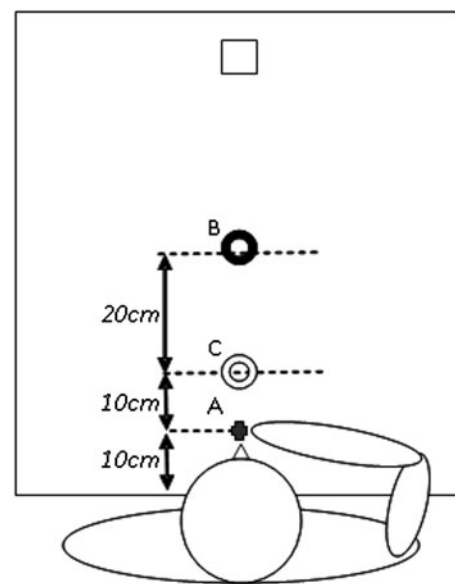

Fig. 1 Schematic diagram of the set-up of Experiment 1. '*A*' represents the starting position, where the participant's hand started at the beginning of each block, and where it was brought back to between trials. '*B*' represents the starting position of the object in all trials, whilst '*C*' is the location that the object was moved to in grasp-to-place blocks. The *square* represents the Polhemus transmitter unit

auditory signal, the participant moved their hand from the starting position (location A; 10 cm from the table edge, and approximately 20 cm from their body, in front of them) to the object location (location C; 40 cm from the table edge), grasped the object and placed it in location B (20 cm from the table edge). Participants were told to hold their hand steady in the 'placed' position (location B) until a second auditory signal three seconds after the first, at which point they were to move the object back to location C and immediately return their hand to the starting position to await the next trial. In the grasp-to-eat conditions, the participants moved their hand from location A to the object, before bringing the object from location C to their mouth, and holding it just in front of their mouth until the second auditory signal. They then returned the object to location C and moved their hand back to location A. To make the grasp-to-eat movements as natural (i.e. as similar to an eating movement, without the object actually being put into the mouth) as possible, the participants were told to perform the action as if they were going to eat the object, so that the mouth opened as the object approached the mouth, and the final position was the object held at the open mouth. The movement to be performed was demonstrated to the participants by the experimenter before the start of each block, and the participants were told when to move relative to the auditory signals.

Kinematic data acquisition began immediately prior to the first auditory signal and continued for 3 s. EMG data were acquired continuously and later segmented offline using trigger signals sent from the experimental control computer to the data acquisition computer.

Data analysis

Kinematic data

Filtering and extraction of variables The kinematic data (X, Y, Z position in cm) were filtered with a second-order dual-pass Butterworth filter with a high-frequency cut-off of 10 Hz. The data of the left-handed participant were mirror-reversed across the midline (inverting the Y values of the markers). The position data were differentiated once to compute velocity and a second time to compute acceleration.

The movement was analysed in two parts: the pre-grasp and grasp phase (henceforth 'reach to grasp'), and the post-grasp phase ('grasp to place' or 'grasp to eat'). For each part of the movement, a total of 38 variables were extracted from the kinematic data. Movement onset (RT) and movement offset (ET) for the pre-grasp reach were defined based on the velocity of the wrist after trial onset: the movement began (RT) when the velocity of the wrist first exceeded 5 cm/s and ended (ET) when the velocity first decreased below 10 cm/s. Movement duration (MT) was calculated

by subtracting RT from ET. The same criteria were used to define the RT, ET and MT of the post-grasp movement, but with the constraint that the RT of the post-grasp movement was at least one sample (25 ms) after the pre-grasp ET. Five variables associated with 'grip aperture' (the distance between the thumb and index finger) were calculated: grip aperture at movement offset (GA_{ET}), peak grip aperture (PGA), time of peak grip aperture (PGAT), peak velocity of grip aperture (PV_{GA}) and the time of peak velocity of grip aperture ($PV_{GA}T$). The following variables were calculated separately for each of the three kinematic markers (thumb, index finger and wrist): peak velocity (PV), peak acceleration (PA), peak deceleration (PD), time of peak velocity (PVT), time of peak acceleration (PAT), time of peak deceleration (PDT), path length (the distance travelled between movement onset and offset) and position at movement offset (X_{ET}, Y_{ET} and Z_{ET}).

Trials were excluded automatically by the analysis script if they met certain criteria, which differed for each part of the action due to the considerable kinematic differences between the pre- and post-grasp movements. Most of the excluded trials were due to hand movement at the start of the trial (before the first auditory signal), unsmooth trajectories or participants missing the start signal. For the pre-grasp, trials were excluded if the RT was less than 100 ms, if the calculated ET was less than 50 ms after the RT or if the path length was shorter than 17 cm or longer than 60 cm. For the post-grasp, trials were automatically excluded if ET was less than 50 ms after the RT, if the ET was within 100 ms (four samples) of the last recorded sample (i.e. very late, slow or long movements), if path length was shorter than 12 cm or longer than 90 cm or if the velocity at the end of the trial was greater than 10 cm/s (i.e. the hand was still moving at trial offset). Further trials were excluded on visual inspection if they were clear outliers within the dataset of the participant. In total, 2.9 % of trials were excluded from further analysis (of 1,600 trials in total, 40 trials were excluded automatically, and a further six trials manually).

Data reduction Because many of the kinematic variables were correlated with one another (e.g. peak velocity and peak acceleration of the wrist in participant 1, $r = 0.822$, $p < .001$), principal component analyses (PCAs) were conducted to reduce the number of redundant kinematic variables, thereby decreasing the number of statistical comparisons required and simplifying the interpretation of the data. It has been suggested that PCA is preferable to factor analysis where the primary goal of analysis is data reduction (de Vaus 2002). Oblique (direct oblimin) rotation was used, as this method of rotation is recommended if it is expected that some components might correlate with each other (e.g. Costello and Osborne 2005).

Pre-grasp A preliminary PCA with all 37 variables (excluding ET, which was redundant given that MT was based on RT and ET) suggested seven components. However, as these were difficult to interpret and the rotation failed to converge, we decided to analyse the variables associated with temporal properties of the movement separately from the spatial variables. Thus, two separate PCAs were conducted with the aim of reducing the 37 variables into meaningful temporal and spatial components. The first of these PCAs comprised 23 temporal variables: RT, MT, PV, PA, PD, PVT, PAT, PDT, PGAT, PV_{GA} and $PV_{GA}T$. The Kaiser–Meyer–Olkin (KMO) measure of sampling adequacy confirmed that the data were suitable for this analysis (KMO = 0.942). The second PCA (KMO = 0.480) was conducted on the 14 spatial variables: ET position (X_{ET}, Y_{ET} and Z_{ET}) and path length for all three markers, in addition to GA_{ET} and PGA.

Post-grasp Whilst our main focus of interest was the pre-grasp movement, the kinematics of the post-grasp movement phase (placing or bringing to the mouth) were nonetheless recorded and analysed. Grasp-to-place and grasp-to-eat movements were analysed separately because of the large kinematic differences between the two. A PCA was conducted with all 32 variables (the same variables as in the pre-grasp analysis, but excluding variables relating to grip aperture, as this did not change during the post-grasp movement).

EMG data

Muscle activity was recorded throughout the whole experiment, but only data arising from the pre-grasp part of the trial were analysed. The data were acquired at a sampling rate of 1 kHz and bandpass filtered at 1–1,000 Hz by the data acquisition software. For offline analysis, the data were then rectified and filtered with a second-order dual-pass Butterworth filter with a bandpass of 1–15 Hz.

EMG data were analysed by three paired *t* tests conducted on each sample. Due to the large number of data points generated and analysed for every trial, bootstrapping was carried out to provide 95 % confidence intervals for any significant differences found in muscle activity between different conditions. Bootstrapping was carried out for three epochs of the data: standardised across the whole pre-grasp movement (by interpolating to 1,000 samples), relative to RT (99 ms before to 100 ms after RT; 200 samples) and relative to the peak acceleration (99 ms before to 100 ms after PAT; 200 samples). For each participant's dataset, the data were randomly resampled with replacement across trials and conditions, separately for each muscle and participant. For each iteration of resampling, within-participants *t* statistics were calculated by comparing the average of two resampled conditions with the average of two others (i.e. similar to the main effects of action, object and their interaction). We then calculated, for each muscle in each dataset, the number of significant samples (i.e. where one data point was significantly higher ($t(9) > 2.26$, $p < .05$, two-tailed) for one of the contrasted conditions than the other), as well as the number of sequences and the length of each sequence of significant samples. This process was repeated for 10,000 iterations, and distributions were constructed of: (a) the total number of significant samples per iteration, (b) the number of sequences of significant samples per iteration and (c) the lengths of significant sequences of samples. From these null distributions, *p* values were assigned to the sequences of significant samples found in the real data.

All data treatment and analysis were carried out using MATLAB (R2010b) and SPSS (version 19).

Results

Pre-grasp kinematics

Extracted temporal and spatial movement components For both PCAs, components were extracted which had eigenvalues exceeding Kaiser's criterion of 1. In interpreting the components, we referred mainly to the pattern matrix, but loadings in the structure matrix were also considered when the two matrices differed considerably. Variables were interpreted as loading onto a component 'significantly' if they had a loading value of 0.4 or above (Stevens 2002).

The 23 temporal variables were reduced to five components, which together explained 75.1 % of the variance. Component loadings can be seen in Online Resource 1. Component 1 was interpreted as representing 'slowness of movement', with positive loadings of PD, MT, PGAT and PDT, and negative loadings of PV, PA and PV_{GA}. Component 2 had positive loadings of MT, PVT and PDT, so was interpreted as representing long movements with late peak velocities. Component 3 represented time of peak acceleration of the thumb and the index finger, with PAT of both loading negatively. Component 4 had positive loadings of RT and $PV_{GA}T$; thus, a high score represented movements that started later and in which the fastest finger-thumb opening occurred later. Finally, Component 5 represented time of peak acceleration of the wrist, with only this one variable loading significantly.

The 14 spatial variables were reduced to five components, which together accounted for 80 % of the variance. Component loadings can be seen in Online Resource 2. Component 1 seemed to represent movements with a position at ET in which the thumb and index finger were further forward on the object (further from the participant's body) and the wrist was further back (closer to the participant's body), and in which the index finger was further right and

Table 1 Mean (SD) of all pre-grasp kinematic variables

	Thumb	Index	Wrist
RT (ms)	n/a	n/a	317 (100)
MT (ms)	n/a	n/a	732 (136)
PV (cm/s)	80.4 (18.0)	87.9 (18.9)	68.9 (15.8)
PA (cm/s/s)	635 (246)	685 (262)	450 (191)
PD (cm/s/s)	−368 (169)	−434 (193)	−273 (134)
PVT (ms)	331 (88.4)	293 (84.6)	320 (74.7)
PAT (ms)	102 (70.1)	102 (70.1)	111 (68.8)
PDT (ms)	569 (173)	570 (183)	545 (163)
Path (cm)	35.4 (3.10)	38.7 (3.28)	29.8 (2.75)
X_{ET} (cm)	36.6 (0.834)	30.6 (0.768)	44.8 (1.74)
Y_{ET} (cm)	−1.45 (0.938)	1.52 (1.28)	7.99 (2.12)
Z_{ET} (cm)	1.23 (0.611)	2.79 (0.977)	7.05 (1.33)
PGA (cm)		3.65 (1.23)	
PGAT (ms)		541 (191)	
PV_{GA} (cm/s/s)		20.3 (9.25)	
$PV_{GA}T$ (ms)		251 (151)	
GA_{ET} (cm)		2.63 (1.14)	

the thumb further left. Component 2 comprised high positive loadings of X_{ET} position of the thumb and index finger (i.e. the thumb and index finger were further back on the object), and high positive loadings of Z_{ET} for all markers (i.e. the thumb, index finger and wrist were all higher up at ET). This component was interpreted as grasp position; specifically, a high score represented a grasp position in which the hand was further back and higher up on the object. Component 3 represented path length, a high score on this component representing a short path. Component 4 represented an ET position in which the thumb and wrist were further to the left (negative loadings of Y_{ET}). Component 5 had negative loadings of PGA and GA_{ET}. The mean and standard deviation of all the individual kinematic variables prior to the PCA are provided in Table 1.

Effects of action and object type on movement components Bonferroni correction was used to protect against type 1 error. This was done separately for the temporal and spatial analyses. Because there were five components extracted for each of these, the alpha significance criterion for all tests was decreased to 0.01.

Separate analyses of variance (ANOVAs) were conducted to assess the effects of action and object on each of the extracted components. Main effects of action on both Component 3 (PAT of the index finger and thumb; $F(1,9) = 12.91$, $p = .006$, $\eta^2 = 0.589$) and Component 5 (PAT of the wrist; $F(1,9) = 17.21$, $p = .002$, $\eta^2 = 0.657$) were revealed. In both cases, peak acceleration occurred earlier in grasp-to-eat than in grasp-to-place movements. There was also a significant interaction between action

and object on Component 5 ($F(1,9) = 12.88$, $p = .006$, $\eta^2 = 0.588$). Post hoc ANOVAs showed that peak acceleration occurred earlier in grasp-to-eat than grasp-to-place movements for both the plum and the ball, although the simple effect of action was larger for actions towards the ball ($F(1,9) = 32.44$, $p < .001$, $\eta^2 = 0.783$) than the plum ($F(1,9) = 5.60$, $p = .042$, $\eta^2 = 0.384$). Separate analyses of placing and eating actions showed that peak acceleration was reached earlier for grasp-to-place actions towards the plum than those towards the ball ($F(1,9) = 5.46$, $p = .044$, $\eta^2 = 0.378$), whereas there was no significant difference between grasping-to-eat the plum and grasping-to-eat the ball ($F(1,9) = 3.70$, $p = .086$, $\eta^2 = 0.291$). The average peak acceleration times for each condition are plotted in Fig. 2.

Because PAT of the wrist was the only variable to load significantly onto Component 5, additional analyses were carried out using the original variable. These confirmed the same main effect ($F(1,9) = 11.25$, $p = .008$, $\eta^2 = 0.555$) and interaction ($F(1,9) = 6.48$, $p = .031$, $\eta^2 = 0.018$). The same post hoc tests performed on the original PAT variable showed significant differences between grasp-to-eat plum and grasp-to-eat ball actions ($F(1,9) = 6.02$, $p = .037$, $\eta^2 = 0.400$), and between grasp-to-eat and grasp-to-place actions towards the ball ($F(1,9) = 26.35$, $p = .001$, $\eta^2 = 0.745$).

Analyses of the spatial components revealed a significant main effect of action and a marginal effect of object on grasp position (Component 2). Objects were grasped higher up and further back in grasp-to-place as compared to
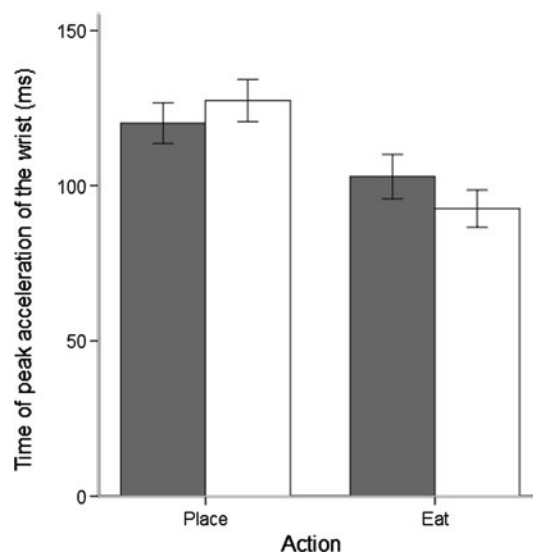
Fig. 2 Interaction between action type and object type on the time (in milliseconds) of peak acceleration of the wrist (Experiment 1). The *grey bars* represent actions towards the plum, and the *white bars* represent actions towards the ball. *Error bars* represent 95 % confidence intervals

grasp-to-eat actions ($F(1,9) = 13.56$, $p = .005$, $\eta^2 = 0.601$), and the grasp was higher and further back on the plum than on the ball ($F(1,9) = 10.20$, $p = .011$, $\eta^2 = 0.531$). These were the only effects which reached significance after Bonferroni correction, but there were also marginally significant effects of object on Component 1 ($F(1,9) = 7.94$, $p = .020$, $\eta^2 = 0.469$) and of action on Component 3 ($F(1,9) = 6.78$, $p = .029$, $\eta^2 = 0.430$). Actions with the plum had higher scores on Component 1 than actions with the ball; thus, participants' grip on the plum was different to their grip on the ball. The second marginal effect indicated shorter path lengths for grasp-to-place as compared to grasp-to-eat actions.

Post-grasp kinematics

Extracted temporal and spatial movement components

Grasp to place   Analysis of all 32 variables (KMO = 0.866) revealed six components. Component loadings are shown in Online Resource 3. Component 1 was interpreted as representing 'slowness of movement' as it was characterised by positive loadings of RT, MT, PD and PVT, and negative loadings of PV and PA. Component 2 represented movements with a late PD of the index finger and an ET position in which the thumb and index were further forward, the thumb was to the left and the index finger to the right and low down on the object. Component 3 was characterised by a long path length and an ET position in which the wrist was further back on the object. Component 4 was characterised by a late PV and late PA time of the thumb and the index finger. Component 5 was characterised by a late PD of the wrist, and an ET position in which the wrist was further to the left. Component 6 represented movements with a late PA of the wrist, and an ET position in which the wrist was further forward, and both the wrist and the thumb were higher up.

Grasp to eat   Analysis of all 32 variables (KMO = 0.858) revealed five components; component loadings can be seen in Online Resource 4. Component 1 represented movements with a late RT, long MT, low and late PV, low PA, and a high and late PD. Component 2 represented movements with long path lengths and in which the thumb, index finger and wrist were all closer to the body at ET. This was interpreted as representing either the distance from location A to the participant's mouth, or how close to their mouth the participants held the object. Component 3 represented grasp position, a high score on this component representing movements in which the thumb, index finger and wrist were all further right, and the index finger and wrist were higher up at ET. Component 4 represented movements with late PA times for all markers, and late PV of the thumb and index finger. Component 5 represented movements with a short

path length of the thumb and in which all markers were lower at ET; thus, a high score on this component could represent movements in which the hand was held lower at the face.

Effects of object type on grasp-to-place and grasp-to-eat movement components   There were no significant effects of object on the post-grasp movement after Bonferroni correction. In both the grasp-to-place and grasp-to-eat data, the only effect of object which was near-significance was on Component 1. In both cases, this component appeared to represent 'slowness of movement', a high score on this component representing movements with a long RT, long MT, low and late PV, low PA, and high and late PD in all markers. For the grasp-to-eat movement, this component also had significant loadings of the position ('left–right') of the thumb and index, with both being further to the left at ET. In both movements, it was found that actions with the plum were slower than actions with the ball (*grasp to place:* $F(1,9) = 6.25$, $p = .034$; *grasp to eat:* $F(1,9) = 6.80$, $p = .028$).
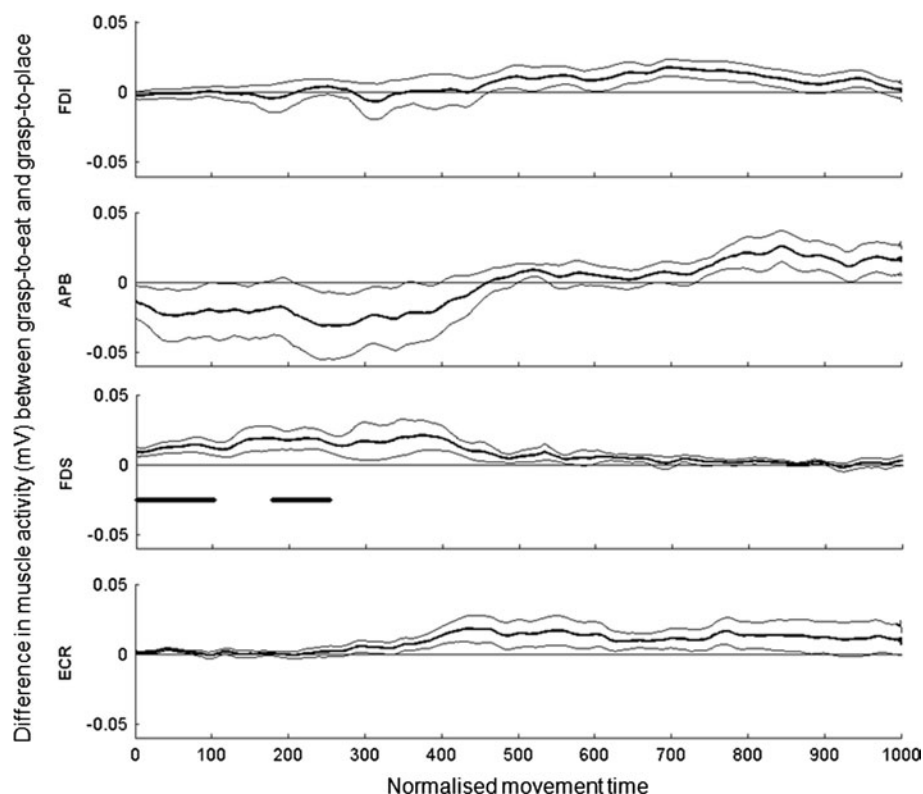
EMG data

Based on the multiple comparisons carried out on data from four different muscles, differences in muscle activity between conditions (eat vs. place; plum vs. ball; interaction between action and object) were only considered significant when p was .01 or lower. Contrasting the grasp-to-eat and grasp-to-place trials revealed differences in activity in the FDS. For the standardised data (1,000 interpolated samples across the whole pre-grasp movement, from four samples before RT to four samples after ET), activity in the FDS was significantly higher (bootstrapped $p < .0001$) in grasp-to-eat than in grasp-to-place movements at two phases of the pre-grasp movement. The first significant sequence of time-points started from trial onset, showing higher activation in the FDS in grasp-to-eat trials from approximately 300 ms (average RT) before the movement had started (a sequence of 102 consecutive samples; $p < .0001$). The second phase at which activation was greater in grasp-to-eat movements was from approximately 170 ms after trial onset (76 samples; $p = .0053$). The greater activity in eating compared to placing trials was confirmed by the analysis of the data relative to RT, with one significant sequence starting 100 ms before the RT (117 samples; $p < .0001$). A plot of the activity in all muscles, comparing grasp-to-eat with grasp-to-place actions, is provided in Fig. 3.

Discussion

The initial movements involved in object-directed actions vary depending on the properties of the object itself (e.g.

Fig. 3 Differences between conditions in EMG activity recorded over four muscles of the hand and forearm (Experiment 1). *Bold lines* represent mean activity, and *fine lines* represent the standard error. The plot compares activity in each of the muscles during grasp-to-eat and grasp-to-place actions; zero on the y-axis represents no difference between the two conditions. The *black bars* below the FDS data highlight the points at which the data deviate significantly from zero, that is, where activity was significantly greater in the grasp-to-eat than in the grasp-to-place conditions

Marteniuk et al. 1987) and the action following the initial movement (e.g. Schuboe et al. 2008). Our data confirm these previous observations, demonstrating effects of both target object and subsequent action on reach-to-grasp movements. In addition, we found an interaction between object and action type, which could reflect an incongruity effect of grasping-to-eat a non-food item, or simply an effect of object which is only apparent when the item has to be moved upwards to the mouth.

Our finding that peak acceleration occurs earlier in grasp-to-eat than in grasp-to-place actions might be due to the fact that the subsequent hand-to-mouth action requires greater control or precision than placing the object. This would support the results of Schuboe et al. (2008), who reported peak acceleration occurring earlier in reaching movements when the post-grasp action involved pouring liquid from the grasped object compared to when the object was simply placed on a shelf. The difference between grasp-to-eat and grasp-to-place actions is especially interesting in the light of the recent finding that the MNS responds differently to observing the initial stages of movement depending on whether the object is subsequently placed or brought to the mouth (Fogassi et al. 2005). Although Fogassi and colleagues' control measure (the inclusion of a grasp-to-place movement in which the object was placed in a container next to the mouth) indicated that differences in MNS responses to eating and placing actions could *not* be explained by

kinematic differences, this does not exclude the possibility that kinematic differences can be detected by the MNS and contribute to the MNS response in humans.

The interaction between post-grasp action and target object in our data is a novel finding, which could be interpreted in different ways. We investigated the effects on time of peak acceleration by analysing both the component scores and the original variable. As peak acceleration time was the only variable to contribute significantly to the component, this discussion will focus on the differences revealed when the raw peak acceleration time was compared between the conditions. Whilst no difference was found between reaching for the plum and reaching for the ball in the grasp-to-place condition, peak acceleration occurred significantly earlier in reaches towards the ball than in reaches towards the plum when the subsequent action was bringing to the mouth. If an earlier peak acceleration reflects more care being taken in the movement (e.g. for movements requiring greater precision), then it is possible that participants took more care over movements in which the post-grasp action and target object were incongruent, that is, 'eating' the ball. Indeed, an effect of object action congruency was found by Begliomini et al. (2007), who looked at the kinematics of 'natural' movements, in which the type of grasp was appropriate to the object (a precision grip for a small object, or a whole hand grasp for a larger object), and 'constrained' movements, in which the grasp type was not the most

appropriate for the object (a whole hand grasp of the small object, or precision grip for the large object). Begliomini et al. found that the time of movement initiation, as well as the time of peak grip aperture, occurred later for constrained than for natural movements.

Alternatively, the earlier peak acceleration time in this case might simply reflect a more 'awkward' movement, as the action is not one that we would normally perform. It is equally possible that the interaction may simply reflect the fact that grasping to eat is an action which requires more care as the object is transported upwards to the mouth, and so the effect of object is apparent only for this action, that is, if grasp-to-eat movements require more care or precision, the kinematics may be more susceptible to properties such as the smoothness of the object. As discussed below, the difference in grasp position could indicate the need for a more secure grip on the ball than the plum. If this is the case, the interaction between action and object on peak acceleration time could reflect a combination of the more 'careful' movement and less graspable object. This interpretation would be consistent with the findings of Sartori et al. (2011a, b) and their suggestion that there is an interplay between object affordances and the end-goal of actions. Sartori and colleagues compared grasp-to-move and grasp-to-pour movements towards a bottle which was either full or half-full of water, and either concave (easier to grasp) or straight-edged. Movement time was found to be longer when the action was 'pouring' compared to when it was simply moving the bottle, arguably due to the greater precision and care required for pouring actions. This difference, however, was *not* found when the bottle was a concave shape, indicating that the effect of action was only present for the less graspable object. Furthermore, some effects of action and object shape (greater peak grip aperture for pouring than moving, and for pouring from the straight bottle compared to pouring from the concave bottle) were only present when the bottle was half-empty (i.e. it weighed less). The findings of Sartori and colleagues, and our own finding of an object–action interaction, could indicate that effects of action type (namely, how precise an action is) are dependent on the stability of the grasp on the object. When the grasp is relatively secure (for example on the plum compared to the ball, or on the concave bottle compared to the straight bottle in Sartori's experiment), there are no discernible effects of the action itself.

The difference in grasp position between the plum and the ball—specifically, that the index finger and thumb were placed further back and higher up on the plum than on the ball—could be due to the fact that a plum would more often be grasped with the intention to eat, and this grasp position would result in the fingers being less of an obstacle when the plum is bitten into. As this difference between the objects was not influenced by the subsequent action (i.e. there was no interaction between action and object in this variable), this would have to be an automatic positioning of the hand in response to an object that could be eaten, rather than a grasp determined by the immediate intention of the actor. Another possibility is that the grasp on the ball, with the thumb and index finger lower down and further forward on the object, would have enabled a more secure grip on the ball, which had a more slippery surface than the plum. It could be argued that the higher-friction surface of the plum, as well as its less symmetrical shape, 'affords' grasping more than does the texture and shape of a table tennis ball. Indeed, affordances such as the shape and texture of objects are known to influence the kinematics of reaching and grasping (e.g. Mon-Williams and Bingham 2011; Flatters et al. 2012). The effect of action on grasp position indicated that the finger and thumb were placed lower down on the object when it was to be brought to the mouth rather than placed on the table. As well as potentially providing a more secure grip on the object when it was going to be brought to the mouth rather than placed down, this could also reflect an effect of the final position of the object, supporting previous findings that grasp height is inversely related to final position height (Cohen and Rosenbaum 2004; Schuboe et al. 2008).

In terms of movement execution, our results confirm what has been found previously. The fact that kinematics are influenced from an early stage by the end-goal indicates forward planning of movements, with movements either following an internal model defined before the movement begins, or being corrected online during the movement based on sensory feedback resulting from movement execution (see Desmurget and Grafton 2000, for review). These data could also have implications for the recognition of actions during action observation; if the kinematics of movement differ according to what is going to be done with an object before the object is reached, perhaps it is possible to predict actions from seeing only the beginning of movements. Based on these findings, Experiments 2a and 2b explored whether people can predict actions based on viewing the initial reach-to-grasp stage of movements alone.

Experiment 2a

In this experiment, participants viewed videos of the same reach-to-grasp actions that were performed in Experiment 1 and were asked to predict whether the object was going to be placed or eaten. The duration of movement viewed by participants on each trial was determined by their (correct or incorrect) response on the previous trial according to an adaptive staircase procedure. This enabled us to estimate how much of the action participants needed to see to correctly predict the movement outcome.

Methods

Participants

Twelve healthy participants, aged between 19 and 55 years ($M = 29.2$; $SD = 11.1$), were recruited from the School of Psychology and Clinical Language Sciences at the University of Reading. None of the participants were actors in the video stimuli. The procedures of Experiments 2a and 2b were approved by the local ethics committee (refs: 2012/035/NH; UREC 11/11). Participants gave written, informed consent, and the experiments were conducted in accordance with the Declaration of Helsinki.

Stimuli

Stimuli consisted of 96 unique video clips, taken from three actors, each showing a hand reaching for and grasping either a plum (48 videos) or a ball (48 videos). The actors in the videos were all white Caucasian; one was female and two were male. The plum and ball featured in the videos were of the same type as those used in Experiment 1. The actors were filmed whilst performing the movement as per the protocol of Experiment 1 (performing the same grasp-to-place and grasp-to-eat actions, in time with the same auditory signals as used in the first experiment). As in Experiment 1, after the grasp, the object would either be brought to the mouth or placed in location B (see Fig. 1). The videos were filmed from three perspectives: above the actor, in front of the actor and from the left-hand side of the actor. Faces were occluded to eliminate distractions from the movement itself, and cues in the actors' head position or facial expression that might have provided information about the actors' intentions. In the 'above' and 'side' views, only the reaching arm was visible, whilst the 'front' views also showed the actors' chests, but not their necks or heads. The object was visible throughout the video clips. Of the 96 videos, 48 showed grasp-to-place actions and 48 showed grasp-to-eat actions. Within each of those subsets, 24 were actions towards the plum and 24 were towards the ball, and within each of those subsets, 8 were 'front', 8 were 'above', and 8 were 'side' views. The videos were presented using MATLAB (R2010a) and the Psychophysics Toolbox version 3 (Brainard 1997).

Design

The video clips were presented in four blocks of 24 trials, in a pseudorandomised order for each participant. A QUEST (Quick Estimation of Threshold) adaptive staircase procedure (Watson and Pelli 1983) was used to determine the threshold proportion of the video required for correct discrimination between eating and placing movements. Due to the kinematic and muscle activity differences between grasping the two different objects (revealed in Experiment 1), separate thresholds were determined for predicting the goal of actions towards the plum and the ball. Each threshold was found twice, in counterbalanced order across participants: once with the video duration based on the proportion of the pre-grasp movement only (M1), and once based on the proportion of the whole movement duration (M2). These two different threshold methods were used because, whilst the two movements (grasp to eat and grasp to place) were different in duration, the initial reach-to-grasp duration was similar. On each trial, the QUEST procedure updated the underlying probability distribution function for the threshold, based on the participant's responses on the previous trials. Thus, depending on whether the participant made a correct or incorrect prediction of the post-grasp movement, they would be shown a lesser or greater proportion (respectively) of the movement in the next trial. The standard Psychtoolbox QUEST parameters were used (beta = 3.5, delta = 0.05, grain = 0.01, pThreshold = 0.82), and staircases began with a stimulus duration corresponding to the pre-grasp and grasp movement.

Procedure

Participants were seated in front of a computer screen and keyboard, and were asked to observe the presented actions closely. After each video, they made a judgement as to whether the action would result in the object being brought to the mouth ('EAT') or placed on the table in location B (Fig. 1; 'PLACE'). On each trial, after the QUEST-determined length of video was played, a screen displaying the question 'Eat or place?' was presented and remained until the participant made a key press response. Participants were told to press the 'e' key on the keyboard if they thought the object would be brought to the mouth, or the 'p' key if they thought the object would be placed. Feedback was given on each trial: the word 'Correct' or 'Incorrect' was presented immediately after participants made their response.

Data analysis

For both M1 and M2, threshold was generated for each participant for both ball and plum conditions. These threshold proportions were then adjusted by multiplying M1 with the mean M1 video duration and M2 with the mean M2 video duration. This gave a threshold measured in numbers of frames (i.e. the number of frames participants needed to view in order correctly to predict the outcome of the action). A 2×2 repeated measures ANOVA was used to look for differences in threshold, with threshold type (M1 and M2) and object type (plum and ball) as predictor variables. The percentage of 'eat' responses given by the participants

was calculated separately for the ball and plum trials, and a paired t test was conducted to assess whether there was any bias in participants' prediction of action depending on whether the action was towards a plum or a ball. A further t test was run to assess whether there was any difference in the total number of 'eat' and 'place' responses given. To investigate whether participants were better at predicting the actions from one angle than another, thresholds were calculated for each of the three angles (front, above and side), and a within-subject ANOVA was performed with accuracy as the dependent and angle as a predictor variable.

Results

There was no significant effect of threshold method ($F(1,11) = 4.292$, $p = .063$ $\eta^2 = 0.281$), or object ($F(1,11) = 0.549$, $p = .474$, $\eta^2 = 0.048$), and no interaction between threshold type and object ($F(1,11) = 1.572$, $p = .236$, $\eta^2 = 0.125$). The mean threshold duration for M1 was 28.3 ± 0.3 frames and for M2 was 27.8 ± 0.3 frames. The mean threshold for plum was 27.9 ± 0.2 frames and for ball was 28.1 ± 0.3 frames. The overall mean duration was 28 ± 0.2 frames. Whilst there was no difference between plum and ball trials in the percentage of 'eat' responses given by participants ($t(11) = -1.747$, $p = .108$), participants were significantly more likely to judge actions as 'eat' (53 %) than 'place' (47 %; $t(11) = 3.246$, $p = .008$).

To confirm that the participants were not able accurately to predict the subsequent action from viewing the pre-grasp alone, and to find out how many frames were required for participants to perform significantly above chance level, we calculated th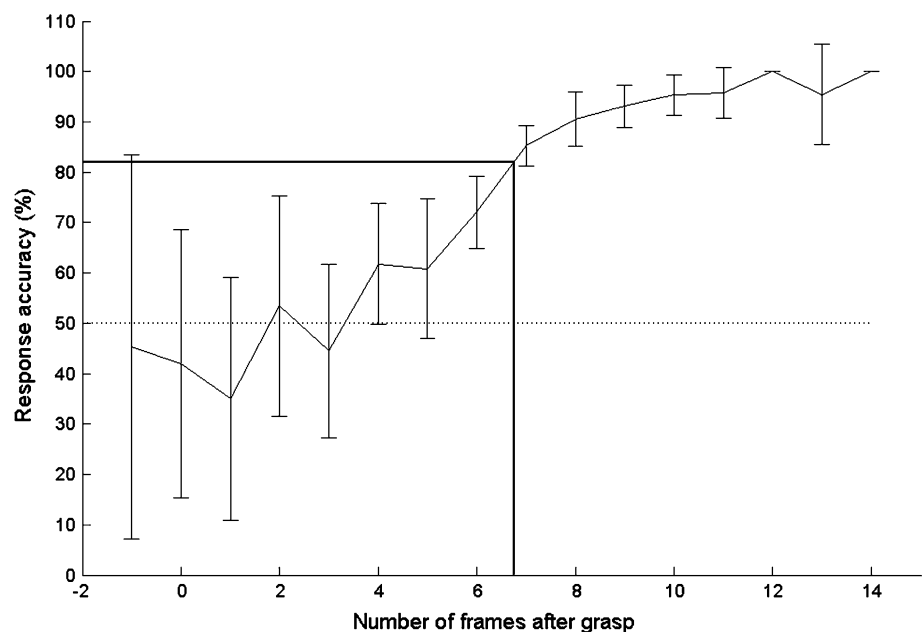e accuracy of the participants' predictions after seeing different lengths of videos. Figure 4 shows the percentage accuracy across all participants, for each proportion of movement viewed (ranging from one frame before the grasp to 14 after it). Because the number of frames viewed on each trial was based on each participant's accuracy on previous trials, not all participants saw all lengths of video. Therefore, there are some proportions of movement (for example, six frames before the grasp) for which the percentage accuracy is based on very few trials. Consequently, the number of frames before or after the grasp was included in Fig. 4 only if the number of trials available fell inside the central 95 % of the distribution of trials per frame number. The figure clearly shows that participants needed to see at least six frames after the grasp, in order to perform at a level significantly above chance (50 %).

Separate analyses of participants' responses to each camera angle revealed mean thresholds of 26, 30 and 27 frames, respectively, for the front, above and side angle trials. Thus, participants needed to see approximately 16 % (front), 37 % (above) and 20 % (side) of the post-grasp movements in order to accurately predict the action. The ANOVA showed that the participants' predictions were most accurate when viewing the videos filmed from the 'front' angle, and least accurate when viewing the videos taken from the 'above' angle ($F(1.7, 18.6) = 24.36$, $p < .001$).

Discussion

The results of Experiment 2a indicate that people need to see at least part of the post-grasp action before they can correctly predict the action outcome. The mean duration

Fig. 4 Percentage accuracy of predictions based on viewing different proportions of movement. The average percentage accuracy (across all participants) on the y-axis is plotted against the number of frames viewed relative to the 'grasp' frame. *Error bars* represent 95 % confidence intervals. The *solid black horizontal line* on the figure depicts the number of frames required to perform at 82 % accuracy (the threshold level used by QUEST in our experiment). The *dotted black line* marks the 50 % accuracy (chance) level, showing that participants had to see six or more frames after the grasp to perform significantly above chance

required for accurate prediction was 28 frames (~1167 ms), which represented slightly different stages of the action in each of the videos used, but was always later than the time at which the kinematic differences were detected in our first experiment. The average duration of M1 (up until the start of the lift) shown in the videos was 916 ms, and the duration of the post-grasp movement was 945 ms. Therefore, participants needed to see around 27 % (251 ms) of the post-grasp movement in order to correctly predict the final action.

The absence of a significant effect of object indicates that there was no difference in participants' ability to predict the outcome of actions towards the plum and the ball. There was also no difference between the proportions of 'eat' and 'place' responses when participants were observing actions towards the plum compared to when they were observing actions towards the ball. So, perhaps surprisingly, viewing a plum did not appear to bias participants towards an 'eat' response (nor did the ball bias participants towards a 'place' response). Interestingly, the number of 'eat' responses was higher overall than the number of 'place' responses, indicating that people were more likely to interpret actions as eating than placing.

The fact that the participants were more accurate in predicting actions viewed from the front, and least accurate for those viewed from above, may be explained as an effect of familiarity. Both eating and placing actions are commonly viewed from a frontal viewpoint. In social eating contexts, it is common for people to eat meals facing each other. Similarly, we often view placing actions from the front, for example, when a person hands us an object or takes an object from us. In contrast, it is quite rare for us to view actions from above, so it is likely that the participants had little experience of viewing the actions from this angle. The increased performance for the front view compared to the side view is perhaps the most interesting difference, as it is not uncommon to view grasp-to-eat or grasp-to-place actions from the side. One explanation for the difference is that people are better at predicting actions viewed from the front because we pay greater attention to actions directed towards us, and thus have greater visual experience of the finer details of these movements. When a hand is reaching towards an observer's body (as is perceived in the 'front' view video clips), it is likely that the observer is expected to perform an action themselves (for example, in the case of shaking hands, or when giving or receiving an object). Therefore, it would make sense that we pay more attention to actions viewed from this angle and would consequently be better at predicting the outcome of such actions. It must be noted, however, that even from the 'front' viewpoint, the participants could only correctly distinguish eating and placing actions after seeing a considerable portion of the post-grasp movement.

In summary, the data from Experiment 2a indicate that participants need to see more than the initial phase of a reaching action before they can judge the intention of that action. Whilst there may be distinct differences in grasp kinematics and muscle activity associated with pre-grasp movements of grasp-to-eat and grasp-to-place actions (Experiment 1), observers are either not able to detect these differences, or do not use them to predict whether a grasping action will lead to eating or placing.

Experiment 2b

Our final experiment considered whether people are able to predict post-grasp actions based on observing (exclusively) the hand's position on an object. Experiment 1 showed that the index finger and thumb are placed lower down and further forward on the target object when the object is going to be brought to the mouth, compared to when it is going to be placed. Although the results of Experiment 2a indicate that observers are unable to infer the subsequent action based on viewing the grasp position, we wanted to confirm this by isolating the view of the hand on the object. In the videos presented in Experiment 2a, the grasp itself was always preceded by the pre-grasp movement, so it is possible that other factors impeded participants' ability to predict the action. By isolating grasp position, we aimed to establish whether observers can predict actions based on the differences in grasp position alone. To this end, participants in this study were presented with a single frame of video which showed the hand's final position on the grasped object before the object was lifted from its starting position.

Methods

Participants

Twelve healthy participants aged 18–33 years ($M = 25.5$, $SD = 4.43$) were recruited from the School of Psychology and Clinical Language Sciences at the University of Reading. None of them had participated in Experiment 2a. Two of the authors (KN and AR) were participants.

Stimuli

The same video clips presented to participants in Experiment 2a were used in this experiment, but this time only the 'grasp' frame of each video was presented. For videos in which more than one video frame showed the hand grasping the object in its starting location, the frame immediately before the hand started to lift the object was selected.

Design and procedure

All 96 video frames were presented in a pseudorandomised order for each participant, in four blocks of 24 trials. On each trial, the single video frame was presented for 1,000 ms. As in Experiment 2a, this was followed by an 'Eat or place?' prompt, which remained on the screen until the participant responded by pressing the 'e' or 'p' key to denote 'eat' or 'place'.

Data analysis

We used the binomial distribution to assess whether the number of correct responses for each participant was greater or lesser than that expected by chance and a *t* test against the chance level of 0.5 across participants. As participants were more likely to give an 'eat' response in Experiment 2a, we also ran a *t* test to compare the number of 'eat' and 'place' responses in this experiment.

Results

The number of correct predictions ranged from 42 to 55 ($M = 49.5$, $SD = 3.90$), so the mean percentage of correct responses was just, but not significantly, higher than chance ($M = 51.6$ %, $SD = 4.06$; $t(11) = 1.334$, $p = .209$). The binomial tests confirmed that none of the participants performed significantly above or below chance. In addition, there was no difference between the number of 'eat' and 'place' responses given by participants ($t(11) = -0.650$, $p = .529$).

Discussion

These data confirm the results of Experiment 2a, that observers are not able to predict whether an object is going to be placed or brought to the mouth, based on seeing either the pre-grasp movement or the grasp position alone.

General discussion

Studies on the neural effects of action observation have suggested that the mirror neuron system (MNS) can anticipate action outcomes from an early stage in the observed action (Umiltà et al. 2001; Fogassi et al. 2005; Villiger et al. 2011). The present experiments aimed to investigate whether the predictive ability of the MNS might be due to visible differences between movements with different goals. To address this question, we compared muscle activity and movement kinematics between grasp-to-eat and grasp-to-place actions, and between actions towards food and non-food objects. After discovering differences in kinematics and muscle

activity based on the subsequent action and object type, we ran two behavioural experiments to assess whether people are able to detect these differences and use them to predict what is going to be done with an object after it has been grasped.

The results of Experiments 2a and 2b indicate that, despite differences in the pre-grasp stage of movement, participants are not able to distinguish grasp-to-eat and grasp-to-place movements until they have seen at least part of the post-grasp movement. This suggests that either observers do not detect the early kinematic (and muscular) differences, or that they do not utilise such differences to predict the outcome of observed actions. This finding is surprising, as the results of previous studies suggest that observers can predict and recognise actions, and even infer properties of the acting individual and the object, based on viewing the kinematics of movements (e.g. Runeson and Frykholm 1983; Manera et al. 2011; Stapel et al. 2012). We know from previous studies that adult participants are good at making goal predictions on the basis of action observation, including predicting whether an action is going to be cooperative or competitive (Manera et al. 2011; Sartori et al. 2011a), predicting the weight of an object to be lifted (from the way the actor approaches the object), and predicting whether or not an actor has 'deceptive' intentions (Runeson and Frykholm 1983; Sebanz and Shiffrar 2007).

There remains the possibility that the kinematic differences between the grasp-to-eat and grasp-to-place actions depicted in our stimuli were too subtle to guide observers' predictions. However, this seems unlikely to be the case given that action prediction in other studies can often occur in particularly pared down circumstances. For example, in work by Stapel et al. (2012), observers had to predict whether a walking individual was going to start crawling or to continue walking. Observers were able to predict the subsequent action accurately, even in trials in which all contextual information was eliminated.

Our preferred interpretation of our findings is that most people are not able to detect subtle kinematic differences between, specifically, pre-grasp movements with different subsequent outcomes. This has important implications for the MNS literature, as it places limitations on the apparent ability of the MNS to infer action goals (e.g. Villiger et al. 2011) on the basis of kinematic differences in reaching behaviours. As suggested by Fogassi et al. (2005), the MNS response may rely on cues such as the context in which the action is observed (e.g. an actor opening an empty container immediately before grasping an object), or the type of object being acted upon (e.g. a food item is likely to be taken to the mouth). Fogassi and colleagues did find that mirror neurons that were selective for grasp-to-eat actions responded more strongly to grasp-to-place actions directed towards food than grasp-to-place actions

directed towards non-food objects. This could suggest that the chain of motor commands associated with eating (i.e. the 'eating chain'; Fogassi et al. 2005, p. 666) is activated whenever an observer sees a food object, regardless of the subsequent action. In other words, seeing a person reaching towards an object which *could* be eaten may lead to activation which represents the 'eating' goal of the action rather than another possible goal such as 'placing'. In our experiment, participants would have learned quickly that both the food and non-food object could be 'eaten' or 'placed', so we did not necessarily expect participants to predict the action based on object suitability. In a 'real-world' context, however, perhaps seeing a plum would lead observers to predict a 'grasp-to-eat' rather than 'grasp-to-place' action.

It is, of course, possible that MNS responses are based on a combination of kinematic and contextual cues, so that, when the final goal of an action cannot be inferred from the kinematics of a movement, context can be used to infer intention. Indeed, Stapel et al. (2012) showed that action prediction is more accurate when contextual cues are available, but that actions can be inferred using kinematic cues alone.

The fact that participants were unable to report the kinematic differences in our study does not preclude the possibility that the MNS is nonetheless able to detect differences in movement kinematics. It is possible that our participants did not recognise these kinematic differences to an extent that allowed them consciously to know whether an action was going to bring the object to the mouth, but that, nonetheless, the differences were detected by a mechanism that influences the mirror neuron response. Indeed, there is evidence that some of our perception of actions takes place at an unconscious level (e.g. see Blake and Shiffrar 2007 for a review), so it is feasible that kinematic differences are 'mirrored' but not recognised by the observer. It should be noted, however, that implicit processing of kinematic differences between the actions would likely enhance the participants' performance on the action prediction task even if they had no conscious awareness of the differences, so we find this explanation unlikely.

In conclusion, the present findings indicate that there are early kinematic differences in the reach-to-grasp phase of eating and placing actions, but these appear to be too subtle to be detected by an observer. This places an important qualification on the putative ability of the MNS to distinguish reaching actions with different goals (e.g. eating vs. placing; Fogassi et al. 2005) on the basis of kinematic differences between those actions. We speculate that, where intention cannot be inferred from kinematics, action prediction may be based on contextual cues such as the type of object to be acted on.

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